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VOL. I.

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# ANATOMY OF VERTEBRATES.

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VOL. I.

FISHES AND REPTILES.

BY

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## PREFACE.



THE PRESENT WORK completes the outline of the Organisation of the Animal Kingdom which was begun in that on the Invertebrates.<sup>1</sup> They may be regarded as parts of a whole, having the same general aim, and, together, form a condensed summary of the subjects of my 'Lectures on Comparative Anatomy and Physiology, according to the Classes of Animals,' delivered in the Theatre of the Royal College of Surgeons of England in the years 1852, 1853, and 1854.

In the choice of facts, as then and since acquired by science, I have been guided by their authenticity and their applicability to general principles.

In the first, regard has been had to the agreement of several observers, or to the nature of the fact as making it acceptable on the testimony of a single expert. Appearances that require helps to vision are those that call for multiplied concurring testimony, and on such alone are offered the descriptions and illustrations of the microscopical characters of 'tissues' premised to most of the chapters.

In the second aim, the parts and organs, severally the subjects of these chapters, are exemplified by instances selected with a view to guide or help to the power of apprehending the unity which underlies the diversity of animal structures; to show in these structures the evidence of a predetermining Will, producing

<sup>1</sup> Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals, 8vo. 1843; 2nd ed. 8vo. 1855.

them in reference to a final purpose ; and to indicate the direction and degrees in which organisation, in subserving such Will, rises from the general to the particular.

Anatomy, or the ‘ Science of the Structure of Organised Bodies,’ is primarily divided into ‘ Phytotomy,’ or that of plants, and ‘ Zootomy,’ or that of animals. When particular provinces, classes, or species of animals have monopolised the time and skill of anatomists, such special knowledges have received particular denominations : such as ‘ Malacotomy,’ or anatomy of mollusca ; ‘ Entomotomy,’ or anatomy of insects ; ‘ Ichthyotomy,’ or anatomy of fishes ; ‘ Ornithotomy,’ or anatomy of birds, &c.

An animal may be dissected in order to a knowledge of its structure, absolutely, without reference to or comparison with any other, its species being regarded as standing alone in creation. The knowledge so gained, from the very limitation of the field of enquiry, may be most accurate and minute, most valuable in its application to the repair of accident, the remedy of injury and decay, and the cure of disease. Such, e.g., is ‘ Anthropotomy,’ or the anatomy of man, and ‘ Hippotomy,’ or that of the horse. Besides the numerous and excellent works on these special subjects, I may cite the ‘ *Traité Anatomique de la Chenille du Saule*,’ 4to., 1762, by LYONNET ; the ‘ *Anatome Testudinis Europææ*,’ fol., 1819, by BOJANUS ; the ‘ *Anatomie Descriptive du Melolontha vulgaris*,’ 4to., 1828, and the ‘ *Anatomie Descriptive du Chat*,’ 4to., 2 vols., by STRAUS-DURCKHEIM ; also, in application of the science to art, ‘ *The Camel, its Anatomy, Proportions, &c.*,’ fol., 1865, by ELIJAH WALTON ; as unsurpassed examples of this monographical kind of anatomical science. As applied to Man it is commonly called ‘ Human Anatomy,’ and is, in strictness of speech, one of the manifold ways of human work.

But the anatomist may apply himself to a particular organ instead of a particular species, either exhaustively in one animal, or by tracing such organ or system throughout the animal kingdom. The ‘ Neurotomies’ and ‘ Neurographies’ to which JOSEPH SWAN, e.g., has devoted a laborious life, the ‘ *Ostéographie*’ of



DE BLAINVILLE, and my own 'Odontography,' are examples of this way of anatomy. JOHN HUNTER assembled the evidences of his labours, in the unique and grand department of his Museum illustrative of anatomy properly so called, in series according to the organ, beginning with the simplest form, followed in succession by the progressively more complex conditions of the same organ, the series culminating, in most cases, with that which exists in the human frame. The mechanism of the organ is here unfolded, and its gradations were compared, to discover its mode of working; and, as 'Physiology' mainly consists in such determinations of functions or final aim, this kind of investigation of organic structures might be termed 'Physiological Anatomy.'<sup>1</sup>

'Homological Anatomy' seeks in the characters of an organ and part those, chiefly of relative position and connections, that guide to a conclusion manifested by applying the *same name* to such part or organ, so far as the determination of the namesakeism or homology has been carried out in the animal kingdom. This aim of anatomy concerns itself little, if at all, with function, and has led to generalisations of high import, beyond the reach of one who rests on final causes. It has been termed, grandiloquently, 'Transcendental' and 'Philosophical;' but every kind of anatomy ought to be so pursued as to deserve the latter epithet.

A fourth way of anatomy is that which takes a particular species in the course of individual development, from the impregnated ovum, tracing each organ step by step in its evolution up to the adult condition. It is called 'Embryology' and 'Developmental Anatomy.'

A fifth way of anatomy is that which investigates the structure of an animal in its totality, with the view of learning how the form or state of one part or organ is necessitated by its functional connections with another, and how the co-ordination of organs is adapted to the habits and sphere of life of the species; but does

<sup>1</sup> See 'Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy in the Museum of the Royal College of Surgeons,' 4to. 5 vols. 1832-1840; 2nd ed. vol. i. 1852.

not stop here, having for its main end the comparison of these associated modifications and interdependencies of organs in all the species of animals. As their degrees of affinity and the characters and circumscription of natural groups are hereby illustrated, this way may be termed 'Zoological Anatomy.'

In the hands of the anatomist the microscope has been mainly applied to the constituent parts of an organ, called 'tissues;' and the results of such research, combined with those of chemical tests, constitute a sixth sort of anatomy called 'Histology.' It has been termed 'Microscopical Anatomy,' but this is essentially only a more refined method of the scrutiny of organic parts. In so far, however, as 'Histology' treats of structure according to the proximate tissues common to different organs, it corresponds with the branch of the science which BICHAT, its founder, called, loosely, 'Anatomie Générale.'<sup>1</sup>

Finally, a seventh way in which the highest generalisations in biological science may be aimed at is that which is taken when we pursue investigations of form and structure beyond the animals that *are* to those that *have been*. Here, however, the anatomist is limited, as a rule, to such tissues and organs as are petrifiable, e.g., corals, shells, crusts, scales, scutes, bones, and teeth; but he has been stimulated to a degree of minuteness and accuracy of observation in this field of research to which few of the other ways and aims would have led him. In applying the results of such researches to the restoration of extinct species, physiology has benefited by the study of the relations of structure to function requisite to obtain an insight into the food, habits, and sphere of life of such species; and zoology has gained an immense accession of subjects through such determinations, with improved systems of classification due to the expanded survey of organic nature opened out by 'Palæontology.'

The word 'Anatomy' is still commonly used to signify 'Anthropotomy,' or 'Human Anatomy.' Almost all begin the study of the science, as medical students, with the dissection of the human

<sup>1</sup> Anatomie Générale, appliquée à la Physiologie, &c., Svo. 1801.

body, and most end there ; but no special anatomy can be rightly and fully understood save on the basis of the general science of which it is an integral part. The reason lies in the diversities of organic structure being subordinated to a principle of unity. Of this principle, apprehended as an 'idea' or truth of reason, the understanding receives evidences in number and comprehensibility differing in different natural groups of the animal kingdom. Illustrations of the 'idea' will be found in the chapters on the Articulate Province and other parts of the 'Lectures on Invertebrates,' and, in accordance with the present phase of anatomical science, more abundantly in the present Work. True it is that in the first steps to organisation we seem to see a tendency to disintegration, to a reduction of the primary whole to the subordinate characters of a part. The first centre of sarcode, or undifferenced organic matter, however originated, yet with definite tendencies to formal character and course of growth (as in a Foraminifer, e.g.), buds forth a second centre of identical nature ; this a third, and so on, until a group of such exists as an assemblage of coherent homogeneous or like parts. These, if clothed by a delicate crust of characteristic structure, constitute a chambered shell, straight, bent, or spiral, each chamber occupied by the same vital sarcode, outshooting filamentary food-getting processes through the shell-pores ; in which seeming complexity the incipient unity or 'whole' is reduced to the 'part' called innermost chamber, or is conceivable as a lesser whole in the larger one. The Annelides offer a familiar example of such repetitions of a primal complexly organised whole, by successive buddings in a linear direction ; the nerve-centre, the muscles, the skeleton-segment, perhaps heart and gills, being regularly repeated in each, and thereby reducing the original whole to one of many parts of a segmented unity.

Almost every organ in the progressively differenced organism initiates itself under a similar character of irrelative repetition, suggestive of operance akin to that of inorganic polar growths, as in a group of crystals, wherein each exemplifies the characters

of the mineral or crystalline species, but is subject, like vital growths, to occasional malformation.

As this principle of growth by multiplication of like parts is manifested more commonly and extensively in plants, it is illustrated in the 'Invertebrate Volume'<sup>1</sup> under the term 'Vegetative Repetition.' In the vertebrate series it is exemplified by the hundreds of similar teeth in the jaws of many of that low class (*Pisces*) in which true dentinal teeth first appear in the animal kingdom. The numerous and similar many-jointed terminal divisions of the pectoral limbs of the fishes thence called 'Rays,' the multiplied similar endoskeletal segments of the vertebral column of these and other cartilaginous fishes, of murænoids and serpents, are likewise lingering exemplifications of the low irrelative principle of development.

In the vertebral embryo the first appearance of the parts of the skeleton, in gristle or bone, is a segmental one; in fishes the muscular system shows much, and in all Vertebrates a little, of the like segmental constitution of the trunk; the same idea is suggested by the symmetrical and parial origins of the nerves, and physiologists have mentally recognised a corresponding segmental condition of the myelon or spinal chord, which is visibly exemplified in certain fishes. But these appearances are concealed by the general tegument; not exposed, as in the Articulates, in which the segmented skeleton is at the same time tegument. A Vertebrate may be defined as a clothed sum of segments. But in this highest province of the animal kingdom growth by repetition of parts rapidly gives place to the higher mode of development by their differentiation and correlation for definite acts and complex functions. Nevertheless, I am constrained by evidence to affirm that in the vertebrate as in the invertebrate series there is manifested a principle of development through polar relations, working by repetition of act and by multiplication of like parts, controlled by an opposite tendency to diversify the construction and enrich it with all possible forms, proportions, and modifications of

<sup>1</sup> Op. cit. 2nd ed. p. 541.



parts, conducive to the fulfilment of a pre-ordained purpose and a final aim: these opposite yet reciprocally complementary factors co-operating to the ultimate result, with different degrees of disturbance, yet without destruction, of the evidences of the typical unity.<sup>1</sup>

Thus, the dentition of Vertebrates will be seen to pass from irrelative sameness and multitude to the state in which the teeth in the same jaw are classed according to diversities of form and function, and where each tooth has its own character, bears its own name and symbol.

In like manner may be traced the gradations by which the terminal divisions of the limb ascend from the multitude of many jointed rays, swathed in a common sheath of integument, to individual freedom, with reduction of number and of joints, and with a special form and action; according to which each digit in the human hand, e.g., has its special name and symbol, and can be combined in action with any other digit for a particular purpose. The same principle, through reduction of number with differencing of the parts, is exemplified by the fact that the competent anthropotomist will distinguish and name each of the four and twenty 'true vertebræ' of the human skeleton.

In the Mammalian class there are four muscular pulsatile cavities concerned in the propulsion of blood; but they differ from those cavities in the Annelide, in each having its own special structure and powers, and being in such relation with another cavity that the whole can combine to effect two complete but mutually related systems of circulation, the four pulsatile cavities constituting one complex and perfect 'heart.' The ox has four bags for the digestion of food; but they differ from those cavities of the *Polygastria*, not only in their minor number and more definite structure as bags, but by each performing a distinct part in the process of digestion, and combining with the rest, in mutual

<sup>1</sup> This idea will be found more fully exemplified in my work, 'Principes d'Ostéologie Comparée,' 8vo. (Paris) 1855, p. 366, *et seq.*



subserviency, to the completion of the most perfect act of that function, the conversion, namely, of grass into flesh.

Thus, in tracing through the animal series this course of parts and organs, we pass from the many and the like to the few and the diverse.

A 'homologue' is a part or organ in one organism so answering to that in another as to require the same name.

Prior to 1843 the term had been in use, but vaguely or wrongly.<sup>1</sup> 'Analogue' and 'analogy' were more commonly current in anatomical works to signify what is now definitely meant by 'homology.' But 'analogy' strictly signifies the resemblance of two things in their relation to a third; it implies a likeness of ratios. An 'analogue' is a part or organ in one animal which has the same function as a part or organ in another animal. A 'homologue' is the same part or organ in different animals under every variety of form and function.

In the *Draco volans* (Vol. I. fig. 163) the fore-limbs are 'homologous' with the wings of the bird (Vol. II. fig. 1); the parachute is 'analogous' to them.

Relations of homology are of three kinds; the first is that above defined. When the 'basilar process of the occipital bone' in Man is shown to answer to the distinct bone called 'basioccipital' in the fish, the *special homology* of that anthropotomical process is determined; as such homologies are multiplied, the evidence grows that man and fish are constructed on a common type.

A wider relation of homology is that in which a part or series of parts stands to such general type. When the 'basilar process of the occipital bone' is determined to be the 'centrum' of the last cranial vertebra, its *general homology* is enunciated.

The archetype skeleton represents the idea of a series of essentially similar segments succeeding each other in the axis

<sup>1</sup> 'Les organes des sens sont *homologues*, comme s'exprimerait la philosophie allemande; c'est-à-dire, qu'ils sont analogues dans leur mode de développement.'—Geoffroy St. Hilaire, *Annales des Sciences Nat.*, tom. xii. 1825, p. 341.

of the body ; such segments being composed of parts similar in number and arrangement. Accordingly, a given part or appendage in one segment is repeated in another, just as one bone is represented in the skeletons of different Vertebrates ; and this representative relation in the segments of the same skeleton is 'serial homology.' As, however, the parts can be namesakes only in a general sense, as 'centrums,' 'ribs,' &c., and since they must be distinguished by special names according to their special modifications, as 'basioccipital,' 'mandible,' 'coracoid,' 'humerus,' &c., I have called such serially related or repeated parts 'homotypes.' The basioccipital is the homotype of the basisphenoid, and the humerus is the homotype of the femur : when the basioccipital is shown to repeat in its 'vertebra' the element which the 'odontoid process' represents in the succeeding vertebra, or the basisphenoid in the preceding one, its 'serial homology' is indicated.

The extent to which serial homologies can be determined shows the degree in which vegetative repetition prevails in the organisation of an animal.

The study of homologies is comparatively recent ; much of this field of research remains for future cultivators, especially in regard to the muscular and nervous systems.

When engaged in the 'third way' of anatomy, and in making known the results of such labour as applied to the skeleton,<sup>1</sup> I found a great impediment in the want of names of bones. For these, when first studied, had been mostly described under phrases suggested by forms, proportions, or likeness to some familiar object, which they present in the human body. A reform of this nomenclature was an essential first step, and it is gradually making its way against the usual impediments.

The best workman uses the best tools. Terms are the tools of the teacher ; and only an inferior hand persists in toiling with a clumsy instrument when a better one lies within his reach. But 'he has been used to the other.' No doubt ; and some extra

<sup>1</sup> On the Archetype and Homologies of the Vertebrate Skeleton, 8vo. 1848 ; and On the Nature of Limbs, 8vo. 1849.

practice is necessary to acquire the knack of applying the new tool. But in this acquisition a small capital of trouble will have been invested with a sure return of large profits. A single substantive term is a better instrument of thought than a paraphrase.<sup>1</sup> But the substitution of such terms for definitions is still more advantageous when they are susceptible of becoming adjectives by inflection. Thus the term 'notochord' for 'chorda dorsalis' or 'dorsal chord' enables one to predicate of species or groups of vertebrates as being 'notochordal;' that single epithet implying that the embryonal body in question is, in them, persistent. A like advantage cleaves to 'myelon' for 'chorda spinalis' or 'spinal chord;' the Physiologist, e.g., can then speak of 'myelonal functions,' and the Pathologist of 'myelonal' disease, with the certainty of being understood to signify properties and affections of the 'spinal chord;' not, as in 'spinal disease,' that of its case, or 'spinal column.' In regard to the part so called and its constituent 'vertebræ,' their modifications are so many, so characteristic, so important, especially in the application of Anatomy to Palæontology, that I was early compelled in the latter kind of labour to substitute single pliable terms for the phrases 'transverse process,' 'oblique' or 'articular process,' 'body of the vertebra,' 'vertebral lamina,' 'vertebral rib,' 'sternal rib,' &c., by which the parts of the 'vertebra' were then designated.

But the single names of parts and constituents of the skeletal segment called 'osteocomma' or 'vertebra' have not merely the advantage above illustrated, as where the adjective 'neurapophysial' can be applied to a 'ridge,' notch, or 'foramen,' in the vertebral lamina (neurapophysis); the vertebral terminology in use in the present Work indicates a profound truth which is hidden by the language of anthropotomy. The terms 'pleurapophysis' and 'hæmapophysis' imply parts of the segment corre-

<sup>1</sup> 'Superoccipital,' e.g., for 'pars occipitalis stricte sic dicta partis occipitalis ossis spheno-occipitalis' of the eminent anthropotomist SOEMMERING. (See TABLE OF SYNONYMS, &c., appended to Vol. II.) Similarly, in the present Work, I use the word 'Vertebrate' as a substantive. We do not speak of a 'Confederate' animal, and the added word is as unnecessary in regard to the 'Vertebrate' one.

lative in independency of development and elemental grade with the 'neurapophysis,'—a fact of high generalisation not only ignored but impliedly contradicted by the reckoning of the 'vertebral rib' and the 'sternal rib,' or 'rib-cartilage,' as bones distinct from, and countable with, that which the anthropotomist equally holds to be a single bone under the name 'vertebra.' Furthermore, as each distinctly recognisable part or thing must have its verbal sign, for the purposes of intelligible predication of its nature and qualities, the course of knowledge of the vertebral column would have enforced the origination of such signs irrespective of the abstract need of improving the mental tools of anatomy.

When it came to be discovered that 'the transverse process of a cervical vertebra' was other, and more than, as well as formally different from, the 'transverse process of a dorsal vertebra,' and that this process was a different thing from the 'transverse process' of a 'lumbar' or 'sacral' vertebra, the results of such analysis necessitated the creation of a correspondent nomenclature.

'Transverse processes,' as such, are, as JOHANNES MÜLLER first pointed out, of two kinds; they are, in relation to horizontally disposed vertebrates, 'upper' and 'lower'—in our nomenclature, 'diapophyses' and 'parapophyses.' Both kinds exist in the 'transverse processes' of the neck from the crocodile upwards; and the seeming unity of the outstanding part in birds and mammals is caused by the soldering thereto of a third element—the 'cervical rib' of the herpetotomist, the 'styloid process' of the ornithotomist.<sup>1</sup>

Referring to the 'Introductory Chapter' of the 'Archetype of the Vertebrate Skeleton,'<sup>2</sup> for further illustrations of the advantage of single well-defined terms, I will here only show how such advantage may be affected by reason of an unsettled definition.

The anatomical term 'organ' has diverse significations. The

<sup>1</sup> Macartney, Art. 'Birds,' Rees' Cyclopædia.

<sup>2</sup> Op. cit.



chief constituent idea is 'work for a special end:' thus, the heart is the 'organ' of circulation; the lungs, the 'organ' of respiration; the liver, the 'organ' of bilification, &c. But also, incipient stages in the development or formation of parts are called the 'organs' of such; e.g., the periosteum is the 'organ of bone,' the pulp is the 'dentine organ;' other parts of the growing complex tooth are the 'enamel organ,' 'cement organ,' &c. The parts in which independent cells, with special powers, originate, are also called the 'organs' of such; as, e.g., the ovary is the 'organ of ovulation;' the testis the 'organ of semination.' It is obvious, however, that the part which the more or less condensed cellular basis, or 'stroma,' of the ovary or the testis may take in the production of the germ-cells or sperm-cells and spermatozoa is very different from that which the heart performs in the motion of the blood, or the lungs in the mutation of the air inspired.

Zoological anatomy is now an indispensable instrument to the classifier, if not to the determiner, of the species of animals. The anatomist properly so called, but commonly qualified as the 'comparative' one, makes known the results and applications of his comparisons of structure in zoological as well as homological or anatomical works. The '*Règne Animal*' and the '*Leçons d'Anatomie Comparée*' of CUVIER exemplify these different applications and ways of exposition of his science.

As a zoologist or classifier, the anatomist avails himself of the definite modification and full development of a part or organ, indicating, and predicating of such conditions by special terms, for the required characters. The 'fin,' the 'hoof,' the 'paw,' the 'foot,' the 'hand,' are to him so many kinds of limbs, the presence or absence of which serve to differentiate his groups; anthropotomical terms of parts of the brain reaching their full and characteristic development in Mammals or in Man, e.g., 'fornix,' 'corpus callosum,' 'hippocampus minor,' 'posterior cerebral lobe,' &c., serve and are used, absolutely, for the same end; so likewise



with regard to special forms and proportions of teeth indicated by the terms ‘canine,’ ‘carnassial,’ ‘tusk,’ &c.

The absolute way in which the things or characters so designated are affirmed or denied in zoological definitions is essential to their purpose.

Amongst the characters by which CUVIER differentiated the hoofed quadrupeds which he had restored from their fragmentary fossil remains in the building-stone of Paris, the most important in his estimation was ‘the presence of canines’ in one (*Palæotherium*), their absence in the other (*Anoplotherium*).<sup>1</sup> Nevertheless, Homological Anatomy easily indicates in the series of nine teeth in the ‘morceau de conviction,’<sup>2</sup> on which the character was founded, the teeth answerable to those which, because their pointed crowns projected beyond their neighbours in the Palæothere, were called and characterised as ‘canines.’ Now here was a temptation to an aspirant to scientific notoriety ‘to meet’ the great anatomist ‘by a flat contradiction,’ and ‘affirm that the *Anoplotherium* possessed canine teeth.’ I allude to such abuse because, of late, a practice has been creeping in, to the opprobrium of some of our English zootomists, of representing a zoological definition of a part which an anatomist may have given in a classificatory work, as the exponent of his homological knowledge and descriptions of such part in its various modifications and grades of development.

CUVIER, in his characters of the order *Bimana*, affirms that Man is the only animal possessing ‘hands’ and ‘feet:’—‘L’homme est le seul animal vraiment *bimane* et *bipède*.’<sup>3</sup> The *Quadrumana* are distinguished as having ‘hands’ instead of ‘feet,’ a ‘hand’ being defined as having the thumb opposable—‘le pouce libre et opposable aux autres doigts, qui sont longs et flexibles.’<sup>4</sup>

The aim of the author in the zoological work above cited was to impart obvious and easily apprehended differential characters

<sup>1</sup> ‘Le plus important fut celui qui m’apprit que cette espèce n’a point de dents canines.’—*Recherches sur les Ossemens Fossiles*, 4to. 1822, tom. iii. p. 14.

<sup>2</sup> *Ibid.*

<sup>3</sup> *Règne Animal*, tom. i. p. 70. 1829.

<sup>4</sup> *Ibid.* p. 85.

of the organ which observation had shown to define the groups. The naturalist, thus enabled to place his subject in its proper class or order, is not concerned, as such, in knowing the homological or transcendental relations of the part or character which has afforded him the means of effecting what he wished to do.

LINNÆUS, to whom mainly is due the discernment of the powerful instrument of well-defined terms in acquiring a systematic Science of Nature, and to whom we owe our best knowledge of its use, so named the guiding parts of plants and animals, for such arbitrary or special application, in botany and zoology: to this end he differentiates the 'bract,' the 'spath,' the 'sepal,' the 'petal,' from the 'leaf,' as things distinct.

What would be thought of the botanical critic who, quoting the definition of the flowers of Cyperaceous plants, as consisting, for example, of 'glumes,' should meet the statement by affirming that they were 'nothing but little bracts,' and who, then, with a show of profounder research, should proceed to expound the 'bract' as being the first step by which the common leaf is changed into a floral organ? The answer is obvious. But what next might be said, if it were pointed out that the objector had obtained this very notion from the 'Prolepsis Plantarum,' or other homological writings of the author criticised, where such philosophical considerations, foreign to the classificatory work, were the proper aim and object? So, with regard to the zoological definitions and characters of CUVIER. Those which I have cited are open to the opposite averment that, 'The "hind hands" of the Quadrumana are nothing but "feet;"' and the contradictor might then proceed to demonstrate, with much show of original research, the homology of the 'astragalus,' 'calcaneum,' 'cuboides,' 'cuneiform bones,' &c., in order to establish his discovery that a hand and foot are all one.

It is true that if the homological descriptions in the 'Leçons d'Anatomie Comparée' had been quoted, as well as the zoological definitions in the 'Règne Animal,' the immortal author of the latter work would be shown to have had previous possession of the pretended discovery. Moreover, in the 'Cinquième Leçon,

Articles VII.–IX. “Des os du pied,”<sup>1</sup> the frame of the hind feet of Man, Ape, Lion, Seal, Elephant, &c., is shown to consist of homologous bones. Nevertheless the great zootomist, in his labour and character as zoologist, does not hesitate to define and differentiate the ‘foot,’ the ‘hand,’ the ‘paw,’ the ‘fin,’ and the ‘hoof,’ respectively: nor does he deem the demonstration of the unity underlying the diversity to make the ‘man’ an ‘elephant’ or a ‘seal,’ any more than it makes him a ‘dog’ or an ‘ape’!

The ‘corpus callosum’ is defined as ‘a horizontal mass of transverse fibres covering the lateral ventricles, and exposed by divaricating the cerebral hemispheres.’ If a group of mammals want such commissural fibres, and another group possess them, the classifier will avail himself of a well-defined term expressing such difference, without prejudice to his reception of any homological determination of the parts, or their rudiments,<sup>2</sup> in anatomical works of the applier of the term.

Only by ignoring such indication of the ‘rudimental commencement of the corpus callosum,’ may a semblance of superior knowledge be assumed by him who asserts, as an antagonistic proposition to an affirmation of its absence as a zoological character, that the Marsupialia, e.g., do possess the ‘great commissure,’ or ‘corpus callosum.’<sup>3</sup>

So likewise with other well-defined parts of the human brain, the homologues of which may not be traceable to the same extent down the mammalian series. KUHLE, e.g., in *Ateles Belzebuth*,<sup>4</sup> TIEDEMANN in the Macaque<sup>5</sup> and Orang,<sup>6</sup> VAN DER KOLK and VROLIK in the Chimpanzee,<sup>7</sup> and myself in the Gorilla,<sup>8</sup> had

<sup>1</sup> Leçons d’Anat. Comparée, vol. i. 1799.

<sup>2</sup> As given in the ‘Philosophical Transactions’ for 1837, p. 41.

<sup>3</sup> Proceedings of the Royal Society, No. 72, and March 23, 1865.

<sup>4</sup> Beiträge zur Zoologie und vergleichenden Anatomie, 4to. 1820, zweite Abtheilung, p. 70, Taf. vii.

<sup>5</sup> Icones cerebri Simiarum, fol. 1821, p. 14, fig. iii. 2.

<sup>6</sup> Treviranus, Zeitschrift für Physiologie, Bd. ii. S. 25, Taf. iv.

<sup>7</sup> Nieuwe Verhandlingen der eerste Klasse van het Koninkl. Nederlandsche Instituut. Amsterdam, 1849.

<sup>8</sup> Fullerian Lectures on Physiology, Royal Institution (March 18, 1861); reported, with copies of diagrams, in ‘Athenæum,’ March 23rd, 1861, p. 395.

severally shown all the homologous parts of the human cerebral organ to exist, under modified forms and grades of development, in *Quadrumana*. But because the presence or absence of the 'ergot,' or 'pes hippocampi minor,' as defined by TIEDEMANN (see Vol. II. p. 273 of the present Work), had been used as a zoological character, the anatomical world has been deluged, since the date of the last under-cited work, with descriptions and figures of the homologous part in the *Orang* and other *Quadrumana*, as a new discovery mainly serviceable as a battery of contradictory affirmations.

Nevertheless the distinctive characters of the human brain, such as the manifold and complex convolutions of the cerebral hemispheres, their extension in advance of the olfactory lobes and farther back than the cerebellum, thereby defining a posterior lobe, with the corresponding 'horn of the lateral ventricle' and 'hippocampus minor,' are as available to the zoologist in classification as are the equally peculiar and distinctive characters of the calcaneum, hallux, and other structures of the foot.

So much, in connection with the 'fifth way' and application of anatomy, I regret to find myself compelled to state, in order to expose and stigmatise procedures which consist in representing the homological knowledge and opinions of an author by his definitions in a purely zoological work, and in suppressing all reference to the descriptions and statements in the anatomical writings of the same author, where his actual knowledge and opinions on the nature and homology of parts are given, and where alone they can be expected to be found.

Somewhat analogous to the course of observation pursued through the animal kingdom, from the lowest to the highest species, is that which traces each organ through the several phases of its development in the same species.

The right use of sense, in both ways, stores the understanding, empirically, with a series of facts, as the raw material for reasoning up to their principles. But Embryology has this inferiority, that



every species is such *ab initio*, and takes its own course to the full manifestation of its specific characters, agreeably with the nature originally impressed upon the germ.

A perch, a newt, a dog, a man, does not begin to be such only when the embryologist may discern the dawning of their respective specific characters. The embryo derived its nature, and the potency of self-development according to the specific pattern, from the moment of the impregnation; and each step of development moves to that consummation as its end and aim.

This truth has been masked to some apprehensions by the course of the developmental steps from the general to the particular; the initial ones, more especially, offering likenesses or analogies to finished lower species exemplifying degrees of organisation in the animal kingdom. Each step differs in degree of difference from the analogous grade at which a lower species rests, and inversely as the advance of such species. Accordingly, the less the degree of difference, and the wider the resemblance or analogy spreads between the embryonal phase and the parallel grade in the series of species.

The formation of the germ-mass (Vol. I. figs. 1-4, 422, 452)—the first step after impregnation—is a general phenomenon in animality (Vol. 'On Invertebrates,' figs. 48-56, 73, 74, 80-84, 181, 209-212, 232); thereat and thereby the man resembles and behaves like the monad.<sup>1</sup> But, the germ-mass completed, the vertebrate at once circumscribes itself or withdraws into its vertebrality. The proteine substance is the seat of a chemical differencing, leading to excess of albumen along one tract, balanced by excess of gelatine along a parallel tract. Thus are laid down the bases of the myelencephalon and vertebral axis. The 'notochord' is soon followed by the protovertebral specks in double parallel series (Vol. I. fig. 5; Vol. II. fig. 133): the embryonal trace is established, and it is one of a vertebrate.

The formation of neural and hæmal arches next follows; and

<sup>1</sup> Compare the above-cited figures with fig. 17, 'Lectures on Invertebrates,' 2nd ed. p. 29.

the phenomenon of the appearance of the latter, in which the blastema is accompanied by a vascular arch, with clefts intervening between contiguous arches, especially at the fore part of the embryo, has led to the idea that a reptile, bird, or mammal, is a fish before it becomes what it is tending to. True it is, that the embryos of these air-breathers float in fluid, and not any of them breathe the air until birth or exclusion, or near to exclusion; but they do not breathe water: the oviparous air-breather has one kind of temporary lung, the mammiferous embryo another kind, each alike special to the class. From the vascular loops accompanying the hæmal arteries branchiæ are not developed; one only of the interhæmal fissures is deepened on each side, brought into communication with the pharynx, and straightway converted into the 'eustachian tube,' according to the precocious rate of growth and development characteristic of the special organs of sense and their appendages. No true branchial or piscine breathing apparatus is at any time, or in any degree, manifested in the embryo of an air-breathing vertebrate. The deepening and opening of several interhæmal fissures in the embryo of a perch, and the subsequent course of development therewith of gill-arches and gills, with their subservient mechanism of branchiostegal rays and the opercular lid or door, are as distinctive manifestations of the original nature of the fish, as is the vascular lining of the egg that of the bird, or the vascular arrangement for borrowing breath from the mother that of the fœtal mammal.

At the incipient stages of these provisional and deciduous respiratory conditions the circulation in the embryo lizard, fowl, beast, is like that of a fish in its simplicity; but, as TREVIRANUS<sup>1</sup> rightly remarked, it is far from being identical; there are, indeed, characters of the circulating organs at this grade of simplicity, which not only distinguish the embryo of the air-breather from that of the water-breather, but also the embryo of the mammal from that of the bird or reptile; so soon is the course of development affected by the specific taint!

<sup>1</sup> G. R. in 'Zeitschrift für Physiologie,' vol. iv.; and 'Edinburgh New Philosophical Journal,' 1832, vol. xiii. p. 75-86.



Marked deviations from the archetype characterising existing species are directly approached in the progress of development.

If, as, e.g., in a thoracic or jugular fish, the position of the pelvic limbs departs from the typical one, these limbs bud out in the embryo in that special and anomalous place. When a higher species departs from type by a thoracic position of the scapular or occipital limbs, they likewise bud out in such special position. In both cases the hæmal arch, sustaining such appendages, is liberated from the rest of its segment for the special needs of the species, and the embryo of such never shows it fixed. At most, perhaps, the general character and typical connections may be indicated by the closer contiguity of the detached scapular arch to the rest of its proper occipital segment; as, e.g., in the embryo of birds and long-necked ruminants, to be removed to a distance determined by the later growth of the series of vertebræ intervening between head and chest.

To infer from such developmental phenomena that the throat-fins of the cod are not the displaced homologues of the hind legs or pelvic limbs of air-breathers, and that the fore-legs of such are not the homologues of the typically situated and connected scapular limbs of fishes, is an abuse or misuse of the empirical facts ascertained by observation of embryonal phenomena.

In like manner the developmental phenomena of the skull of an avian and mammalian species, succeeding those that broadly and intelligibly mark out the four pairs of neurapophyses and corresponding hæmal arches, plainly indicating the segmental or vertebral type of the skull, depart therefrom to attain the particular character of the face and mouth of the species. After the first budding indications of the halves of the maxillary (foremost cranial hæmal) arch, the development of it, as upper jaw, with that of the palate, pterygoid, and zygomatic appendages, obeys the impress of impregnation, and proceeds directly to establish the specific characters of such jaw in the particular bird or beast; the points of ossification, their deposit in membrane or gristle, and subsequent growth, having no other or deeper signifi-

cation. If a species be gifted with acute hearing, and the movements of the ear-drum require several ossicles, these, like the labyrinth, grow to full size in the embryo, appropriating the blastema of the contiguous hæmal arch, and proportionally reducing, by arresting the development of, the pleurapophysis of such arch. The inherited tendency to a special or specific form which thus influences early developments and growth of parts has misled some who have mistaken such for homological or archetypal characters. But the determination of these characters is arrived at by other routes of research; and, so reached, such determination serves to explain many of the phenomena of development which otherwise would remain as mere empirical facts.

Embryology, e.g., shows that in the human foetus the sternum is developed from a series of ossific centres (Vol. II. p. 555, fig. 364), whilst the co-articulated clavicle—as long a bone—is developed from a single ossific centre, and a contiguous rib, though of greater length, is also hardened from a single ossific centre; but embryology affords no explanation of the reason of such difference. That is afforded by a knowledge of the archetype skeleton, which teaches that the sternum—reckoned as a single bone in anthropotomy—consists of a series of vertebral elements, but that the rib and the clavicle are single elements.

Embryology shows that the canon-bone of a ruminant, regarded as a single bone by the veterinarian, is developed from five ossific centres; two on the same transverse line near the middle, one on the upper, and a pair which soon coalesce at the lower end. But no clue is afforded to the signification of these several centres: embryology is no criterion of their homologies; these are determinable on other grounds or ‘ways of anatomy.’

A knowledge of the ‘Nature of Limbs,’ derived from homological studies leading to a recognition of the archetype, could alone determine that two only out of those five centres represent distinct bones in the typical pentadactyle foot of the mammal; the rest having no such signification, but serving to perfect the ultimate growth as ‘epiphyses.’ So likewise with the collar-bone

and rib. At a period long subsequent to the deposition of the first centre of bone, a second appears at the sternal end of the human clavicle, and two are added to complete the head and tubercle of the rib, the shaft of which had been ossified by growth from a single centre.

Recognition of the archetype skeleton elucidates the empirical facts of embryology, and teaches us to distinguish between the points of ossification of a bone in a higher vertebrate which signify or answer to bones that retain their distinctness in lower vertebrates, and the points of ossification which merely help out the growth or have their final purpose in the exigencies of the young animal. A lamb or foal, e.g., can stand on its fore legs shortly after it is born, and soon begins to run and bound. The shock to the limbs themselves is broken at this tender age by the cushions of cartilage at the ends of the shafts, and which continue for some time to be interposed between the 'epiphyses' and 'diaphysis.' The jar that might affect the large and pulpy brain of the immature man is similarly diffused and intercepted by the 'epiphysial' extremities of the vertebral centrums.

Such final purpose in the several centres of ossification of the vertebral bodies and the long bones of the limbs of mammals does not apply to those of reptiles; and no epiphyses with interposed cartilage attend the growth of the limb-bones of saurians and tortoises. But, when the reptile moves by leaps, ossification of the long limb-bones by distinct centres again prevails; the extremities of the humeri and femora are 'epiphyses' in the frog.

Embryology affords no criterion between the ossific centres that have a 'homological' and those that have a 'teleological' signification. A knowledge of the archetype skeleton is requisite to teach how many and which of the separate centres that appear and coalesce in the human, mammalian, or avian skeleton, represent and are to be reckoned as distinct bones, or elements of the archetype vertebra. For the want of this guide great and estimable anatomists have gone astray. Thus CUVIER, commenting on the arbitrary enumeration of the single bones in the human

skeleton, affirmed that to learn their true number in any given species we must go to the first osseous centres as these are manifested in the fœtus;<sup>1</sup> and GEOFFROY ST. HILAIRE<sup>2</sup> concurred in this view.

In the cartilages called ‘epiphysial,’ that eke out the ends and margins of bones, ossification begins later than does that of the bone itself. The times of appearance of the osseous nucleus in the coracoid process and acromion of the human scapula well exemplify this difference; in the coracoid, e.g., at the first year, in the acromion at the fifteenth year. Embryology teaches the facts but affords not the reason.

Special homology shows that the coracoid is a distinct bone, the acromion a mere process, in the vertebrate series. General homology gives the ground of the distinctness—the coracoid being the hæmapophysis of the hæmal arch of which the scapula proper is the pleurapophysis. In most mammals this hæmapophysis is stunted and terminates freely, like that of the last (floating) rib. In Monotremes it attains and articulates with its hæmal spine, as in the ‘true rib,’ and keeps this normal extent and condition through all the lower vertebrates. It is the typical state of the coracoid, which is departed from in all vertebrates above Monotremes: but such typical state is not passed through in the course of their development. As in that of other modified hæmal arches, the maxillary, e.g., so in the scapular arch, the special condition of the aborted hæmapophysis is gained directly, not through any intervening transitory manifestation of the general character. So far is embryology from being a criterion of homology.

In regard to what I have reckoned a ‘seventh way of ana-

<sup>1</sup> ‘Pour avoir le véritable nombre des os de chaque espèce, il faut remonter jusqu’aux premiers noyaux osseux tels qu’ils se montrent dans le fœtus.’—*Leçons d’Anatomie Comparée*, 8vo. ed. 1835, tom. i. p. 120.

<sup>2</sup> ‘Ayant imaginé de compter autant d’os qu’il y a de centres d’ossification distincts, et ayant essayé de suite cette manière de faire, j’ai eu bien d’apprécier la justesse de cette idée.’—*Annales du Muséum*, tom. x. p. 344. See, however, the remarks on this point in my ‘*Lectures on the Comparative Anatomy of the Vertebrate Animals*,’ 8vo. 1846, p. 37, et seq.



tomy,' I would remark that the existing kinds of vertebrates constitute part only, perhaps but a small proportion, of those which have lived. Two large primary groups of fishes have almost wholly passed away; but the Polypterus, Lepidosteus, and sturgeon yield the anatomist some insight into the structural modifications of the *Ganoidei* of AGASSIZ; whilst the shark, the skate, and the cestracion give a fuller knowledge of those of the *Placoidei*.

Present reptiles form a mere fragmentary remnant of the great and varied class of cold-blooded air-breathing vertebrates which prevailed in the mesozoic age. More than half of the ordinal groups of the class, indicated by osteal and dental characters, have perished; and it is only by petrified fœces or casts of the intestinal canal, by casts of the brain-case, or by correlative deductions from characters of the petrifiable remains, that we are enabled to gain any glimpse of the anatomical conditions of the soft parts of such extinct species: by such light some of the perishable structures of these animals are indicated in the text.

As vertebrates rise in the scale and the adaptive principle predominates, the law of correlation, as enunciated by CUVIER,<sup>1</sup> becomes more operative. In the jaws of the lion, e.g., there are large laniaries or canines, formed to pierce, lacerate, and retain its prey. There are also compressed trenchant flesh-cutting teeth, which play upon each other like scissor-blades in the movement of the lower upon the upper jaw. The lower jaw is short and strong; it articulates to the skull by a transversely extended convexity or condyle, received into a corresponding concavity, forming a close-fitting joint, which gives a firm attachment to the jaw, but almost restricts it to the movements of opening and closing the mouth.

<sup>1</sup> 'Tout être organisé forme un ensemble, un système unique et clos, dont les parties se correspondent mutuellement, et concourent à la même action définitive par une réaction réciproque. Aucune de ces parties ne peut changer sans que les autres changent aussi; et par conséquent chacune d'elles, prise séparément, indique et donne toutes les autres.'—*Discours sur les Révolutions de la Surface du Globe*. 4to. 1826, p. 47. In this definition Cuvier apprehended, exclusively, the operance of the differencing and adapting pole, and the law becomes limited in its application accordingly.

The jaw of the Carnivore develops a plate of bone of breadth and height adequate for the implantation of muscles, with power to inflict a deadly bite. These muscles require a large extent of surface for their origin from the cranium, with concomitant strength and curvature of the zygomatic arch, and are associated with a strong occipital crest and lofty dorsal spines for vigorous uplifting and retraction of the head when the prey has been griped. The limbs are armed with short claws, and endued with the requisite power, extent, and freedom of motion, for the wielding of these weapons. These and other structures of the highly-organised Carnivore are so co-ordinated as to justify CUVIER in asserting that ‘the form of the tooth gives that of the condyle, of the blade-bone, and of the claws, just as the equation of a curve evolves all its properties; and exactly as, in taking each property by itself as the base of a particular equation, one discovers both the ordinary equation and all its properties, so the claw, the blade-bone, the condyle, the femur, and all the other bones individually, give the teeth, or are given thereby reciprocally; and in commencing by any of these, whoever possesses rationally the laws of the organic economy will be able to reconstruct the entire animal.’<sup>1</sup>

The law of correlation receives as striking illustrations from the structure of the herbivorous mammal. A limb may terminate in a thick horny hoof. Such a foot serves chiefly, almost exclusively, for locomotion. It may ‘paw the ground,’ it may rub a part of the animal’s hide, it may strike or kick; but it cannot grasp, seize, or tear another animal. The terminal ungulate phalanx gives, as CUVIER declares, the modifications of all the bones that relate to the absence of a rotation of the fore-leg, and those of the jaw and skull that relate to the mastication offered by broad-crowned complex molars.

But there are certain associated structures for the coincidence of which the physiological law is unknown. ‘I doubt,’ writes

<sup>1</sup> Op. cit. p. 49.



CUVIER, 'whether I should have ever divined, if observation had not taught it me, that the ruminant hoofed beasts should all have the cloven-foot, and be the only beasts with horns on the frontal bone.'<sup>1</sup> I may add that we know as little why horns should be in one or two pairs in those ungulates only which have hoofs in one or two pairs; whilst in the horned ungulates with three hoofs there should be either one horn, or two odd horns placed one behind the other, in the middle line of the skull; or why the ungulates with one or three hoofs on the hind foot should have three trochanters on the femur, whilst those with two or four hoofs on the hind foot should have only two trochanters.<sup>2</sup>

'However,' continues CUVIER, 'since these relations are constant, they must have a sufficing cause; but as we are ignorant of it, we must supply the want of the theory by means of observation. This will serve to establish empirical laws if adequately pursued, as sure in their application as rational ones.'<sup>3</sup> 'That there are secret reasons for all these relations observation may convince us, independently of general philosophy.' 'The constancy between such a form of such organ and such another form of another organ is not merely specific, but one of class with a corresponding gradation in the development of the two organs.'<sup>4</sup>

'For example, the dentary system of non-ruminant ungulates is generally more perfect than that of the bisulcates; inasmuch as the former have almost always both incisors and canines in the upper as well as the lower jaw; the structure of their feet is in general more complex, inasmuch as they have more digits or hoofs less completely enveloping the phalanges, or more bones distinct

<sup>1</sup> Op. cit. 50.

<sup>2</sup> Quarterly Journal of the Geological Society, p. 138. 1847.

<sup>3</sup> 'Puisque ces rapports sont constants, il faut bien qu'ils aient une cause suffisante, mais comme nous ne la connaissons pas, nous devons suppléer au défaut de la théorie par le moyen de l'observation.'—Op. cit. p. 50.

<sup>4</sup> 'En effet, quand on forme un tableau de ces rapports, on y remarque non seulement une consistance spécifique, si l'on peut s'exprimer ainsi, entre telle forme de tel organe et telle autre forme d'un organ différent; mais l'on aperçoit aussi une constance classique et une gradation correspondante dans le développement de ces deux organes, qui montrent, presque aussi bien qu'un raisonnement effectif, leur influence mutuelle.'—Op. cit. p. 51.

in the metacarpus and metatarsus, or more numerous tarsal bones; or a more distinct and better developed fibula; or a concurrence of all these modifications. It is impossible to assign a reason for these relations; but, in proof that it is not an affair of chance, we find that whenever a bisulcate animal shows in its dentition any tendency to approach the non-ruminant ungulates, it also manifests a similar tendency in the conformation of its feet.' After citing similar instances of such constant relations, CUVIER again declares that the palæontologist 'must avail himself of the method of observation' as a supplementary instrument when the reason or law of such relations is undiscovered; and that he is most successful in the reconstruction of a whole from a part, who applies to the task 'efficacious comparison,' guided by 'tact (*adresse*) in discerning likeness.'<sup>1</sup>

As we descend in the scale of life from the grade illustrative of 'Cuvier's Law,' the method of empirical observation becomes more and more essential, the tact with which it is applied being, however, in the ratio of the discernment of the correlations of structures. The results of the combined methods of interpreting fossil remains are leading to views of life transcending the gains to zoology as a record of well-classed species, or to physiology as illustrative of final purpose. A progress from more generalised to more specialised structures, analogous to that exemplified in existing grades of animal life and in successive phases of individual development, is appreciable in the series of species which have succeeded one another upon our planet.

Certain structures which are transitory or rudimental in existing species are persistent and developed in extinct.

The caudal vertebræ are laid down in a gradually decreasing series of cartilaginous nuclei, in the embryo of modern bony fishes; but in the course of ossification they become massed and blended together to form the base of a vertically extended symmetrical tail-fin. In all palæozoic fishes the initial embryo-state persists, and the tail-fin, through the length of the upper lobe retaining the

<sup>1</sup> Op. cit. p. 52.

terminal series of vertebræ, is unsymmetrical. The process of differencing which leads to the 'homocercal' type begins in the mesozoic period and prevails in the neozoic. (See TABLE OF STRATA, &c., p. xxxviii.)

A corresponding modification of the caudal vertebræ prevails in neozoic birds; but the embryos of the existing species show the terminal vertebræ distinct, in a tapering series, before they are massed into the 'ploughshare bone;' and such, doubtless, was the law of development in all the extinct species which have left tertiary ornitholites. But the earliest and as yet sole evidence of the fossil skeleton of a mesozoic bird shows the retention of the embryo condition, with ordinary growth of the vertebræ.<sup>1</sup>

Modern ruminants are hornless when born, and have the metapodials supporting the phalanges of the cloven foot distinct; at an earlier fœtal period rudiments of upper fore-teeth start in the gum but do not get beyond it. The eocene mammal that first indicates the ruminant type retained the transitory, and developed the aborted, characters of its successors. The metacarpals and metatarsals never coalesced to form a 'canon-bone;' the upper canines and incisors were functional, but small and equal-sized; and, as horns never sprouted, CUVIER called the extinct beast 'weaponless' (*Anoplotherium*). In modern horses the digit on each side the one supporting the hoof is undeveloped, and is represented by a concealed rudiment of the metapodial called 'splint-bone.' In the miocene horses these metapodials reached their full length and supported hoofed digits, but of small size, like the 'spurious hoofs' of the ox. The eocene mammal initiating the type had these hoofs so developed as to form a functional tridactyle foot. Moreover, in the *Palæotherium*, certain teeth (symbolised in the present Work as *p* 1) which are rudimental and deciduous in the horse, were persistent and functional. The mesozoic marsupials manifested a lower or less differenced state of dentition, either by the degree of sameness of form (*Phascolothere*), or by the superior number (*Thylacothere*) of the molar series of teeth.

<sup>1</sup> Philosophical Transactions, 1863, pp. 33, 45, pls. I. and III.

The 'rudiments' of parts and organs which are retained undeveloped, or do not acquire the state capable of acting, or 'performing the function' done by them in other species, are of two kinds: one exhibits the totality of the organ in miniature, as, e.g., lacteal glands and nipples of the male mammal; the other is a part of an organ, as, e.g., the few concealed caudal vertebræ in the sloth, to which other vertebræ are added, with concomitant growth, to make the organ perfect for its function, as in the tail of the Megathere. Some rudiments show beginnings of parts which rise to perfection in higher species of the existing series; others are remnants of organs that were fully developed and functional in extinct species. TIEDEMANN'S 'scrobiculus parvus in loco cornu posterioris' in the brain of *Macacus*,<sup>1</sup> and the part which VROLIK believed himself entitled to regard as an indication of the 'hippocampus minor' in the brain of *Troglodytes*,<sup>2</sup> are beginnings of structures which show their full development in the human brain, and merit the nomenclature assigned to them in anthropotomy.

The filamentary limb of *Protopterus* (Vol. I. fig. 101, A), the didactyle limb in *Amphiuma* (*Ib.* B), the tridactyle homologue in *Proteus*, are beginnings of organs which attain full functional development in higher vertebrates. The styliform metacarpals and metatarsals in *Equus*, on the other hand, are remnants of parts of digits which were entire in *Hipparion*, and were functionally developed in *Palæotherium*.

Ruminants which habitually frequent heated arid plains or deserts, as the giraffes and camels, e.g., have lost the digits (*ii* and *v*, Vol. II. fig. 193, *ox*) that add to the resistance of the hoof on swampy ground, as in the bison, elk, and reindeer (*Ib.* fig. 311).

The visual organ degenerates in species inhabiting dark caves or recesses (*Amblyopsis* (Vol. I. fig. 175), *Heteropygii*, *Proteus*,

<sup>1</sup> *Icones cerebri Simiarum*, fol. p. 14, fig. iii. 2.

<sup>2</sup> *Versl. en Mededeel. der Kon. Akad.*, xiii. 1862, p. 7.



the craw-fish of the 'Mammoth Cave,' and numerous insects and arachnidans).

*Lepidopus*, *Trichiurus*, *Stromateus*, exemplify fishes which lose the ventral fins entirely with age; they are rudimental in *Gempylus*, *Psettus* and *Centronotus*; *Soleotalpa* has only the right ventral developed and the left rudimental; the pectoral fins are rudimental in many pleuronectoids, either on both sides, as in *Buglossus* and *Achirus*, or on the blind side only, as in *Monochir* and many species of *Synaptura*. The 'adipose fin' of certain Siluroid and Salmonoid fishes is a rudimental dorsal, sometimes showing traces of rays.

The prevalence of birds in New Zealand without wings (*Dinornis*), or too feebly developed for the purpose of flight (*Apteryx*, *Brachypteryx*, *Notornis*, &c.), is associated with the absence in those islands of any higher form of life exercising destructive mastery of organisation, until the immigration of the human race. The wings of such birds, like the eyes of the cavern fishes and crustaceans, would seem to have degenerated for want of use; their legs, by which locomotion was exclusively exercised, to have gained in size and strength.

LAMARCK,<sup>1</sup> adverting to observed ranges of variation in certain species, affirmed that such variations would proceed and keep pace with the continued operation of the causes producing them; that such changes of form and structure would induce corresponding changes in actions, and that a change of actions, when habitual, became another cause of altered structure; that the more frequent employment of certain parts or organs leads to a proportional increase of development of such parts, and that as the increased exercise of one part is usually accompanied by a corresponding disuse of another part, this very disuse, by inducing a proportional degree of atrophy, becomes an added element in the progressive mutation of organic forms.

Concomitant changes of climate, and other conditions of a coun-

<sup>1</sup> Philosophie Zoologique, tom. i. chaps. iii. vi. vii.



try affecting the sustenance or well-being of its indigenous animals, may lead not only to their modification but to their destruction. I have, in another work, pointed out the characters in the animals themselves calculated to render them most obnoxious to such extirpating influences; and have applied the remarks to the explanation of so many of the larger species of particular groups of animals having become extinct, whilst smaller species of equal antiquity have remained.

‘In proportion to its bulk is the difficulty of the contest which, as a living organised whole, the individual of such species has to maintain against the surrounding agencies that are ever tending to dissolve the vital bond and subjugate the living matter to the ordinary chemical and physical forces. Any changes, therefore, in such external agencies as a species may have been originally adapted to exist in, will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be gradually prolonged, the large mammal will suffer from the drought sooner than the small one; if such alteration of climate affect the quantity of vegetable food, the bulky Herbivore will first feel the effects of stinted nourishment; if new enemies are introduced, the large and conspicuous quadruped or bird will fall a prey, whilst the smaller species conceal themselves and escape. Smaller animals are usually, also, more prolific than larger ones.’<sup>1</sup>

The actual presence, therefore, of small species of animals in countries where larger species of the same natural families formerly existed, is not the consequence of any gradual diminution of the size of such species, but is the result of circumstances, which may be illustrated by the fable of the ‘Oak and the Reed;’ the smaller and feebler animals have bent and accommodated themselves to changes which have destroyed the larger species. They have fared better in the ‘battle of life.’

Accepting this explanation of the extirpation of species as true,

<sup>1</sup> On the Genus *Dinornis* (Part iv.), Zool. Trans., vol. iv. p. 15 (February 1850).

MR. WALLACE<sup>1</sup> has applied it to the extirpation of varieties; and as these do arise in a wild species, he shows how such deviations from type may either tend to the destruction of a variety, or to adapt a variety to some changes in surrounding conditions, under which it is better calculated to exist, than the type-form from which it deviated.

No doubt the type-form of any species is that which is best adapted to the conditions under which such species at the time exists; and as long as those conditions remain unchanged, so long will the type remain; all varieties departing therefrom being in the same ratio less adapted to the environing conditions of existence. But if those conditions change, then the variety of the species at an antecedent date and state of things may become the type-form of the species at a later date, and in an altered state of things.

In his work ‘On the Origin of Species by Natural Selection,’<sup>2</sup> MR. DARWIN more fully exemplifies, conjecturally, the reciprocal influence of external conditions and inherent tendencies to variety, in carrying on, as he believes, the deviations from type to specific and higher degrees of difference.

All these, however, are conceptions of what may have, not observations of what have, originated a species. Applied to the structures which differentiate *Troglodytes* from *Homo*,<sup>3</sup> or *Chiromys* from *Lemur*,<sup>4</sup> they are powerless to explain them: and the structural differences in these instances are greater than in many other species maintaining their distinction by sexual incapacity to produce fertile hybrids.

An innate tendency or susceptibility in an offspring to differ from a parent is a fact of observation: when carried beyond a certain point the issue is called, from its rarity, a ‘monster.’ But this tendency and its results are independent of internal volitions and external influences.

<sup>1</sup> Proceedings of the Linnean Society, August 1858, p. 57.      <sup>2</sup> 8vo. 1859.

<sup>3</sup> On the Classification and Geographical Distribution of the Mammalia, 8vo. 1859, p. 92.

<sup>4</sup> Transactions of the Zoological Society, vol. v. p. 86.

Therefore, with every disposition to acquire information and receive instruction as to how species become such, I am still compelled, as in 1849, to confess ignorance of the mode of operation of the natural law or secondary cause of their succession on the earth. But that it is an 'orderly succession,' or according to law,<sup>1</sup> and also 'progressive' or in the ascending course, is evident from actual knowledge of extinct species.

The inductive basis of belief in the operation of natural law or 'secondary cause' in the succession and progression of organised species, was laid by the demonstration of the unity of plan underlying the diversity of animal structures, as exemplified by the determinations of special and general homology; by the discovery of the law of 'Irrelative repetition;' by observation of the analogies of transitory embryonal stages in a higher animal to the matured forms of lower animals; and by the evidence that in the scale of existing nature, as in the development of the individual, and in the succession of species in time, there is exemplified an ascent from the general or lower to the particular or higher condition of organism.

The most intelligible idea of homologous parts in such series is that they are due to inheritance. How inherited, or what may be the manner of operation of the secondary cause in the production of species, remains in the hypothetical state exemplified by the guess-endeavours of LAMARCK, DARWIN, WALLACE, and others.

In the lapse of ages, hypothetically invoked for the mutation of specific distinctions, I would remark that Man is not likely to preserve his longer than contemporary species theirs. Seeing the greater variety of influences to which he is subject, the present characters of the human kind are likely to be sooner changed than those of lower existing species. And, with such

<sup>1</sup> BADEN POWELL, quoting from my Work 'On the Nature of Limbs,' 8vo. 1849, p. 86, writes:—'To what actual or secondary cause' ('Essays on the Unity of Worlds,' 1855, p. 401), instead of, 'To what natural laws or secondary cause the orderly succession and progression of species may have been committed, we are, as yet, ignorant.'

change of specific character, especially if it should be in the ascensive direction, there might be associated powers of penetrating the problems of zoology so far transcending those of our present condition, as to be equivalent to a different and higher phase of intellectual action, resulting in what might be termed another species of zoological science.

With the present psychical and structural characteristics of the human species, it may be reasonably concluded that those of other existing species, especially of the distinctly marked vertebrate classes, will be, at least, concurrent and co-enduring; and, in that sense, we may accept the dictum of the French zoologist:—‘*La stabilité des espèces est une condition nécessaire à l’existence de la science d’Histoire Naturelle.*’ At the same time, indulging with LAMARCK in hypothetical views of transmutative and selective influences during æons transcending the periods allotted to the existence of ourselves and our contemporaries, as we now are, we may also say:—‘*La nature n’offre que des individus qui se succèdent les uns aux autres par voie de génération, et qui proviennent les uns des autres. Les espèces parmi eux ne sont que relatives, et ne le sont que temporairement.*’





# CONTENTS, OR SYSTEMATIC INDEX.



## CHAPTER I.

### CHARACTERS OF VERTEBRATES.

SECTION	PAGE
1. Developmental characters . . . . .	1
2. Structural characters . . . . .	3
3. Piscine modification . . . . .	4
4. Reptilian modification . . . . .	5
5. Avian modification . . . . .	6
6. Mammalian modification . . . . .	6
7. Genetic and thermal distinctions . . . . .	6
8. Sub-classes of Hæmatoerya, or Cold-blooded Vertebrates . . . . .	7
9. Orders of Hæmatoerya . . . . .	9

## CHAPTER II.

### OSSEOUS SYSTEM OF HÆMATOCRYA.

10. Composition of Bone . . . . .	19
11. Development of Bone . . . . .	21
12. Growth of Bone . . . . .	23
13. Classes of Bone . . . . .	26
14. Type-segment, or Vertebra . . . . .	27
15. Archetype Skeleton . . . . .	29
16. Development of Vertebrae . . . . .	30
17. Vertebral column of Fishes . . . . .	34
18. Vertebral column of Batrachia . . . . .	46
19. Vertebral column of Ichthyopterygia . . . . .	50
20. Vertebral column of Sauropterygia . . . . .	51
21. Vertebral column of Ophidia . . . . .	53
22. Vertebral column of Lacertia . . . . .	57
23. Vertebral column of Chelonia . . . . .	60
24. Vertebral column of Crocodilia . . . . .	65
25. Vertebral column of Pterosauria . . . . .	70
26. Development of the Skull . . . . .	71
27. Skull of Plagiostomi . . . . .	76
28. Skull of Protopteri . . . . .	82

SECTION	PAGE
29. Skull of Batrachia . . . . .	85
30. Skull of Osseous Fishes . . . . .	92
31. Skull of Chelonia . . . . .	126
32. Skull of Crocodilia . . . . .	135
33. Skull of Ophidia . . . . .	146
34. Skull of Lacertilia . . . . .	154
35. Skull of Ichthyopterygia . . . . .	158
36. Skull of Dicynodontia . . . . .	159
37. Skull of Pterosauria . . . . .	161
38. Scapular arch and appendages of Hæmatoerya . . . . .	161
39. Pectoral limb of Fishes . . . . .	163
40. Pectoral limb of Reptiles . . . . .	169
41. Pelvic arch and limb of Fishes . . . . .	179
42. Pelvic arch and limb of Reptiles . . . . .	181
43. Dermoskeleton of Fishes . . . . .	193
44. Dermoskeleton of Reptiles . . . . .	198

## CHAPTER III.

## MUSCULAR SYSTEM OF HÆMATOCRYA.

45. Structure of Muscles . . . . .	200
46. Myology of Fishes . . . . .	202
47. Myology of Reptiles . . . . .	215
48. Locomotion of Fishes . . . . .	243
49. Locomotion of Serpents . . . . .	259
50. Locomotion of Limbed Reptiles . . . . .	262

## CHAPTER IV.

## NERVOUS SYSTEM OF HÆMATOCRYA.

51. Nervous Tissues . . . . .	266
52. Myelencephalon of Fishes . . . . .	268
53. Myelencephalon of Reptiles . . . . .	290
54. Myelencephalic membranes in Hæmatoerya . . . . .	296
55. Nerves of Fishes . . . . .	297
56. Nerves of Reptiles . . . . .	309
57. Sympathetic nervous system . . . . .	318
58. Sympathetic nervous system of Fishes . . . . .	320
59. Sympathetic nervous system of Reptiles . . . . .	321
60. Appendages of the Nervous System . . . . .	323
61. Organ of Touch in Hæmatoerya . . . . .	325
62. Organ of Taste in Reptiles . . . . .	327
63. Organ of Smell in Hæmatoerya . . . . .	328
64. Organ of Sight in Fishes . . . . .	331
65. Organ of Sight in Reptiles . . . . .	337
66. Organ of Hearing in Fishes . . . . .	342
67. Organ of Hearing in Reptiles . . . . .	347
68. Electric Organs of Fishes . . . . .	350

## CHAPTER V.

## DIGESTIVE SYSTEM OF HÆMATOCRYA.

SECTION	PAGE
69. Dental Tissues . . . . .	359
70. Teeth of Fishes . . . . .	368
71. Teeth of Reptiles . . . . .	385
72. Alimentary canal of Fishes . . . . .	409
73. Liver of Fishes . . . . .	425
74. Pyloric appendages and pancreas of Fishes . . . . .	428
75. Alimentary canal of Reptiles . . . . .	433
76. Liver of Reptiles . . . . .	448
77. Pancreas of Reptiles . . . . .	453

## CHAPTER VI.

## ABSORBENT SYSTEM OF HÆMATOCRYA.

78. Connective tissue : serosity . . . . .	455
79. Absorbents of Fishes . . . . .	456
80. Absorbents of Reptiles . . . . .	458

## CHAPTER VII.

## CIRCULATING AND RESPIRATORY SYSTEMS OF HÆMATOCRYA.

81. Blood of Fishes . . . . .	463
82. Veins of Fishes . . . . .	464
83. Heart of Fishes . . . . .	470
84. Gills of Fishes . . . . .	475
85. Arteries of Fishes . . . . .	488
86. Air-bladder of Fishes . . . . .	491
87. Blood of Reptiles . . . . .	500
88. Veins of Reptiles . . . . .	501
89. Heart of Reptiles . . . . .	505
90. Gills of Batrachians . . . . .	512
91. Arteries of Reptiles . . . . .	516
92. Lungs of Reptiles . . . . .	521
93. Larynx of Reptiles . . . . .	527
94. Respiratory actions of Reptiles . . . . .	530

## CHAPTER VIII.

## URINARY SYSTEM OF HÆMATOCRYA.

95. Kidneys of Fishes . . . . .	533
96. Kidneys of Reptiles . . . . .	537
97. Adrenals of Hæmatocrya . . . . .	542

## CHAPTER IX.

## TEGUMENTARY SYSTEM OF HÆMATOCRYA.

SECTION	PAGE
98. Composition of Tegument . . . . .	545
99. Teguments of Fishes . . . . .	546
100. Teguments of Reptiles . . . . .	550

## CHAPTER X.

## PECULIAR AND DUCTLESS GLANDS AND REPRODUCIBLE PARTS.

101. Scent-glands of Reptiles . . . . .	562
102. Poison-glands of Reptiles . . . . .	563
103. Thyroid body or gland of Hæmatocrya . . . . .	564
104. Thymus body or gland of Reptiles . . . . .	565
105. Reproducible parts in Hæmatocrya . . . . .	566

## CHAPTER XI.

## GENERATIVE SYSTEM OF HÆMATOCRYA.

106. Male organs of Fishes . . . . .	568
107. Female organs of Fishes . . . . .	571
108. Male organs of Batrachians . . . . .	576
109. Male organs of Reptiles . . . . .	579
110. Female organs of Batrachians and Reptiles . . . . .	583

## CHAPTER XII.

## GENERATIVE PRODUCTS AND DEVELOPMENT OF HÆMATOCRYA.

111. Semination of Hæmatocrya . . . . .	589
112. Ovulation in osseous Fishes and Batrachians . . . . .	592
113. Ovulation in cartilaginous Fishes and scaled Reptiles . . . . .	597
114. Fecundation in Fishes . . . . .	599
115. Development of Fishes . . . . .	601
116. Growth and nests of Fishes . . . . .	611
117. Fecundation in Reptiles . . . . .	614
118. Oviposition in Reptiles . . . . .	616
119. Development of Batrachians . . . . .	619
120. Development of Reptiles . . . . .	630

## ERRATA.

- Below Cuts 134, 135, 136, 137, *for* 'XXXIII,' *read* 'XXIII'
- Page 396, eight lines from top, *for* 'premaxillary,' *read* 'vomericine.'
- ,, 448, eighteen lines from top, *for* 'tunical,' *read* 'tumid.'
- ,, 512, eleven lines from bottom, *transpose* 'fig. 399, R' to tenth line, after 'ventricle.'
- ,, 625, four lines from top, *for* 'fig. 435,' *read* 'fig. 424, b.'
- ,, 630, five lines from bottom, *for* 'bodies,' *read* 'borders.'

## ANATOMY OF VERTEBRATES.



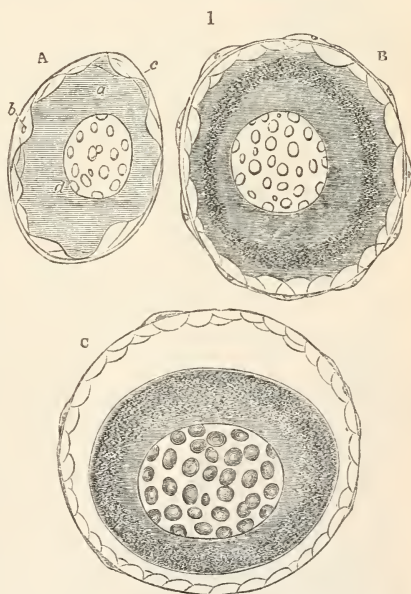
## CHAPTER I.

## CHARACTERS OF VERTEBRATES.

§ 1. *Developmental characters.*—Vertebrates, like lower animals, begin in a semifluid nitrogenous substance called ‘plasma,’ fig. 1, A, *a*; primarily differentiating into albumen, fibrine, lemma, ib. *b*, *c*<sup>1</sup>, nuclei and cells; in which latter form the individuality of the new organism first dawns as a nucleated ‘germ-cell’ or germinal vesicle, ib. *d*.

By the evolution of albuminous granules and oil-particles plasma becomes ‘yolk,’ fig. 1, B, C; the germinal vesicle may be obscured by endogenous multiplication of granules, granular cells and oil-globules, which combine with those of the yolk to form its germinal part: an outer layer of ‘lemma,’ D, *ch*, completes the unimpregnated vertebrate egg.

For further development another principle is needed, viz. the hyaline nucleus or product of the sperm-cell, fig. 2, called ‘spermatozoon.’ Its reception by the egg, as at *a*, *b*, fig. 3, is followed by the formation of a germ-mass. This mass is due

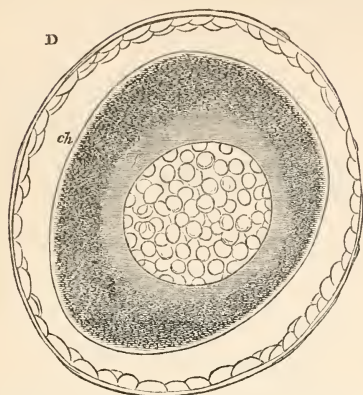


Stages of development of the ovarian egg of a vertebrate animal (*Gasterosteus*). CLXXVI.

<sup>1</sup> Gr. *lemma*, skin; also called ‘primary’ or ‘basement’ membrane; distinguished, through its relations, as ‘neurilemma, sarcolemma, adenolemma’ or the limitary membrane of gland-follicles, &c.



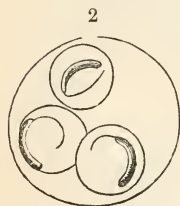
to a series of self-splittings of the impregnated centre, which 'fissiparous' progeny assimilate or incorporate more or less of the yolk. In fig. 4, *A*,



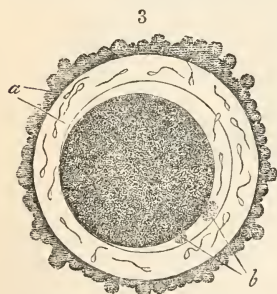
Stages of development of the ovarian egg of a vertebrate animal (continued). CLXXVI.

*d* is the impregnated germ-yolk; *e* the fluid between it and the zona; *f*; *f'* is albumen from which the chorion, *cho*, arises. In *B*, fig. 4, is shown the first division or segmentation of the germ-yolk; *C* shows the second division; and *D*, a later stage in which the properties of the impregnated centre have been diffused and distributed by fissiparous multiplication amongst the countless nucleated cells which form the germ-mass.

Thus far the vertebrate germ resembles in form, structure, and behaviour, the infusorial monad and the germ-stage of invertebrates. The next step impresses upon the nascent being its 'vertebrate' type. Linear rows of the nucleated cells coalesce and become converted into the nervous axis, which under the form or appearance of a double chord, fig. 5, *ch*, marks the dorsal or 'neural' aspect of the embryonal rudiment. The nutritive organs grow from the opposite side. Along the interspace is laid the basis of the skeleton, as a gelatinous cylinder, in a membranous sheath, called 'notochord,'<sup>1</sup>



Sperm-cell, with three spermatozoa, and their nucleus the 'spermatozoon' (Cock). CLXXVII.



Vertebrate egg, impregnated by the spermatozoa (Rabbit). CLXXVI.

which develops a pair of plates 'neurad'<sup>2</sup> to enclose the nervous axis, and a pair of plates 'hæmad'<sup>3</sup> to enclose the vascular axis and organs of vegetative life. Flesh and skin coextend with the enclosing plates.

This formation of two distinct parallel cavities—'neural' and 'hæmal'—under symmetrical guidance in the vertical or 'neuro-hæmal' direction, with a repetition of parts on the right and left sides, establishing transverse or 'bi-lateral'

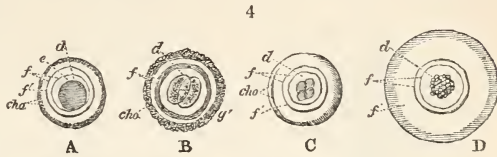
<sup>1</sup> The 'chorda dorsalis' of embryologists.

<sup>2</sup> Backward in man, upward in beasts.

<sup>3</sup> Forward in man, downward in beasts.

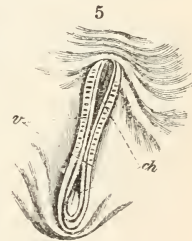
symmetry, constitutes the chief developmental characteristic of the vertebrate animal.

The twofold symmetry is shown in the bone-segment, fig. 7; also in the flesh-segment surrounding the skeletal one in fig. 6, in which the mid point marks the 'notochord;' with the neural canal above, the hæmal canal below; both surrounded by the two neural and two hæmal masses of muscles on each side.



Stages of development of a vertebrate germ (Rabbit), CVII.

The lancelet, *Branchiostoma*, fig. 23, superinduces its distinctive characters upon this stage. Aponeurotic septa accompany the pairs of nerves and divide the longitudinal muscular masses into segments. At the next rise segmentation is shown by the development of cartilage, forming pairs of plates, fig. 5, v, commonly corresponding with the pairs of nerves sent off from the neural axis, and with the pairs of vessels from the hæmal axis. As these plates ossify, ossification commonly also begins at corresponding points of the notochord, dividing it into as many central parts as there are peripheral plates or arches, and constituting skeletal segments or 'vertebræ;' according, or reducible to, the type, fig. 7.



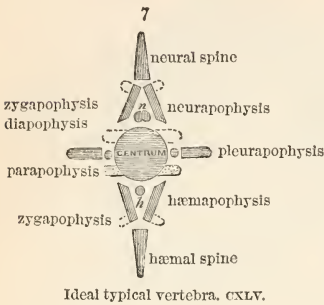
Germ of a Rabbit (Barry)

§ 2. *Structural characters.* — The series of 'vertebræ,' under their several modifications, as the neural or hæmal organs may predominate, constitute the vertebral column. The neural axis consists of 'encephalon' or brain, and of 'myelon' or spinal chord. The organs of the five senses — touch, taste, smell, hearing, and sight — are usually present. The blood-discs, fig. 8, speedily acquire the red colour which, by their number and minuteness, they impart to the whole blood. The heart is a compact muscular organ, of two or more cavities, propelling the blood, through a closed system of arteries and veins, directly to the breathing-organ, and, in most vertebrates, directly also to the body. The breathing-organ communicates with the pharynx. The alimentary canal has distinct receptive and expellent apertures, usually at opposite ends of the trunk. The mouth is provided with two jaws, placed one above or before the other, working in the direction of the axis of the body. The muscles surround



Section of a 'myocomma' or flesh-segment; tail of a Mackerel. XXI.

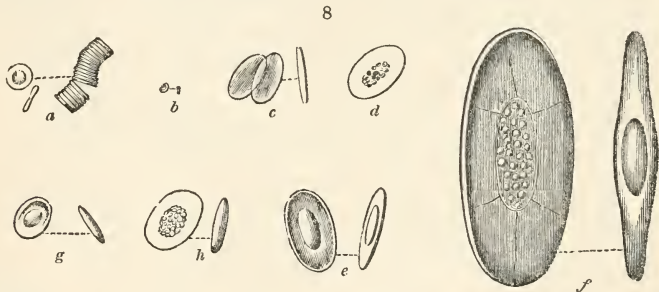
the bony or gristly levers on which they act. The limbs do not exceed two pairs. The sexes are distinct, and the individual is developed directly from an impregnated ovum. Under the vertebrate plan of structure animals grow to a greater size and live a longer time, than under any of the invertebrate plans.



Ideal typical vertebra. CXLV.

§ 3. *Piscine modification.* — All vertebrates, during more or less of their developmental life-period, float in a liquid of similar specific gravity to themselves. A large proportion, constituting the lowest organised and first developed forms of the province, exist and breathe in water,

and are called 'fishes.' Of these a few retain the primitive vermiform condition and develop no limbs: in the rest they are 'fins,' of simple form, moving by one joint upon the body, rarely adapted for any other function than the impulse or guidance



Blood-discs, each magnified 300 diameters linear. a, Man; b, Musk-deer; c, Goose; d, Crocodile; e, Frog; f, Siren; g, Cod-fish; h, Skate. CXLV.

of the body through the water. The shape of the body is usually such as is adapted for moving with least resistance through a liquid medium. The surface of the body is either smooth and lubricous, or is smoothly covered by overlapping scales, is rarely defended by bony plates or roughened by tubercles, still more rarely armed with spines.

The neural axis presents but one local enlargement, at the fore end, forming the 'encephalon;' it is small, and consists of a succession of simple ganglionic masses, most of which are appropriated to the function of a nerve of special sense. Touch is feebly exercised, and an organ for that sense rarely developed.

The tongue, as an organ of taste, is hardly conspicuous; the framework supporting it relates chiefly to the mechanism of swallowing and breathing, and is suspended to a pedicle common to it and the mandible. Of the organ of hearing there is no outward sign; but the essential internal part or 'labyrinth' is present, and its semicircular canals are, in most fishes, largely developed. The labyrinth is devoid of a 'cochlea,' and is rarely provided with a proper chamber, but is lodged, in common with the brain, in the cranial cavity. The eyes are usually large, seldom defended by eyelids, and never served by a lacrymal apparatus. The alimentary canal is commonly short and simple, with the divisions less clearly marked than in higher vertebrates; the short and wide gullet being hardly distinguishable from the stomach. The pancreatic function appears to be performed by commonly more or fewer cæcal appendages to the duodenum. The heart consists essentially of one auricle receiving the venous blood, and one ventricle propelling it to the gills, or organs submitting that blood in a state of minute subdivision to the action of aerated water. From the gills the arterial blood is carried over the entire body by vessels, the circulation being aided by the contraction of the surrounding muscles. The blood is cold, or with a temperature rarely above that of the surrounding medium. The coloured discs are, in some fishes, subcircular, fig. 8, *g*; in others, subelliptical, ib. *h*, or elliptical; comparatively large, but not the largest amongst vertebrates. The primordial renal glands (*corpora Wolffiana*) are persistent, and secrete the urine from venous blood. Such are the leading anatomical characters of the class *Pisces*—Fishes.

§ 4. *Reptilian modification*.—Many fishes have a bladder of air between the digestive canal and kidneys, which, in some, communicates by an air-duct with the gullet; but its office is chiefly hydrostatic. When, in the rise of structure, this air-bladder begins to assume the vascular and pharyngeal relations, with the form and cellular structure of lungs, the limbs acquire the character of feet; at first, as in *Lepidosiren*, fig. 41, 99, thread-like and many-jointed—then bifurcate, or two-fingered, with the ordinary elbow and wrist-joints of land-limbs (*Amphiuma*), fig. 100, B, D,—next, three-fingered, as in *Proteus*,—or four-fingered, but reduced to the pectoral pair, as in *Siren*. From these gill-retaining transitional forms, up to and including crocodiles, all cold-blooded vertebrates, with lungs, breathing air directly, are called Reptiles (*Reptilia*, Cuv.). The heart has two auricles; the ventricle, in most, is imperfectly divided, and more or less of



the venous blood is mixed with the arterial blood which circulates over the body. The lungs retain the form of bags, with cellulovascular walls, varying as to thickness, and are situated, with the other organs of vegetative life, in a common thoracic-abdominal cavity.

§ 5. *Avian modification.*—When the lungs become spongy, and the cavity of the air-bag is obliterated by the multiplication of vascular cellules, and when a four-chambered heart transmits the venous blood to the lungs, and pure arterial blood to the body, the temperature is raised, and is maintained at from 90° to 105° Fahr., whatever may be that of the surrounding medium. Of these hot-blooded vertebrates, one class has the lungs fixed, and communicating with air-cells extending into the abdomen, and usually other parts of the body; this class is oviparous, is clothed with feathers, and has the pectoral limbs modified as wings; it is called *Aves* — Birds.

§ 6. *Mammalian modification.*—In the other class of warm-blooded animals, the spongy lungs are freely suspended and confined to a thoracic cavity, defined by a midriff from the abdomen; the class is hair-clad, viviparous, and suckles the young, whence it is called *Mammalia* — Mammals.

§ 7. *Genetic and thermal distinctions.*—The broad and well-marked characters afforded by the respiratory system will probably give permanence to the division, so convenient for most purposes, of the vertebrate province into the four great classes above defined, viz. *Pisces*, *Reptilia*, *Aves*, *Mammalia*.

But many important relations and affinities are thereby masked. Although the last two classes agree, as ‘hot-blooded vertebrates,’ in their higher cerebral development, and in the more complex heart and lungs, birds, by genetic and developmental characters, as well as by the general plan of their organisation, are more intimately and naturally allied to the oviparous saurians than to the viviparous mammals. In their generation and development, modern batrachians differ from other cold-blooded air-breathers, and agree with fishes. Present knowledge of extinct forms more clearly exposes the artificial nature of the primary groups of the oviparous vertebrates. An important link, the *Pterosauria*, or flying reptiles, with wings and air-sacs, fig. 108, more closely connecting birds with the actual remnant of the reptilian class, has passed away. Other extinct orders (*Ganocephala* and *Labyrinthodontia*) have demonstrated the artificial nature of the distinction between fishes and reptiles, and the close transitions that connect together all the cold-blooded vertebrates.



Thus vertebrates might be binarily divided into oviparous, I. II. III., and viviparous, IV.; into anallantoic or branchiate and allantoic or abranchiate; into *Hæmatothermal*,<sup>1</sup> having the four-chambered heart, spongy lungs, hot blood, and *Hæmatocryal*,<sup>2</sup> having less perfect breathing organs, less complex heart, with cold blood; and each of such divisions are artificial and convenient. It suits my present purpose to adopt the latter.

§ 8. *Subclasses of Hæmatocrya.*—With the best insight—peering into the dark vistas of the remote past—that one can command into the nature of the strange forms which then perished, and combining with palæontological research the results of anatomical and developmental scrutiny of existing vertebrates, the following seem to be the best defined cold-blooded groups, each with such characters in common as leads to their being called ‘natural,’ and of a value which may be expressed by the term ‘sub-class.’

I. DERMOPTERI.	III. PLAGIOSTOMI.
II. TELEOSTOMI.	IV. DIPNOA.
V. MONOPNOA.	

Subclass I. DERMOPTERI.—Body vermiform, limbless; endoskeleton membrano-cartilaginous and notochordal,<sup>3</sup> ribless; skin scaleless, lubricous; a vertical fin-fold bordering the hind part of the body, without fin-rays; myelon opaline, ductile, elastic; no sympathetic nerve; organ of smell single; eyes wanting, or very small; optic nerves not crossing each other; auditory labyrinth of one or two semicircular canals; mouth jawless, or suctorial; alimentary canal straight, simple, without cæcal appendages, pancreas, or spleen. Branchial function independent of the mouth; heart, without ‘bulbus arteriosus;’ a pulsatile portal sinus; no swim-bladder; testes and ovaria elongated plates without ducts; generative outlet peritoneal; ova numerous, small, simultaneously developed, and impregnated externally; cleavage of yolk entire; no amnios or allantois; a metamorphosis, as, e. g. from *Ammocetes* to *Petromyzon*, after the third year from the egg.

Subclass II. TELEOSTOMI.<sup>4</sup>—Body pisciform, with medial and

<sup>1</sup> Gr. *haima*, blood; *thermos*, hot.

<sup>2</sup> Gr. *haima*, blood; *cruos*, cold.

<sup>3</sup> Retaining the notochord or primitive basis of the vertebral column.

<sup>4</sup> This word (from Gr. *telos*, end or completion; *stoma*, mouth;) refers to the completion of the mouth by opposing upper and lower jaws, and also to its terminal position, opening at the fore end of the head.

parial fins, supported by rays; endoskeleton in most, more or less ossified; hyoid arch attached to tympanic pedicle; scapular arch attached to the occiput; no sternum: skin defended by scales or plates; brain with predominant mesencephalon; myelon opaque, inelastic; a sympathetic nerve; organ of smell double; eyes usually large, with bony sclerotic; auditory labyrinth with three semi-circular canals, in the cranial cavity; mouth formed by upper and lower jaws, opening at the fore part of the head, and admitting the respiratory currents; intestine, in most, with pyloric appendages and spleen; anus in front of urethra; air-bladder in most; gills, free; branchial outlet single on each side, defended by a branchiostegal flap, with one or more rays; testes ('milt') and ovaries ('roe') large, with continuous ducts in most; ova very numerous and small, simultaneously developed, and impregnated, usually, externally; no amnios or external allantois.

Subclass III. PLAGIOSTOMI. — Endoskeleton cartilaginous, or partially ossified; scapular arch detached from occiput; exoskeleton as osseous granules or tubercles; body with medial and parial fins, the hinder pair pelvic in position; caudal-fin with produced upper lobe; brain with the prosencephalon predominant; auditory labyrinth in a special chamber; mouth, in most, a wide transverse slit, opening below the head; intestine with a spiral valve, pancreas, and spleen; no air-bladder; bulbus arteriosus with numerous rows of valves; gills, in most, fixed, and with several branchial outlets on each side; testes of moderate size, with sperm-duct and copulatory apparatus; ovaries with few and large ova, successively developed and conveyed away by a detached oviduct; ova impregnated and, in some, developed internally; embryo without amnios or allantois, and with deciduous external gills.

Subclass IV. DIPNOA. — Endoskeleton more or less ossified; ribs wanting, or short and free; parial members as legs; brain with predominant prosencephalon; optic nerves not decussating; auditory labyrinth in a special chamber, but with only the 'fenestra vestibuli;' nostrils communicating with the mouth; intestine, with pancreas and spleen; air-bladder as a pair of lungs, communicating by a duct and glottis with the hæmal side of the pharynx; heart, in most, with one ventricle and two auricles. Testes of moderate size, with sperm-ducts, but no intromittent organs or claspers; ovaries with detached oviducts; ova simultaneously developed, and, in most, impregnated externally. Embryo without amnios or allantois, and with external gills.

Subclass V. MONOPNOA. — Endoskeleton ossified; exoskeleton in most as horny scales, in some as bony scutes; one occipital condyle; vomer usually single; trunk-ribs long and curved. Brain with predominant prosencephalon. Labyrinth with both fenestra vestibuli and fenestra rotunda; a tympanum in most; lungs; heart with two auricles, and with the ventricle more or less completely divided. Testes with ducts and intromittent organ. Ovaria with detached oviducts. Ova successively developed, impregnated with copulation. An amnios and allantois. No metamorphosis.

### § 9. Orders of HÆMATOCRYA.

#### Subclass I. Order I. CIRROSTOMI.

Body compressed; mouth a longitudinal fissure with sub-rigid cirri on each side. Pulsating vessels or sinuses in place of heart. Blood pale; free pharyngeal branchial filaments, and a branchial dilatation of the œsophagus.

Gen. *Branchiostoma*. Ex. Lancelet.

#### Order II. CYCLOSTOMI.

Body cylindrical; heart distinct; branchial artery without bulb; branchiæ sacciform, with external spiracles, six or seven on each side, blood red. Mouth subcircular, suctorial, but longitudinal when closed. Olfactory sac communicating with, or produced into, a canal.

Gen. *Myxine*. Ex. Hag-fish.

*Petromyzon*. Ex. Lamprey.

Subclass II. A. Arterial bulb with one pair of valves; optic nerves decussating; vertebræ biconcave.

#### Order III. MALACOPTERI.

Skin, in most with cycloid scales, in a few with ganoid plates; rarely naked. Fins supported by rays, all of which (save the first in the dorsal and pectoral, in some) are 'soft,' or many-jointed; a swim-bladder and air-duct; peritoneal outlets in many.

## Suborder I. APODES.

- Fam. 1. *Symbranchidæ*. Ex. Cuchia.  
 2. *Murænidæ*. Ex. Eel.  
 3. *Gymnotidæ*. Ex. Gymnotus.

## Suborder II. ABDOMINALES.

- Fam. 1. *Heteropygii*. Ex. Amblyopsis.  
 2. *Clupeidæ*. Ex. Herring.  
 3. *Salmonidæ*. Ex. Salmon.  
 4. *Scopelidæ*. Ex. Saurus.  
 5. *Characinidæ*. Ex. Myletes.  
 6. *Galaxidæ*. Ex. Galaxias.  
 7. *Esocidæ*. Ex. Pike.  
 8. *Mormyridæ*. Ex. Mormyrus.  
 9. *Cyprinodontidæ*. Ex. UMBER.  
 10. *Cyprinidæ*. Ex. Carp.  
 11. *Siluridæ*. Ex. Sheat-fish.  
 12. *Alepisauridæ*. Ex. Marine Sheat-fish.

## Suborder III. PHARYNGOGNATHI.

- Fam. 1. *Scomber-esocidæ*. Ex. Saury-Pike.

## Order IV. ANACANTHINI.

Endoskeleton ossified; exoskeleton in some as cycloid, in others as ctenoid scales; fins supported by flexible many-jointed rays; ventrals beneath or in advance of the pectorals, or wanting; swim-bladder, when present, without a duct.

- Fam. 1. *Ophididæ*. Ex. Ophidium.  
 2. *Gadidæ*. Ex. Cod.  
 3. *Pleuronectidæ*. Ex. Plaice.

## Order V. ACANTHOPTERI.

Endoskeleton ossified; exoskeleton, in most, as ctenoid scales; fins with one or more of the first rays unjointed or inflexible spines; ventrals, in most, beneath or in advance of the pectorals; duct of swim-bladder obliterated.

## Suborder I. PHARYNGOGNATHI.

- Fam. 1. *Chromidæ*. *Ex.* Chromis.  
 2. *Cyclo-labridæ*. *Ex.* Wrasse.  
 3. *Cteno-labridæ*. *Ex.* Pomacentrus.

## Suborder II. ACANTHOPTERI VERI.

- Fam. 1. *Percidæ*. *Ex.* Perch.  
 2. *Squammipennes*. *Ex.* Chætodon.  
 3. *Sparidæ*. *Ex.* Sea-bream, Gilthead.  
 4. *Sciænidæ*. *Ex.* Maigre.  
 5. *Labyrinthobranchii*. *Ex.* Anabas or Tree-climber.  
 6. *Mugilidæ*. *Ex.* Mullet.  
 7. *Atherinidæ*. *Ex.* Sand-smelt.  
 8. *Sphyrænidæ* (cycloid). *Ex.* Barracuda.  
 9. *Scomberidæ* (cycloid). *Ex.* Mackerel.  
 10. *Sclerogenidæ*. *Ex.* Gurnard, Miller's thumb.  
 11. *Tænioidei*. *Ex.* Riband-fish.  
 12. *Teuthydæ*. *Ex.* Lancet-fish.  
 13. *Fistularidæ*. *Ex.* Pipe-mouth.  
 14. *Gobiidæ*. *Ex.* Goby.  
 15. *Blenniidæ* (cycloid). *Ex.* Wolf-fish.  
 16. *Lophiidæ* (skin muricate or naked). *Ex.* Angler.<sup>1</sup>

## Order VI. PLECTOGNATHI.

Endoskeleton partly ossified; exoskeleton as ganoid scales, plates, or spines; ventrals wanting in most; maxillary and pre-maxillary immoveably connected on each side of the jaw; swim-bladder without air-duct.

## Suborder SCLERODERMI.

- Fam. 1. *Balistini*. *Ex.* File-fish.

## Suborder APLEURI (ribless).

- Fam. 1. *Ostraciontidæ*. *Ex.* Trunk-fish.  
 2. *Gymnodontidæ*. *Ex.* Globe-fish.

<sup>1</sup> This selection of the chief family-diversities of the vast acanthopterous order is designed, like the families cited under other orders, merely to exemplify it by familiar fishes with vernacular names. For the characters and affinities of all the present known acanthopterous families, see Dr. Günther's excellent work, CLXXIV., vol. iii.



## Order VII. LOPHOBANCHII.

Endoskeleton partially ossified, without ribs; exoskeleton ganoid; gills tufted; opercular aperture small; swim-bladder without air-duct. Males marsupial.

Fam. 1. *Hippocampidæ*. *Ex.* Sea-horse.

2. *Syngnathidæ*. *Ex.* Pipe-fish.

B. Arterial bulb muscular, with more than one row of valves. Optic nerves not decussating.

## Order VIII. GANOIDEI.

Endoskeleton cartilaginous, partly bony, or ossified; in a few recent and in most palæozoic extinct forms, notochordal; exoskeleton as ganoid scales or plates; fins usually with the first ray a strong spine; caudal fin in most unsymmetrical; a swim-bladder, often cellular, and with an air-duct; intestine in many with a spiral valve.

## Suborder I. LEPIDOGANOIDEI.

Fam. 1. *Salamandroidei*. *Ex.* *Lepidosteus*, *Polypterus*.

2. *Pycnodontidæ*. *Ex.* *Pycnodus*.

3. *Lepidoidei*. *Ex.* *Dapedius*.

4. *Leptolepidæ*. *Ex.* *Leptolepis*.

5. *Acanthodei*. *Ex.* *Acanthodes*.

6. *Dipteridæ*. *Ex.* *Dipterus*.

7. *Cœlacanthi*. *Ex.* *Cœlacanthus*.

8. *Holoptychidæ*. *Ex.* *Holoptychius*.

## Suborder II. PLACOGANOIDEI.

Fam. 1. *Sturionidæ*. *Ex.* *Sturgeon*.

2. *Ostracostei*. *Ex.* *Pterichthys*.

## Subclass III. Order IX. HOLOCEPHALI.

Endoskeleton cartilaginous, subnotochordal; cranial wall complete; tympanic pedicle confluent therewith; endoskeleton as placoid granules. Anterior dorsal fin with a strong spine; mouth terminal, beak-shaped; dental plates and columns fused with the jaws. Optic nerves not decussating. Valves of bulbous arteriosus multiserial. Gills laminar, with a small proportion of

the border free; a single external gill-aperture on each side; opercular and branchiostegal rays. Oviparous; ova few and large.

Fam. 1. *Chimæridæ*. *Ex.* Chimæra, Callorhynchus.

2. *Edaphodontidæ*. *Ex.* Edaphodus, Ischiodus, Elasmodus.

## Order X. PLAGIOSTOMI.

Endoskeleton cartilaginous or partially ossified; vertebræ biconcave; exoskeleton as placoid granules or tubercles, spiny in some. Mouth transverse on the lower surface of the head. Optic nerves commissurally united, not decussating. Valves of bulbus arteriosus multiserial. Gills attached to the skin by the outer margin, with intervening gill-apertures, five or more in number, on each side; no operculum.

### Suborder I. CESTRAPHORI.<sup>1</sup>

(Spine in front of each dorsal fin; back teeth obtuse.)

Fam. 1. *Hybodontidæ*. *Ex.* Hybodus.

2. *Cestraciontidæ*. *Ex.* Cestracion.

### Suborder II. SELACHII. (Sharks, branchial apertures lateral.)

Fam. 1. *Notidanidæ*. *Ex.* Grey Shark.

2. *Spinacidæ*. *Ex.* Piked Dog-fish.

3. *Scylliadæ*. *Ex.* Spotted Dog-fish.

4. *Nictitantes*. *Ex.* Tope.

5. *Lamnidæ*. *Ex.* Porbeagle.

6. *Alopecidæ*. *Ex.* Fox Shark.

7. *Scymniidæ*. *Ex.* Greenland Shark.

8. *Squatina*. *Ex.* Monk-fish.

9. *Zygænidæ*. *Ex.* Hammer-head Shark.

### Suborder III. BATIDES. (Rays, branchial apertures inferior.)

Fam. 1. *Pristidæ*. *Ex.* Saw-fish.

2. *Rhinobatidæ*. *Ex.* Rhinobates.

3. *Torpedinidæ*. *Ex.* Electric ray.

4. *Raiidæ*. *Ex.* Skate.

5. *Trygonidæ*. *Ex.* Sting Ray.

6. *Myliobatidæ*. *Ex.* Eagle Ray.

7. *Cephalopteridæ*. *Ex.* Cephalopterus.

<sup>1</sup> *Kestra*, a weapon; *phero*, I bear. Many extinct species of this group are known only by their fossil weapons, called 'Ichthyodorulites.'

## (Transitional) Order XI. PROTOPTERI.

Endoskeleton notochordal, partly cartilaginous, partly osseous; no occipital condyle; vomer undivided; temporal fossæ roofed over by bone; pleurapophyses short, with free extremities; exoskeleton as subcuticular cycloid scales; scapular arch attached to occiput; proximal ends of hyoidean and tympano-mandibular arches distinct. Vertical fin a continuous border to the compressed tail. Pectoral and ventral fins subulate, many jointed; the former fringed beneath; the latter pelvic in position; the pelvis unattached to the spine; gills filamentous, free, in a branchial chamber with a single vertical outlet; branchial arches unconnected with the hyoid; air-bladder double, lung-like, with air-duct, glottis, and pulmonary vein. Prosencephalon predominant in brain; nasal sacs sublabial with two remote extra-buccal apertures; auditory labyrinth in a distinct chamber; bulbus arteriosus long, with two longitudinal valves; intestine with a spiral valve, vent anterior to urethra; ovaria distinct from oviducts.

Fam. *Sirenoidei*. Ex. *Lepidosiren*.

Subclass IV. Order XII. GANOCEPHALA. (*Extinct.*)

Endoskeleton notochordal and osseous; no occipital condyle; vomer divided; temporal fossæ roofed over by bone; hyoid arch not connected with tympanic pedicle; branchial arches(?) unconnected with hyoid; exoskeleton as subganoid scales; pleurapophyses short and free. Teeth with converging inflected folds of cement at their basal half. Pectoral and pelvic limbs short, slender, three or four digitate; natatory.

Genus *Dendrerpeton*.

*Archegosaurus*.

Order XIII. LABYRINTHODONTIA. (*Extinct.*)

Head defended, as in Ganocephala, by a continuous casque of externally sculptured and unusually hard and polished osseous plates, including the supplementary "post-orbital" and "super-temporal" bones, but leaving a "foramen parietale." Two occipital condyles. Vomer divided and denticigerous. Vertebral bodies, as well as arches, ossified, biconcave. Pleurapophyses of the trunk, long and bent. Exoskeleton, in some, as small ganoid

scales. Teeth rendered complex by undulation and side branches of the converging folds of cement, whence the name of the order.

Genus *Rhombopholis*.  
*Labyrinthodon*.

#### Order XIV. BATRACHIA.

Endoskeleton ossified; two occipital condyles; vomer divided, in most dentigerous; temporal fossæ unroofed; scapular arch detached from occiput; ribs as processes, or short, straight and free; skin nude, often lubricous. Limbs digitate, trisegmental. Intestine without spiral valve, vent posterior to urethra. Embryonal gills, in some retained, in most lost; with a metamorphosis associating a tail-less body with pulmonary respiration and a heart of two auricles and one ventricle.

##### Suborder I. OPHIOMORPHA.

Fam. *Cæciliadæ*. *Ex.* Cæcilia.

##### Suborder II. ICHTHYOMORPHA.

Fam. *Proteidæ*. *Ex.* Siren, Proteus.

*Salamandridæ*. *Ex.* Newt, Salamander.

##### Suborder III. THERIOMORPHA. *Anura*.

Fam. 1. *Aglossa*. *Ex.* Pipa or Surinam Toad.

2. *Ranidæ*. *Ex.* Frog.

3. *Hylidæ*. *Ex.* Tree-frog.

4. *Bufonidæ*. *Ex.* Toad.

#### Subclass V. Order XV. ICHTHYOPTERYGIA.<sup>1</sup> (*Extinct.*)

Body fish-like, without neck; limbs natatory, with more than five multiarticulate digits; vertebræ many, short, biconcave; no sacrum; anterior trunk-ribs with bifurcate heads; an episternum and clavicles; post-orbital and supra-temporal bones; a foramen parietale; maxillaries small; premaxillaries long and large. Teeth confined to maxillary, premaxillary, and premandibular bones, implanted in a common alveolar groove, penetrated by converging folds of cement at the base; nostrils two, small, near

<sup>1</sup> Gr. *ichthys*, a fish; *pteryx*, a fin.

the orbits; orbits large; a circle of sclerotic plates. Skin naked, forming a vertical tail-fin (inferential).

Genus *Ichthyosaurus*.

#### Order XVI. SAUROPTERYGIA. (*Extinct.*)

Body, in most, with a long neck; limbs natatory, with not more than five digits; an episternum and clavicles; vertebræ with flattened, or slightly cupped, articular surfaces; a sacrum of one or two vertebræ for the attachment of the pelvic arch, in some; ribs with simple heads; no post-orbital and supra-temporal bones; large temporal and other vacuities between certain cranial bones; a foramen parietale; two antorbital nostrils; teeth simple, in distinct sockets of premaxillary, maxillary, and premandibular bones, rarely on the palatine or pterygoid bones; maxillaries larger than premaxillaries.

Genera *Plesiosaurus*, *Pliosaurus*, *Nothosaurus*, *Placodus*.

#### Order XVII. ANOMODONTIA. (*Extinct.*)

Teeth wanting, or limited to a single maxillary pair, having the form and proportions of tusks; a 'foramen parietale;' two external nostrils; tympanic pedicle fixed; vertebræ biconcave; anterior trunk-ribs with a bifurcate head, ischiopubic symphysis continuous.

Fam. *Dicynodontia*.

A long ever-growing tusk in each maxillary bone; pre-maxillaries connate, forming with the lower jaw a beak-shaped mouth, probably sheathed with horn. Sacrum of more than two vertebræ. Limbs ambulatory. *Ex.* *Dicynodon*.

Fam. *Cryptodontia*.

Upper as well as lower jaw edentulous; premaxillaries distinct and produced. *Ex.* *Rhynchosaurus*.

Premaxillaries confluent, short. *Ex.* *Oudenodon*.

#### Order XVIII. CHELONIA.

Trunk-ribs broad, flat, suturally united, forming with their



vertebræ, the sternum, and dermal bones, an expanded thoracic-abdominal case, into which the limbs, tail, and, usually, the head, can be withdrawn; sacrum of more than two vertebræ; no teeth; external nostril single, a cavum tympani; body covered by horny scales in most; ventricle of heart single.

Limbs natatory. Genus *Chelone*. (Turtles.)

Limbs amphibious.  $\left\{ \begin{array}{l} \textit{Trionyx}. \text{ (Mud turtles.)} \\ \textit{Emys}. \text{ (Terrapenes.)} \end{array} \right.$

Limbs terrestrial. *Testudo*. (Tortoises.)

### Order XIX. LACERTILIA.

Vertebræ procœlian, with a single transverse process on each side, and with single-headed ribs; sacral vertebræ wanting, or not exceeding two; two external nostrils; eyes with moveable lids; body covered by horny, sometimes bony, scales.

Limbs natatory, no sacrum. *Ex. Mosasaurus*. (Extinct.)

Limbs ambulatory, a sacrum. *Ex. Lacerta, L.*

Limbs abortive, no sacrum. *Ex. Anguis*.

### Order XX. OPHIDIA.

Vertebræ very numerous, procœlian, with single-headed hollow ribs; no sacrum; no visible limbs; two external nostrils; no cavum tympani; eyeball covered by an immoveable transparent lid. Body covered by horny scales. Teeth anchylosed to jaw.

### Order XXI. CROCODILIA.

Teeth in a single row, implanted in distinct sockets; external nostril single and terminal or sub-terminal. Anterior trunk vertebræ with par- and di-apophyses, and bifurcate ribs; sacral vertebræ two, each supporting its own neural arch; this arch usually articulated by suture. Tail long, vertically compressed; feet short, webbed. Skin protected by bony, usually pitted, plates. Ventricle of heart double.

Suborder AMPHICÆLIA (vertebræ cupped at both ends).

*Ex. Teleosaurus*.

Suborder OPISTHOCÆLIA (vertebræ convex in front, concave behind). *Ex. Streptospondylus*.

Suborder PROCÆLIA (vertebræ concave in front, convex behind). *Ex. Crocodilus*.

## Order XXII. DINOSAURIA. (Extinct.)

Cervical and anterior dorsal vertebræ with par- and di-apophyses, articulating with bifurcate ribs; a few anterior vertebræ more or less convex in front and cupped behind; the rest with flat or slightly concave articular ends; dorsal vertebræ with a neural platform; sacral vertebræ exceeding two in number; body supported on four strong, ambulatory, unguiculate limbs. Skin in some armed by bony scutes. Teeth confined to upper and lower jaws; implanted in sockets. Ventricle of heart double (inferential).

Genera, *Iguanodon*, *Scelidosaurus*, *Megalosaurus*.

## Order XXIII. PTEROSAURIA. (Extinct.)

Pectoral members, by the elongation of the anti-brachium and fifth digit, adapted for flight. Vertebræ procælian; those of the neck very large, those of the pelvis small. Anterior trunk-ribs with bifurcate heads. Most of the bones pneumatic. Head large; jaws long, and armed with teeth. Ventricle of heart double (inferential).

Genera, *Dimorphodon*, *Ramphorhynchus*, *Pterodactylus*.

## CHAPTER II.

## OSSEOUS SYSTEM OF HÆMATOCRYA.

§ 10. *Composition of bone.*—The vertebrate organisation will be first described as manifested in the great cold-blooded series, under the diverse modifications, and progressive stages, indicated by the characters of the foregoing subdivisions of the class. But before entering upon the details of the osseous system, some observations must be premised on the vertebrate skeleton in general.

The original substance of all animals consists of a fluid with granules and cells. In the course of development tubular tracts are formed, some of which become filled with ‘neurine’ or nervous matter; others with ‘myonine’ or muscular matter; other portions are converted into vessels, glands, &c.; but a great proportion of substance, akin to primordial, remains as ‘cellular tissue.’ This, as a rule, becomes hardened in certain parts of the body of vertebrates by earthy salts, chiefly phosphate of lime. Thus the tissues called ‘osteine’ or bone, and ‘dentine’ or tooth, are constituted; between which the chief distinction lies in the mode of arrangement of the earthy particles, in relation to the maintenance of a more or less free circulation of the nutrient juices through such hardened or calcified bodies.

Fishes have the smallest proportion, birds the largest proportion, of the earthy matter in their bones. The animal or soft part in all is chiefly a gelatinous substance.

PROPORTIONS OF EARTHY OR HARD,<sup>1</sup> AND OF ANIMAL OR SOFT, MATTER IN  
THE BONES OF THE VERTEBRATE ANIMALS.

FISHES.			
	Salmon	Carp	Cod
Soft . . . .	60·62	40·40	34·30
Hard. . . .	39·38	59·60	65·70
	<hr style="width: 50%; margin: 0 auto;"/>	<hr style="width: 50%; margin: 0 auto;"/>	<hr style="width: 50%; margin: 0 auto;"/>
	100·00	100·00	100·00

<sup>1</sup> This has been termed inorganic; but that the combination of phosphorus and calcium has ever taken place in nature save under the influences of a living organism, remains to be proved.

## REPTILES.

	Frog	Snake	Lizard
Soft . . . .	35.50	31.04	46.67
Hard . . . .	64.50	68.96	53.33
	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00

## MAMMALS.

	Porpoise	Ox	Lion	Man
Soft . . . .	35.90	31.50	27.70	31.03
Hard . . . .	64.10	69.00	72.30	68.97
	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00

## BIRDS.

	Goose	Turkey	Hawk
Soft . . . .	32.91	30.49	26.72
Hard . . . .	67.09	69.51	73.28
	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00

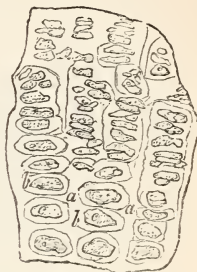
From the above table it will be seen that the bones of the fresh-water fishes have more animal matter, and are, consequently, lighter than those of fishes from the denser element of sea-water; and that the marine mammal called Porpoise differs little from the sea-fish in this respect. The batrachian Frog has more animal matter in its bones than the ophidian or saurian reptiles, and thereby, as in other respects, more resembles the fish. Serpents almost equal birds in the great proportion of the osseous salts, and hence the density and ivory-like whiteness of their bones.

The chemical nature of the hardening particles, and of the soft basis of bone, is exemplified in the subjoined Table, including a species of each of the four classes of Vertebrata:—

## CHEMICAL COMPOSITION OF BONES.

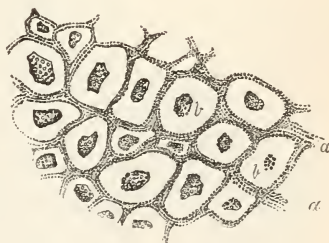
	Hawk	Man	Tortoise	Cod
Phosphate of lime, with trace of fluato of lime . . . . .	64.39	59.63	52.66	57.29
Carbonate of lime . . . . .	7.03	7.33	12.53	4.90
Phosphate of magnesia . . . . .	0.94	1.32	0.82	2.40
Sulphate, carbonate, and chlorate of soda . . . . .	0.92	0.69	0.90	1.10
Glutin and chondrin . . . . .	25.73	29.70	31.75	32.31
Oil . . . . .	0.99	1.33	1.34	2.00
	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00	<hr/> 100.00

§ 11. *Development of bone.*—The primitive basis, or ‘blas-tema,’ of bone is a subtransparent glairy matter containing numerous minute corpuscles. It progressively acquires increased firmness; sometimes assuming a membranous or ligamentous state, usually a gristly consistence, before its conversion into bone. The change into cartilage is noted by the appearance of minute nucleated cells; which increase in number and size, and are aggregated in rows, with intercellular tracts, where the ossification is about to begin, as in fig. 9. These rows, in the cartilaginous basis of long bones, are vertical to its ends; in that of flat bones they are vertical to the margin. The cells furthest from the seat of ossification are flattened and in close contact; nearest that seat they become enlarged and separated. In fig. 9, *a* is the intercellular or ‘intercolumnar’ tissue; *b* the enlarged cell-wall; *c* the nucleus. The first appearance of bone is that of minute granules in the intercolumnar and intercellular tissue, fig. 10, *a*. Canals are next formed in the bone, by absorption, which ultimately receive blood-vessels, and become the ‘vascular canals.’ The immediate nutrition of bone is provided for by the production of minute ‘plasmatic canals’ from the vascular ones.



Section of temporary cartilage, which has undergone the last stage towards ossification. CL.

In most fishes the plasmatic canals are free from partial dilata-tions, and appear as in the magnified section of bone, fig 11; where *a* shows the area of the ‘vascular canal,’ and *b* the orifices of the ‘plasmatic canals,’ exposed in a longitudinal section of a vascular canal. In some fishes, e. g. the Garpike (*Belone*), partial dilatations do occur in the plasmatic canals, of the form shown in fig. 12, *d*; and in a Sea-bream (*Sargus*) of that marked *c*; in the Frog they are wider and more defined, as in the two dilatations shown at *a*. In serpents, e. g. the *Python*, they are commonly, where best defined, of the elongate oval form shown in 1, 2, and 3, fig. 13; but in transverse section they appear as in 5 and 6. In the bird, e. g. the Goldfinch, they have the form shown in *b*, fig. 12. In human bone they assume the forms represented in fig. 14. When so defined they are termed ‘lacunæ’ or ‘bone-cells;’ and, in some



Transverse section of temporary cartilage in the first stage of ossification. CL.



degree, characterise, by their shape and size, the osseous tissue of the respective vertebrate classes. In the concentric laminae sur-

11



Plasmatic canals in a fish-bone. *a* transverse, *b* longitudinal, section of vascular canal (TOMES, CL.)

rounding the vascular canal, fig. 15, *a, a*, the bone-cells are arranged concentrically, between the laminae, with the long axis

12

13



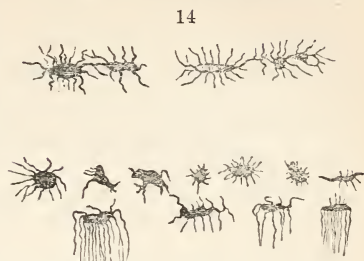
Forms of bone-cells in Python and Boa Constrictor. CL.

in the direction of the circular line of the plate. Most of the plasmatic tubes continued from the bone-cells pierce the plates at

right angles in their course to the vascular canal, with which they communicate; and they form the essential vehicle of the material for future growth.

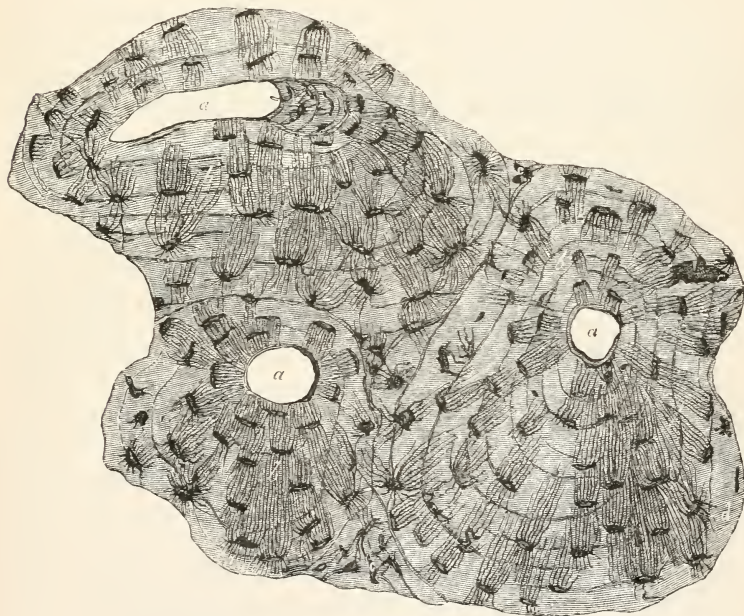
§ 12. *Growth of bone.* — In fishes the bones continue to grow throughout life, and their periphery, whether in the flat bones of the head which overlap each other,

or in the thicker bones that interlock, is cartilaginous or membranous, and the seat of progressive ossification. The long bones of most reptiles retain a layer of ossifying cartilage beneath the terminal articular cartilage; and growth continues at their extremities while life endures.



The forms assumed by the bone-cells in man. CL.

15



Transverse section from the dense portion of the human femur. CL.

Some of the long bones in frogs, birds, and most of those in mammals, have their ends distinct from the body or shaft of the growing bone; these separately ossified ends are termed 'epiphyses': the seat of the active growth of the shaft is in a cartilaginous crust at the ends supporting the epiphyses. When these coalesce with the shaft, growth in the direction of the bone's axis comes to

an end; but there is a slower growth going on over the entire periphery of the bone, which is covered by a membrane, called the 'periosteum.' In this membrane, the vascular system of a bone, except the vessel supplying the marrow-cavity, undergoes the amount of subdivision which reduces its capillaries to dimensions suited for penetrating the pores leading to the vascular canals, figs. 11 and 15, *a, a*.

Thus bone is a living and vascular part, growing by internal molecular addition and change, and having the power of repairing fracture or other injury. The shells and crusts of molluscous and crustaceous animals are unvascular; they grow by the addition of layers to their circumference, may be cast off when too small for the growing body, and be reproduced of a more conformable size. When fractured, the broken parts may be cemented together by newly superadded shell-substance from without; but are not unitable by the action of the fractured surfaces from within.

Extension of parts, however, is not the sole process which takes place in the growth of bone; to adapt a bone to its destined office changes are wrought in it by the removal of parts previously formed. In fishes, indeed, we observe a simple unmodified increase. To whatever extent the bone is ossified, that part remains, and consequently most of the bones of fishes are solid or spongy in their interior, except where the ossification has been restricted to the surface of the primary gristly mould.<sup>1</sup> The bones of the heavy and sluggish turtles and sloths, of the seals, and of the whale-tribe, are solid. But in the active land quadrupeds, the shaft of the long bones of the limbs is hollow, the first formed osseous substance being absorbed, as new bone is being deposited from without. The strength and lightness of the limb-bones are thus increased after the well-known principle of the hollow column, which Galileo, by means of a straw picked up from his prison floor, exemplified, as an evidence of design, in refutation of a charge of Atheism brought against him by the Inquisition. The bones of birds, especially those of powerful flight, are remarkable for their lightness. The osseous tissue itself is, indeed, more compact than in other animals; but its quantity in any given bone is much less, the most admirable economy being traceable throughout the skeleton of birds in the advantageous arrange-

<sup>1</sup> In this case, exemplified in bones of the *Lophius*, *Gyrosteus*, and the lower *Batrachia*, fossilisation, which affects only the ossified crust, leaves the appearance, through the solution of the unossified cartilage, of a wide medullary cavity, which might mislead the Palæontologist in his inferences.

ment of the weighty material. Thus, in the long bones, the cavities analogous to those called 'medullary' in beasts, are more capacious, and their walls are much thinner: a large aperture called the 'pneumatic foramen,' near one end of the bone, communicates with its interior; and an air-cell, or prolongation of the lung, is continued into and lines the cavity of the bone, which is thus filled with rarefied air instead of marrow. The extremities of such air-bones present a light open net-work, slender columns shooting across in different directions from wall to wall, and these little columns are likewise hollow.

In the mammalian class, the air-cells of bone are confined to the head, and are filled from the cavities of the nose or ear, not from the lungs. Such cells are called 'frontal sinuses,' 'antrum,' 'sphenoidal,' and 'ethmoidal sinuses,' in man. The frontal sinuses extend backward over the top of the skull in the ruminant and some other quadrupeds, and penetrate the cores of the horns in oxen, sheep, and certain antelopes. The most remarkable development of cranial air-cells is presented by the elephant; the intellectual physiognomy of this huge quadruped being caused, as in the owl, not by the actual capacity of the brain case, but by the vast extent of the pneumatic cellular structure between the outer and inner plates of the skull-wall.

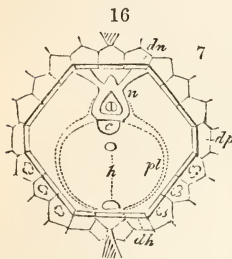
In all these varied modifications of the osseous tissue, the cavities therein, whether mere cancelli, or small medullary cavities as in the Crocodile, or large medullary cavities as in the Ox, or pneumatic cavities and sinuses as in the Owl, are the result of secondary changes by absorption, and not of the primitive constitution of the bones. These are solid in their commencement in all classes, and the vacuities are established by the removal of osseous matter previously formed, whilst increase proceeds by fresh bone being added to the exterior surface. The thinnest-walled and widest air-bone of the bird of flight was first solid, next a marrow-bone, and finally became the case of an air-cell. The solid bones of the Penguin, and the medullary bones of the Apteryx, exemplify arrested stages of that course of development through which the pneumatic wing-bone of the soaring Eagle had previously passed.

But these mechanical modifications do not exhaust all the changes through which the parts of a skeleton, ultimately becoming bone, have passed; they have been previously of a fibrous or of a cartilaginous tissue, or both. Entire skeletons, and parts of skeletons, of vertebrate animals exhibit arrests of these early stages of development; and this quite irrespective of the grade of



the entire animal in the zoological scale. The capsule of the eye-ball, for example, in man, is a fibrous membrane; in the Turtle, it is gristle; in the Tunny, bone. The skeletal framework of the Lancelet (*Branchiostoma*) does not pass beyond the fibrous stage of tissue-change. In the Sturgeon and Skate it stops at the gristly stage, and hence these fishes are called 'cartilaginous.' In most fishes, and all air-breathing vertebrates, it proceeds to the bony stage, with the subsequent modifications and developments above recited.

§ 13. *Classes of bone.*—Bony matter is variously disposed in the bodies of vertebrate animals. The Trunk-fish, fig. 16, *dn*, *dp*, *dh*, the Crocodile, and the Armadillo are instances of its accumulation upon or near the surface of the body; and hence the ball-proof character of the skin of the largest of these mailed examples. The most constant position of bone is around the central masses of the nervous, *ib. n*, and vascular, *ib. h*, *pl*, systems, with rays thence extending into the middle of the chief muscular masses, forming the bases of the limbs. Portions of bone are also developed to protect and otherwise subserve the organs of the senses, and in some species are found encasing mucus-ducts, and buried in the substance of certain viscera—as, e. g. the heart in the Bullock and some other large quadrupeds. Strong membranes, called 'aponeurotic,' and certain tendons, become bony in some animals; as, e. g. the 'tentorium' in the Cat, the temporal fascia in the Turtle, the 'leaders' of the leg-muscles in the Turkey, the nuchal ligament in the Mole, and certain tendons of the abdominal



Segment of neuro- and dermo-skeletons, *Ostracion*

muscles of the Kangaroo, which, so ossified, are called the 'marsupial-bones.' The primary classification of the parts of the osseous system is, therefore, according to their prevalent position, as in the cases above cited. The superficial or skin-bones constitute the 'dermo-skeleton';<sup>1</sup> the deep-seated bones, in relation to the nervous axis and locomotion, form the 'neuro-skeleton';<sup>2</sup> the bones connected with the sense-organs and viscera form the 'splanchno-skeleton';<sup>3</sup> those developed in tendons, ligaments, and aponeuroses, the 'sclero-skeleton.'<sup>4</sup>

<sup>1</sup> Gr. *derma*, skin, and *skeleton*.

<sup>2</sup> Gr. *neuron*, nerve, and *skeleton*.

<sup>3</sup> Gr. *splagchnon*, viscus, or inward part, and *skeleton*.

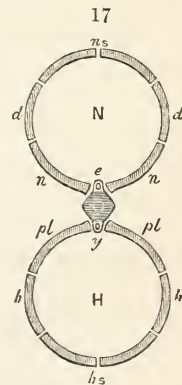
<sup>4</sup> Gr. *scleros*, hard, and *skeleton*.



In the arrangement of the parts of the dermo-, splachno-, and sclero-skeletons, no common pattern is recognisable. One can but discern a purpose gained by such bony plates, cases, or rods, in special relation to the habits and well-being of the creatures manifesting them; but the diversity in the number, size, shape, and relative position of dermal, tendinal, and visceral bones seems interminable. The neuro-skeleton, which is the main part of the osseous system, and might be termed the 'skeleton proper,' exemplifies not only the principle of design and adaptation, but that of unity of composition. Its parts are arranged in a series of segments following and articulating with each other in the direction of the axis of the body.

§ 14. *Type segment or vertebra.*—Each complete segment, called 'vertebra,' consists of a series of osseous pieces arranged according to a type or general plan, exemplified in fig. 17; in which they form a hoop or arch above, and another beneath, a central piece. The upper hoop, encircling a segment of the nervous axis, is called the neural<sup>1</sup> arch, N; the lower hoop, encircling a part of the vascular system, is called the hæmal<sup>2</sup> arch, H: their common centre is termed the 'centrum.'<sup>3</sup> The neural arch is formed by a pair of bones, called 'neurapophyses,'<sup>4</sup> *n, n*, and by a bone sometimes cleft or bifid, called the 'neural spine,' *ns*: it also sometimes includes a pair of bones, called 'diapophyses'<sup>5</sup> *d, d*. The hæmal arch is formed by a pair of bones, called 'pleurapophyses,'<sup>6</sup> *pl*; by a second pair, called 'hæmapophyses,'<sup>7</sup> *h*; and by a bone, sometimes bifid, called the 'hæmal spine,' *hs*. It also sometimes includes parts, or bones, called 'parapophyses.'<sup>8</sup> Bones, moreover, may be developed which diverge as rays from one or more of the above parts.

The parts of a vertebra which are developed from independent centres of ossification are called 'autogenous;' those that grow from previously ossified parts are called 'exogenous:' the autogenous parts of a vertebra are its 'elements,' the exogenous parts are its 'processes.' No part, however, is absolutely autogenous



<sup>1</sup> Gr. *neuron*, nerve.

<sup>2</sup> Gr. *haima*, blood.

<sup>3</sup> Gr. *kentron*, centre.

<sup>4</sup> Gr. for nerve, and *apophysis*, a projecting part.

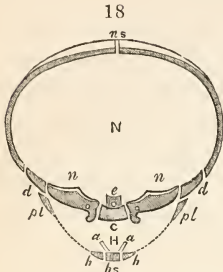
<sup>5</sup> Gr. *dia*, across, and *apophysis*.

<sup>6</sup> Gr. *pleuron*, rib, and *apophysis*.

<sup>7</sup> Gr. for blood, and *apophysis*.

<sup>8</sup> Gr. *para*, transverse, and *apophysis*.

throughout the vertebrate series; and some parts, usually exogenous, are autogenous in a few instances.



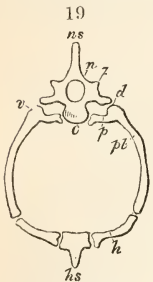
Cranial segment or vertebra

The vertebral elements are, the centrum *c*, the neurapophyses *n*; the neural spine *ns*, the pleurapophyses *pl*, the haemapophyses *h*, and the haemal spine *hs*. The exogenous parts are the diapophysis *d*, the parapophysis *p*, the zygapophysis *z*,<sup>1</sup> the anapophysis *a*,<sup>2</sup> the metapophysis *m*,<sup>3</sup> the hypapophysis, fig. 17, *y*,<sup>4</sup> and the epapophysis, fig. 17, *e*.<sup>5</sup> Of the autogenous parts, the neural spine is most commonly exogenous; of the exogenous parts, the parapophyses,

diapophyses, and hypapophyses, are sometimes autogenous.

Vertebrae are subject to many and great modifications—e. g. as to the number of the elements retained in their composition, as to the form and proportion of the elements, and even as to the relative position of the elements; but the latter modification is never carried to such a degree as to obscure the general pattern or type of the bony segment.

Sometimes, as in the example, fig. 18, of the third segment of the human skeleton, the neural arch, *N*, is much expanded, the haemal one, *H*, is contracted; and, in the expanded neural arch, the autogenous diapophyses, *d d*, are wedged between the neurapophyses, *n*, and the enormously expanded neural spine, *ns*. More commonly, as in the example from the thorax, fig. 19, the haemal arch, *hs*, is much expanded, the neural one *n*, contracted; and the parapophysis is represented sometimes by the exogenous growth from the centrum, commonly by that, *p*, from the rib *pl*. Sometimes, again, as is exemplified in the neck of the bird, fig. 20, and the tail of the Crocodile, both neural and haemal arches are alike contracted, the pleurapophyses, *pl*, being excluded from the latter, and standing out as continuations of the confluent diapophyses and parapophyses; and the haemal arch being formed, either by haemapophyses (Crocodile), fig. 7, or hypapophyses (bird), fig. 20, *hy*. Such vertebrae deviate but little from the ideal type, under its less developed condition, as in fig. 7. The segments are commonly simplified and made



Thoracic segment or vertebra

<sup>1</sup> Gr. *zugos*, junction, and *apophysis*.

<sup>2</sup> Gr. *ana*, backwards, and *apophysis*.

<sup>3</sup> Gr. *meta*, between, and *apophysis*.

<sup>4</sup> Gr. *hupo*, below, and *apophysis*.

<sup>5</sup> Gr. *epi*, above, and *apophysis*.

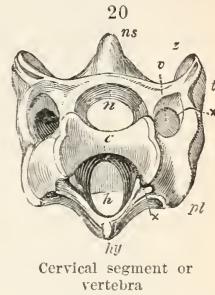
smaller as they approach the end of the vertebral column; one element or process after another is removed, until the vertebra is reduced to its centrum, as in the subjoined diagram, fig. 21, of the archetype vertebrate skeleton.

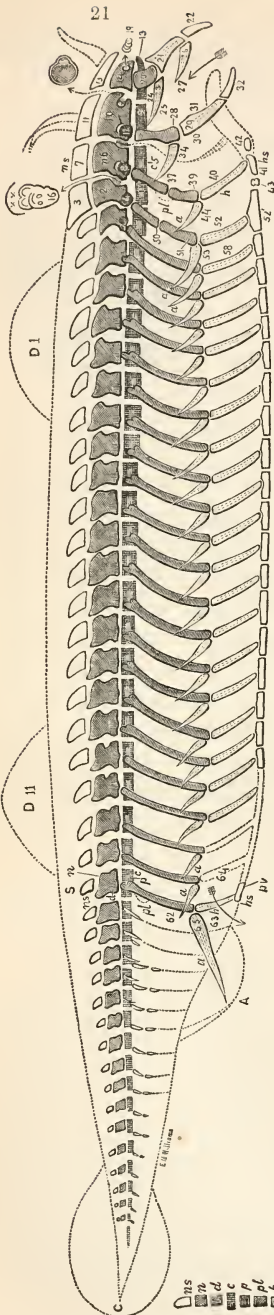
§ 15. *Archetype skeleton.*—In this scheme, which gives a side view of the series of segments or ‘vertebræ’ of which the skeleton is composed, the extreme ones are the seat of those modifications, which, according to their kind and degree, impress class-characters upon the type.

The four anterior neurapophyses, 14, 10, *n* 6, 2, give issue to the nerves, the terminal modifications of which constitute the organs of special sense. That of smell, 4, 19, is situated in advance of its proper (nasal) segment, which becomes variously modified to enclose and protect it. The organ of sight, lodged in a cavity or ‘orbit’ between its own (the frontal) and the nasal segment, is here drawn above that interspace. The nerve of taste perforates the neurapophysis of the third segment, 6, or passes by a notch between this and the frontal segment, to expand in the sense-organ, or ‘tongue,’ which is supported by the hæmal spine, 41, 42, of its own (parietal) segment. The fourth is the organ of hearing, 16, indicated above the interspace between the neurapophysis of its own (occipital) and that of the antecedent (parietal) vertebra, in which it is always lodged; the surrounding vertebral elements being modified to form the cavity for its reception, which is called ‘otocrane.’

The jaws are the modified hæmal arches of the first two segments. The mouth opens at the interspace between these hæmal arches; the position of the vent varies (in fishes), but always opens behind the pelvic arch, *s*, 62, 63, *p*, when this is ossified.


Outlines of the chief developements of the dermoskeleton, in different vertebrates, which are usually more or less ossified, are added to the neuroskeletal archetype; as, e. g. the median horn supported by the nasal spine, 15, in the rhinoceros; the pair of lateral horns developed from the frontal spine, 11, in most ruminants; the median folds, *D* 1, *D* 11, above the neural spines, one or more in number, constituting the ‘dorsal’ fin or fins in fishes and cetaceans, and the dorsal hump or humps in the buffaloes and camels; similar folds are sometimes developed at the end of the tail, forming a ‘caudal’ fin, *C*, and beneath the hæmal spines, constituting the ‘anal’ fin or fins, *A*, of fishes.








Ideal archetype skeleton


The different elements of the primary segments are distinguished by peculiar markings:—

The neurapophyses by diagonal lines, thus — 

The diapophyses by vertical lines— 

The parapophyses by horizontal lines— 

The *centrum* by decussating horizontal and vertical lines— 

The pleurapophyses by diagonal lines— 

The appendages by dots— : : : : :

The neural spines and hæmal spines are left blank.

In certain segments the elements are also specified by the initials of their names:—

- ns* is the neural spine.
- n* is the neurapophysis.
- pl* is the pleurapophysis.
- c* is the centrum.
- h* is the hæmapophysis, also indicated by the numbers 21, 29, 44, 52, 58, 63, 64.<sup>1</sup>
- hs* is the hæmal spine.
- a* is the appendage.

The centrum is the most constant vertebral element as to its existence, but not as to its ossification. There are some living fishes, and formerly there were many, now extinct, in which, whilst the peripheral elements of the vertebra become ossified, the central one remains unossified; and here a few words are requisite as to the development of vertebræ.

§ 16. *Development of vertebræ.*— The central basis of the neuroskeleton is laid down in the embryo of every vertebrate animal as a more or less

<sup>1</sup> See 'TABLE OF SYNONYMS, Special Homologies,' for the names of the bones indicated by numbers.

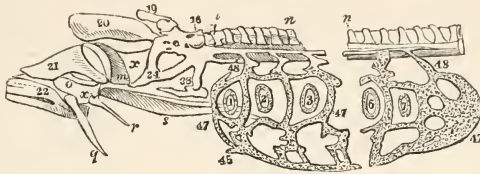






layer of the notochordal capsule has assumed the texture of tough hyaline cartilage; and not only are firm opake cartilaginous neurapophyses present, but also parapophyses, pleurapophyses,

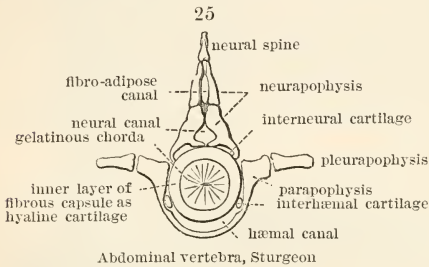
24



Fore part of skeleton, Lamprey (*Petromyzon*)

and neural spines. The part of the neurapophysis bounding the true neural canal is usually distinct from that bounding the fat-filled fissure above. The parapophyses are united by a continuous plate of cartilage forming an inverted arch beneath the

aorta, in the trunk, analogous to that formed by bone in the lower neck-vertebræ of birds, fig. 20.



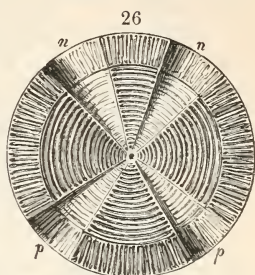
Abdominal vertebra, Sturgeon

In the *Chimara* slender subossified rings appear in the cartilaginous sheath of the notochord, which are more numerous than the neural arches.

These, where unconfluent with each other, are distinct also from the parapophyses, which in the tail bend down to form the hæmal arches. In the Mediterranean Grey Shark (*Notidanus cinereus*) the vertebral centres are still feebly and irrelatively marked out by numerous slender rings of hard cartilage in the notochordal capsule, the number of vertebræ being more definitely indicated by the neurapophyses and parapophyses; but these remain cartilaginous.

In the Lepidosiren the peripheral vertebral elements, fig. 41, *ns*, *p*, *hs*, are ossified, but the notochord, *ch*, with a thicker and condensed capsule, remains. In the Piked Dog-fish (*Acanthias*) the vertebral centres coincide in number with the neural arches, and are defined by a thin plate of bone, shaped like an hour-glass, and forming the conical cavity at each end of the centrum: the rest of which is cartilaginous external to the 'hour-glass,' and subgelatinous within its terminal cavities. In the Spotted Dog-fish (*Scyllium*) the two thin bony cones of each centrum are con-

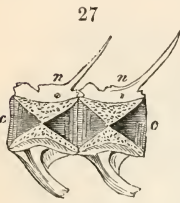
fluent at their apices, which are perforated, and the notochord, reduced to a beaded form, is continued through them: the exterior of the bony cones is occupied by a clear cartilage. In the Porbeagle Shark (*Lamna cornubica*) further ossification of the conical plate has reduced the central communication to a minute foramen. Osseous plates have also been developed in the exterior clear cartilage: these plates are triangular, parallel with the axis of the vertebra, their apices converging towards the centre: the interspaces are filled by cartilage. In the great Basking Shark (*Selache maxima*) fig. 26, the longitudinal bony laminae are more numerous and shorter than in *Lamna*, are peripheral in position, and extend about one-third of the way towards the centre of the interspace between the terminal cones, the rest being occupied by a series of concentric cylinders of bone, interrupted by four conical converging cavities, filled by cartilage; of these, two, *n, n*, are closed by the bases of the neurapophyses, and two, *p, p*, by those of the parapophyses. There is a transition from the cylindrical to the longitudinally lamellar structure, the exterior and largest of the cylinders sending out processes which join the internal margins of the converging lamellae. In the Monk-fish (*Squatina*) the osseous part of the centrum between the terminal cones is entirely in the form of concentric layers, few in number, and decreasing in breadth as they approach the centre. In the Cestracion there are no concentric cylinders, but only longitudinal lamellae, radiating from the centre to the circumference, and giving off short lateral plates as they diverge.



Vertical transverse section of centrum of *Selache maxima*

In the Topes (*Galeus*), the Blue Sharks (*Carcharias*), and in most sharks which possess the nictitating eyelid, may be seen the most advanced stage of ossification in the cartilaginous fishes: the entire centrum, save at the four cavities closed by the neur- and par-apophyses, is occupied by a coarse bone, more compact where it forms the smooth exterior surface and that of the terminal articular cavities. In osseous fishes (most *Teleostomi*) the neur- and par-apophysial cavities are obliterated by bone, and the neur- and par-apophyses are confluent, or suturally joined, with the centrum; but they retain a greater proportion, than in higher classes, of the primitive gelatinous basis, which fills up the deep cone or cup at each end of the centrum, fig. 27, *c c*. Only in the ganoid *Lepidosteus*, among fishes, does ossification so extend

as to obliterate the front cavity, and protrude into the hind cavity of the preceding vertebra, fig. 28; thus establishing a cup-and-ball articulation on the 'opisthocœlian' plan.

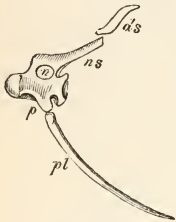


Scarus

The cup-and-ball structure prevails throughout the air-breathing, land-seeking, or terrestrial, *Hæmatocrya*. So interlocked, the vertebræ are better fitted to support the body in air, and transfer its weight to legs. Sometimes the cup is behind, as in the land-salamander, the Surinam toad (*Pipa*), and some extinct crocodiles, thence called *Streptospondylus*; but, as a general rule, existing reptiles have 'procœlian' vertebræ, or with the cup in front.

In many extinct reptiles (*Sauropterygia*, *Dinosauria*) ossification was so advanced as to leave no cavity at either end of the centrum; and these parts were coarticulated by flattened or almost flattened surfaces, as in mammals. Finally, both extinct and recent Reptilia afford instances in which the parts or elements of the vertebra have coalesced into one bone.

28



Lepidosteus

The progressive stages in the development of a vertebra, which have been illustrated by the chief of those at which it is arrested in the cold-blooded series, bear a close analogy to those by which it reaches the coalesced condition as a single bone in the warm-blooded classes. The principal secondary and adaptive modifications will next be pointed out which mark with special characters the collective trunk-vertebræ in *Hæmatocrya*.

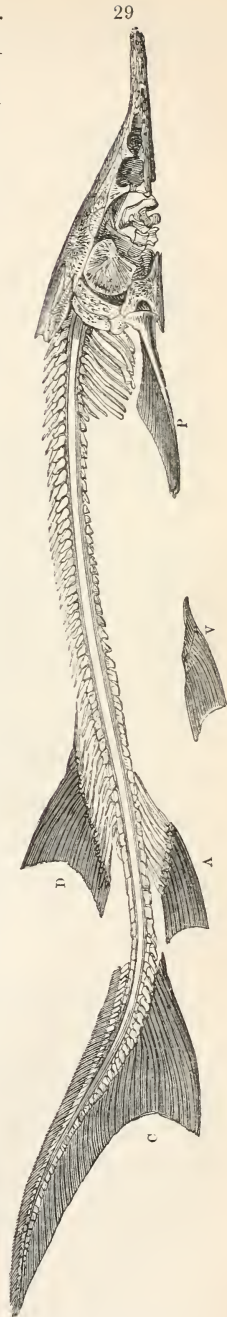
§ 17. *Vertebral column of Fishes.*—In the Sturgeon (*Acipenser*), fig. 29, the first five or six neural arches are confluent with each other and with the parapophyses, forming a continuous sheath of firm cartilage (fig. 62), inclosing the fore part of the notochord, ib. *a*, and myelon, and perforated for the exit of the nerves. The tapering end of the notochord is continued forward into the fused basal elements of the cranial vertebræ, ib. *g*, *g'*, and backward into the base and upper lobe of the tail-fin, fig. 29, *c*. The vertebræ are represented by their peripheral elements, and principally by the neural and hæmal arches. The pleurapophyses are limited to about twelve of the anterior trunk-vertebræ, are articulated by simple heads to parapophyses, fig. 62, *p*, and rapidly shorten in the two or three hinder pairs; the large ones sometimes consist of two or three pieces joined end on end, like the modified occipital rib, called 'scapula.' Vegetative repetition of perivertebral parts

not only manifests itself in the double pleur- and neur-apophyses on each side, but in small interneural and interhæmal cartilages, fig. 25. These peripheral cartilages are more feebly developed in *Spatularia*.

In the Chimæroids (*Holocephali*) the bases of the neur- and par-apophyses of about ten of the anterior trunk-vertebræ coalesce and form a continuous accessory cartilaginous covering of the fore part of the notochord; and the confluent neural spines here form a broad and high compressed plate. Between the neurapophyses are wedged accessory interneural cartilages.

In *Notidanus*, *Acanthias*, *Centrina*, and *Scymnus*, the interneurals, fig. 30, *i*, resemble the neurapophyses, *ib. n*, inverted, and are interposed, like wedges, between them, with the apices reaching the centrum. In *Scyllium*, *Mustelus*, *Sphyrna*, and *Carcharias*, the interneurals resemble the neurapophyses in size and shape, but occupy a position above the intervertebral joint. In *Galeus* the 'vegetative repetition' is further exemplified by four stellate points of ossification, one of which is intervertebral; and above these are rudiments of neural spines. The spinal nerve directly perforates the neurapophysis; or, when the two roots escape separately, one also perforates the interneural. The pleurapophyses are short and simple cartilages, either wedged into the interspaces of the parapophyses (*Notidanus*, *Carcharias*, *Scymnus*), or attached to the ends of the parapophyses (*Galeus*) of, say, the twenty-six anterior vertebræ. In *Acanthias* there may be forty pairs of such riblets, fig. 30, *pl*.

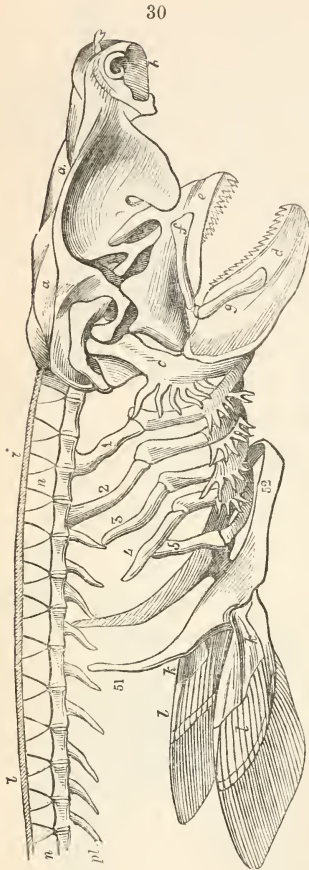
In the flat Plagiostomes (Skates, fig. 64, Rays, Torpedos) vegetative repetition manifests itself in the multiplication of vertebræ, and especially of the central elements; which, as indicated by their rudimentary ossification in *Chimæra*, are commonly more numerous



Skeleton of Sturgeon,  
(*Acipenser Sturio*). CXIV.



than the neural arches; nor are interneural and interhæmal pieces wanting. In *Raia clavata* these 'ossa intercalaria' constitute the



Forepart of skeleton, Piked Dog-fish  
(*Acanthias*). XLIII.

chief part of the neural arch, at the anterior part of the vertebral column; whilst the neurapophyses resume their ordinary share in its formation at the posterior part of the column. In *Zygæna* there are interspinal cartilages. In *Rhinobatus* a single spine answers to two vertebral bodies, and we may well suppose this multiplication of central pieces to have been carried still farther in the primæval fossil Ray (*Spinachorhinus*) from the lower Lias.

In the anchylosed cervical vertebræ of the Skate the short centrums are indicated by transverse bars along the middle of the under part. In the Monk-fish (*Squatina*) the body of the atlas is confluent with the basioccipital, but the neural arch remains distinct.

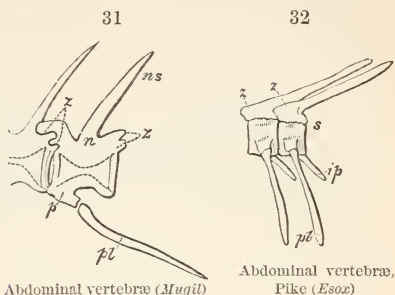
The parapophyses in most Rays pass forward, and then backward, the angle of one fitting, like an articular process, into the notch of the parapophysis in advance: they do not support pleurapophyses; they gradually bend down behind the pelvic arch, and complete the hæmal canal about six vertebræ beyond it; the hæmal spines become flattened in the tail of some Rays.

In osseous fishes a trunk-vertebra consists of a biconcave body, fig. 27, *c*, of a pair of neurapophyses, fig. 31, *n*, usually developing a spine, *ib. ns*, from their point of coalescence above the neural canal; and of a pair of parapophyses, *ib. p*; to which are added in the abdominal region in most fishes, and also in the caudal region of some, a pair of pleurapophyses, *pl*, figs. 31, 32. Ossification usually commences in the bases of the neur- and par-apophyses, and in the terminal cones of the centrum; it may proceed to blend the six points into one bone, and fill



up the hollow outside the cones, as indicated by the dotted tract in the section, fig. 27. But, in some, a communicating aperture is left between the terminal cones, as indicated by the dotted line in fig. 31. In many fishes the plates by which the bone attains the periphery of the centrum leave interspaces permanently occupied by cartilage, forming cavities in the dried or fossil bone, or giving a reticulate surface to the sides of the centrum. The bases of the neur- and par-apophyses sometimes expand so as to wholly inclose the centrum before coalescing therewith; as, for example, in the Tunny, where the line of demarcation may be seen at the border of the articular concavity.

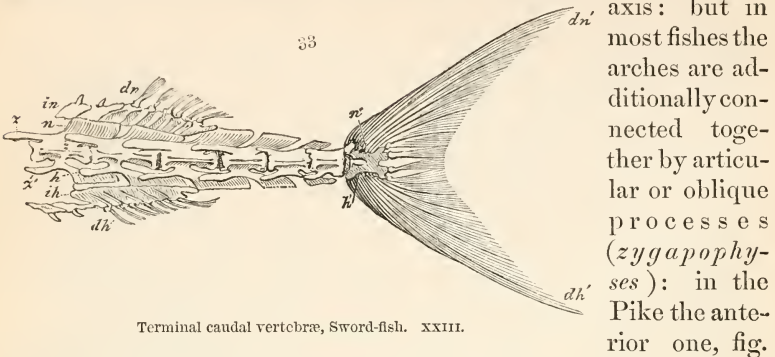
In the Pike the neurapophyses seldom, in the *Polypterus* and *Amia*, never, coalesce with the centrum: the letter *s* shows the neurapophysial suture in fig. 32. In the *Salmonidæ* the neurapophyses remain distinct from both the centrum and from each other, in the anterior vertebræ; where each develops a long and slender spine.<sup>1</sup> The parapophyses remain for some time distinct from the body of the vertebra, as well as from the ribs. In the anterior vertebræ of the Carp the neurapophyses remain distinct, as they do in the atlas of many other fishes, and a suture is observable between the parapophyses and centrum in embryo Cyprioids. In each vertebra the summits of the two neurapophyses usually become anchylosed together, and to their spine; but in the *Lepidosiren*, fig. 41, the spine retains its character as a distinct element, and is always attached by ligament to the top of the neurapophysis, as it is in the Sturgeon, fig. 25. In the anterior abdominal vertebræ of the Tetrodon, each of the neurapophyses, though they coalesce in the interspace of the two spines to form the roof of the neural canal, sends up its own broad truncated spine; and these are not much-developed oblique processes, but gradually approximate and blend together, to form the single normal spine at the fifth abdominal vertebra.<sup>2</sup> In the Barbel the neural arches also support two spines, but one is placed behind the other.



<sup>1</sup> XLIV. vol. i. p. 16, No. 46.

<sup>2</sup> *Ib.* vol. i. p. 81.

The interspaces of the neural arches are occupied by a fibrous aponeurosis—the remains of the primitive covering of the neural



Terminal caudal vertebrae, Sword-fish. XXIII.

axis: but in most fishes the arches are additionally connected together by articular or oblique processes (*zygapophyses*): in the Pike the anterior one, fig. 32, *z*, is present, which barely touches the neural arch in advance; in *Polypterus* it overlaps that part. In the Perch a posterior zygapophysis projects to receive the overlapping anterior one, the relative positions being the reverse of those in most air-breathing vertebrates. But, in some fishes, a second pair of zygapophyses are developed, which resemble the normal pair in higher vertebrates in relative co-adaptation, but seem to grow as exogenous processes, from the centrum itself, fig. 31, *z*. It is also peculiar to fishes to have articular processes developed from the parapophyses, as, e. g. in the abdominal region of the Rays, and from the caudal vertebrae of the Sword-fish, fig. 33, *z*. In the Tunny these processes are branched, and form a network about the hæmal canal. In *Loricaria* peculiar accessory processes are sent out from the neural arch of the seven anterior vertebrae which abut against the lateral shields of the dermo-skeleton. The parapophyses are short in some fishes (*Salmo*, *Clupea*, *Amia*), of moderate size in many, and longest in the Cod-tribe, fig. 34, *p*, where they expand in the abdominal region and sustain the air-bladder which adheres to their under surface. In one species of *Gadus*, the bladder sends processes into deeper cavities of the parapophyses, foreshowing, as it were, the pneumatic bones of birds. The parapophyses gradually bend lower down as they approach the tail, where, in many fishes, they unite to form the hæmal canal. In *Lepidosteus* the canal is formed by the pleurapophyses: whilst these, in *Amia*, *Thynnus*, and some others, are appended to the parapophysial inverted arches, like hæmal spines. In *Lepidosiren* the elements *p*, fig. 41, which in the abdomen represent either pleurapophyses or long parapophyses, bend down in the tail to form the hæmal arch. Not until we reach the Batrachia in the ascensive comparison do we find true hæma-

pophyses,' fig. 43, *h*, forming the hæmal arch in the tail, and coexisting there with par- and pleur-apophyses, *ib. p*, and *pl*.

The pleurapophyses of fishes correspond to what are termed in Comparative Anatomy, 'vertebral ribs,' and in Human Anatomy 'false or floating ribs:' for, with few exceptions, of which the Herring is one, fig. 37, their distal ends are not connected with any bones analogous to sternal ribs or sternum; i. e. the abdomen is unclosed below by the osseous parts completing the hæmal arch. The true homologues of sternal ribs and sternum retain the primitive aponeurotic texture, and may be well seen in the Bream, extending from the ends of the vertebral ribs. These elements, or pleurapophyses, figs. 31, 32, *pl*, are usually appended to the extremities of the parapophyses, *p*, the articulation frequently presenting a reciprocal notch in each. But, in some bony fishes, as *Platax*, the ribs articulate with the bodies of the vertebræ, in depressions behind the parapophyses; and in *Polypterus* beneath the parapophyses, as in the cartilaginous *Heptanchus*, *Carcharias*, and *Alopias*.

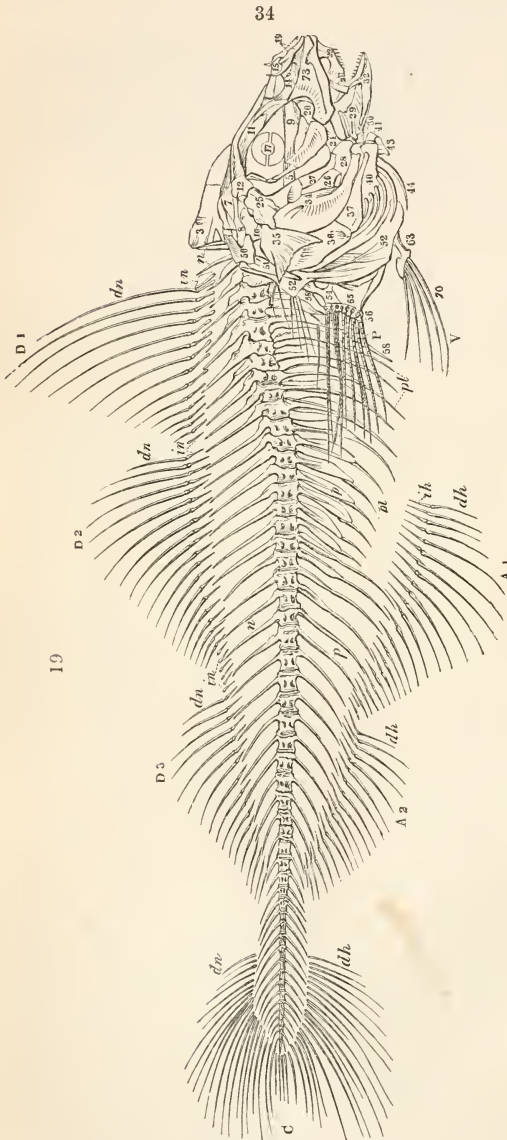
Between the floating ribs extends an aponeurosis, the remains or homologue of the primitive fibrous investment of the abdomen in the Lancelet and Lamprey. In the Salmon and Dory the ribs continue to be attached to some of the parapophyses after they are bent down, as in the *Amia* and Tunny, to form the hæmal canal and spine in the tail. The costal appendages of the first vertebra of the trunk are usually larger than the rest, and detached from the centrum; at least if we regard as such the styliform bones which project from the inner side of the scapulæ, and which have been described as coracoids (Cuvier), and sometimes as displaced iliac bones (Carus): by the muscles attached to these styliform bones the succeeding ribs are drawn forward and the abdomen expanded in the Cyprinoids. Pleurapophyses are entirely absent in the Sun-fish, Globe-fish (*Diodon*), the Tetrodon, the Pipe-fish (*Fistularia* and *Syngnathus*), the Lump-fish and the Angler. Of all osseous, or rather semi-osseous, fishes, *Lophius* presents the simplest vertebral column: the abdominal vertebræ are not only devoid of ribs, but have the feeblest rudiments of parapophyses. The bodies of the vertebræ interlock at their lower and lateral parts by a short angular process fitting into a notch in the next vertebra; the lower border of this notch represents the lower transverse process in other fishes: it is obsolete in the anterior abdominal vertebræ; begins to appear about the middle ones; shows its true character in the tenth; and elongates, bending downward, backward, and inward, to coalesce with its fellow, and form the hæmal arch at the twelfth or thirteenth vertebra, from which the hæmal spine is

developed. The interlocking process of the anterior vertebra disappears as the true inferior transverse process is increased. The side of the neural arch is perforated for the nerve, and that of the hæmal arch for the blood-vessel. The anterior abdominal vertebræ

of the *Tetrodon* are firmly clamped together by the parapophyses.

A vegetative sameness of form prevails in fishes throughout the vertebral column of the trunk, fig. 34, which is made up of only two kinds of vertebræ, characterised by the direction of the parapophyses, *p*: these in the abdominal region are lateral, usually stand out and support ribs: but in the caudal region bend down to form, either by direct coalescence or by the ribs that continue to be attached to them in a vertical position, the hæmal arch.

The atlas is usually distinguished by some modification of the anterior articular end of the centrum, by the persistent suture of the neural arch, or by the absence or detachment of its pleurapophyses. Peculiar processes are sometimes sent off from the

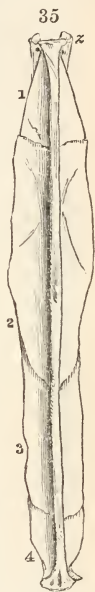


Skeleton of the Haddock (*Gadus aeglefinus*)



under part of the centrum, as, e. g. the two which articulate with the basioccipital in the *Arapaima gigas*. As the centrum of the atlas retains its normal relations to the other elements, and the ordinary mode of articulation with the body of the second vertebra, this shows no 'odontoid process' in fishes.

The number of vertebræ varies greatly in the different osseous fishes: the Plectognathi (*Diodon*, *Tetrodon*) have the fewest and largest: the apodal fishes (Eels, Gymnotes) have the most and smallest, in proportion to their size. It is not easy to determine the precise number, on account of the coalescence of some of the vertebræ, or at least of their central elements, in particular parts of the column. Instances of ankylosis of some of the anterior vertebræ, analogous to that noticed in the cartilaginous Sturgeons, Chimæra, Rhinobates, and some Sharks, occur also amongst the osseous fishes, as in many Siluroid and Cyprinoid species, in *Loricaria* and *Dactylopterus*. Fig. 35 represents the four singularly elongated ankylosed anterior vertebræ in the Tobacco-pipe fish (*Fistularia tabacaria*). A coalescence of several vertebræ is more constant at the opposite end of the column in osseous fishes, in order to form the base of the caudal fin, when this is symmetrical in form, as in fig. 33, and in most existing species of *Teleostomi*. But this modification is arrested at different stages in the piscine class. In *Cyclostomi* the gristly parts of the vertebræ continue distinct, with gradual reduction in size to the taper end of the long tail: in *Protopteri* the bony representatives of the caudal vertebræ behave in the same way: the notochord persists in both orders. In *Murænida*, where it is changed into centrums, these also gradually diminish in size, and remain distinct to the tail-end. The continuous vertical fold of skin bordering the compressed, long, and slender termination of the vertebral column is not specialised as a caudal fin.<sup>1</sup> In *Plagiostomi*, *Holocephali*, *Sturionida*, and many *Ganoidei*, the caudal fin, fig. 29, c, is formed chiefly by the hæmal spines and appendages, developed to support a lower 'lobe;' the vertebræ continue distinct to the end of the tail, which bending upward, seems to form an upper lobe longer than the lower: to this unsymmetrical tail-fin the term 'heterocercal' is applied. By decreased



Ankylosed anterior vertebræ, Pipe-Fish (*Fistularia*)

<sup>1</sup> This primitive embryonal basis of the piscine tail-fin is not to be confounded, because it is symmetrical as to shape, with the extreme stage of developmental modification constituting the true 'homocercal' type of most existing fishes.



number, with progressive confluence, of the caudal vertebræ, the 'upper lobe' becomes gradually reduced in length, until the symmetrical shape is attained. But this coexists in the Salmon, Perch, and many extinct Ganoids with an unsymmetrical bend of the coalesced caudal vertebræ into the base of the upper lobe. In true 'homocercals' the terminal bodies of the caudal vertebræ are not separately established in the primitive notochord, but are continuously ossified to form a common, compressed, vertically extended, and often bifurcated bony plate, fig. 33, *n'l'*, from which the neural and hæmal arches and their spines radiate: from these elements alone can the number of vertebræ of such caudal fin be estimated; normal development proceeding here in the peripheral elements, as throughout the vertebral column in *Lepidosiren*, whilst it is arrested in the central parts of the vertebræ. In the Sun-fish (*Orthogoriscus mola*) it would seem as if a row of rudimental vertebræ had been blended together at right angles to the rest of the column, in order to support the rays of the short, but very deep caudal fin, which terminates the suddenly truncated body of this oddly shaped fish.



Sacrum of a  
Turbot  
(*Rhombus*)

It is rare to find anchylosis save at the ends of the vertebral series in fishes: sometimes, however, in the *Pleuronectidæ*, a kind of sacrum is formed by such bony union of the bodies, *c*, and hæmal spines, *hs*, of the first two of the caudal series, as in fig. 36;<sup>1</sup> in which the broad and deep hæmal spines are concave forwards, and form a sort of pelvic posterior wall of the abdomen. In the Halibut (*Hippoglossus*) the parapophyses of the corresponding vertebræ with those of the last abdominal are similarly united, though the bodies remain distinct. In *Loricaria* both the upper and lower arches of a considerable part of the caudal region are blended together into an inflexible sacrum; but, as a general rule, there exists no such impediment to the lateral inflections of the tail in the present class.

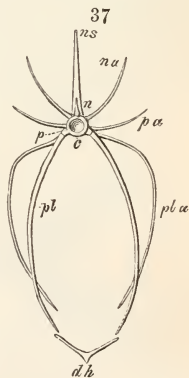
The number of trunk-vertebræ is a useful specific character in Ichthyology; and in counting them the coalesced caudals are usually reckoned as 'one.' In the Sun-fish (*Orthogoriscus*) I find but 8 abdominal and 8 caudal vertebræ by distinct bodies. In a Globe-fish (*Tetrodon*) there are 7 abdominal and 10 caudal vertebræ:

<sup>1</sup> Osteol. Collection, Mus. Coll. Chir. No. 188; XLIV. *z*, p. 50.

total, 17.<sup>1</sup> In the Conger there are 162 vertebræ; in the *Ophidium*, 204; in the *Gymnotus*, 236; and even this number is surpassed in some Plagiostomes.

Although the vertebræ maintain a considerable sameness of form in the same fish, they vary much in different species. The bodies are commonly subcylindrical; as deep, but not so broad, as they are long; more or less constricted in the middle, in some to such a degree as to present an hour-glass figure. In *Spinachorhinus* they are extremely short; in *Fistularia* extremely long; in *Tetrodon*<sup>2</sup> they are much compressed; in *Platycephalus* they are more depressed; in the tail of the Tunny the entire vertebra is cubical,<sup>3</sup> with the ends hollowed as usual, but the four other sides flat, the upper and lower ones being formed, in the connected series, by the neural and hæmal arches of the vertebra in advance, flattened down and, as it were, pressed into cavities on the upper and under surfaces, of the centrum of the next vertebra; so that the series is naturally locked together in the dried skeleton; and these arches cover not the neural and hæmal canals of their own, but of the succeeding, centrum.

The principle of vegetative repetition is manifested, in osseous fishes, by the numerous centres of ossification, from which shoot out bony rays affording additional strength to many of the intermuscular aponeuroses. In this system of bones may be ranked those spines which are attached to, or near to, the heads of the ribs, and extend upward, outward, and backward, between the dorsal and lateral masses of muscles, fig. 32, *i p*, fig. 21, *pl a*. These 'scleral' spines are termed, according to the vertebral element they may adhere to, 'epineurals,' 'epicentrals,' and 'epipleurals'; though each may shift its place, rising or falling gradually along the series of vertebræ. All three kinds are present in the herring, fig. 37, in which *n a* is the 'epineural,' *p a* the 'epicentral,' *pl a* the epipleural spines. The latter have been called 'upper ribs,' and in *Polypterus* are stronger than the ('under') ribs themselves. In *Esox* and *Thymallus* the epineural and epicentral spines are present: in *Cyprinus* the epineural and epipleural ones: in *Perca* and *Gadus* the middle series only is found, passing gradually from the



Abdominal vertebra,  
Herring (*Clupea*)

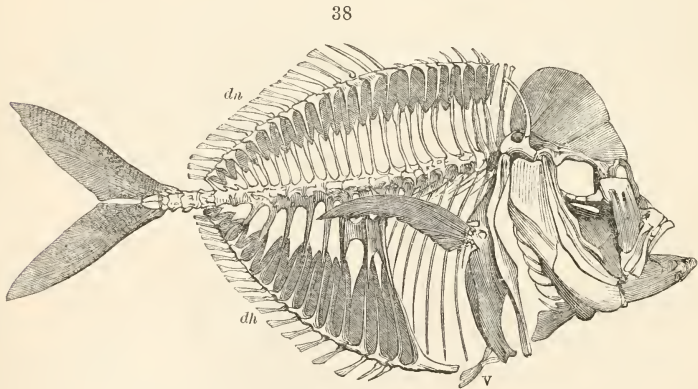
<sup>1</sup> Osteol. Collection, Mus. Coll. Chir. No. 357, p. 81.

<sup>2</sup> Ib. No. 357.

<sup>3</sup> Ib. No. 247. XLIV. *i*, p. 62.

par- to the pleur-apophyses: in *Salmo* only the upper series exists, developed from the second to the antepenultimate abdominal neurapophysis, in *S. Eriox*.<sup>1</sup> There are, however, gristly representatives of epipleurals. In *Glyphisodon* the epipleurals are anchylosed to the ribs, foreshowing their normal condition in the bird's thorax. According to the seat of their development they belong to the 'scleroskeleton:' by their attachments to bone they are 'vertebral appendages.'

The vertical folds of skin from the middle line, constituting the azygos fins, are the seat of ossifications in most fishes, developing a second row of spines, figs. 34, 38, *dn*, *dn*, above the neural, *n*, and a corresponding row, *dh*, *dh*, below the hæmal, *h*, spines. Some of these dermal bones, in certain fishes, project as hard enamelled weapons from the surface of the body. From the bases of the dermal spines, other spines (fig 34, *in*, *ih*) usually shoot downward into the intervals of the neural and hæmal spines. In deep-bodied fishes they are broad and strong, as e. g. in the Cock-fish, fig. 38; in the flat-fishes they are double, figs. 39 and 40; and these modifications are usually repeated above and below. Both interneural and interhæmal spines are commonly shaped like daggers, plunged in the flesh to the hilt, which is re-



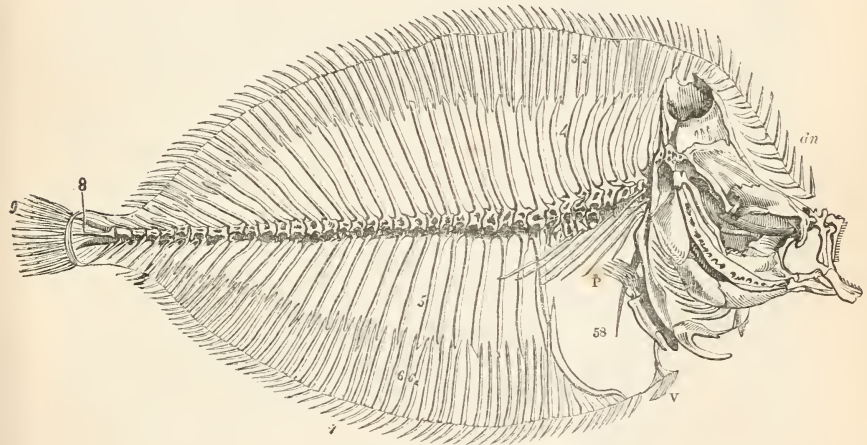
*Argyroscopus scelopinnis*

presented by the part to which the fin-ray (dermoneural or dermohæmal spine) is attached. In the plaice tribe (*Pleuronectidæ*) these superadded dermal ossifications are developed above the cranial as well as the corporal vertebræ (fig. 39, *dn*),

<sup>1</sup> XLIV. i, p. 16. CLIII.

and along the whole hæmal region of the trunk, from the head to the tail. This want of correspondence with the number of the true segments of the endoskeleton, and the seat of development of the inter- and dermo-neurals and inter- and dermo-hæmals, with some minor considerations, led me, in 1845, to substitute for the views and illustration of the typical vertebræ proposed by Geoffroy St.-Hilaire,<sup>1</sup> and then accepted and taught by Professor R. E. Grant<sup>2</sup> in this country and by others abroad, the interpretation of the supposed type-exemplar, which is contrasted with Geoffroy's in fig. 40. The names applied by the French philosophical anatomist to the several parts of the combined endo- and exo-skeletal segment

39



*Pleuronectes Solea.* XLIII.

are opposite the left hand of the reader: those applied to them in my 'Archetype of the Skeleton' are opposite the right hand.

The small exogenous process standing out from the sides of the centrum is a dismemberment of the parapophysis; in the first caudal vertebra it is given off from the base of the parapophysis, increases in length in the second caudal, rises upon the side of the centrum in the third, and becomes distinct from the parapophysis in the fourth: it diminishes and disappears in the ninth and tenth caudal vertebræ. In *Polypterus* and *Muraenoids* a transverse process coexists, from the same cause, with the parapophysis. This, in the twenty-fifth trunk-vertebra of *Muræna Helena*,<sup>3</sup> bifurcates, and in the following vertebræ the

<sup>1</sup> Mémoires du Mus. 4to, ix. 1822, p. 119, pl. v.

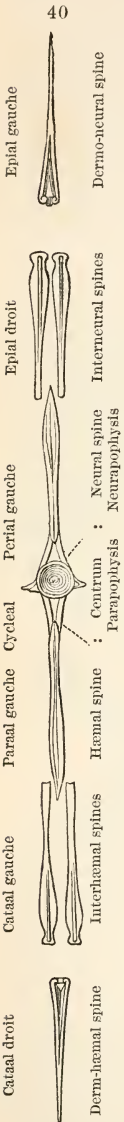
<sup>2</sup> Lectures on Comp. Anat. p. 58.      <sup>3</sup> XLIV. p. 14. No. 37.



fissure deepens and the fork elongates, until at the seventy-third the lower prong descends at a right angle to the upper one, and, meeting its fellow, forms the hæmal arch. There are no true hæmapophyses in the tail of fishes: the elements there composing the hæmal arch are parapophyses, pleura-pophyses, or both combined. In the abdomen only are hæmapophyses represented by the supporting bones of the ventral fins, fig. 41, 64. The slender ossicles along its under part in the Herring, fig. 37, *dh*, are dermal bones, which, like the scutes of serpents, are connected with the lower ends of the ribs, *pl*.

In the subclass *Protopteri* the notochord, fig. 41, *ch*, persists: the neural arches, *n*, *ns*, are ossified: the hæmal arches in the abdomen are represented by parial bones, *p*, attached to the notochordal sheath, and curving outward, like the long parapophyses in the Cod, and the short pleurapophyses in the *Amia* and Salamander, with which they, more probably, are homologous. These riblets bend down and meet at the beginning of the tail, *p*, to form the hæmal arch and support the hæmal spines, *hs*, along that region. As in fishes, the *Lepidosiren* also develops in the continuous vertical fin-fold the accessory ossicles marked *in*, *ih*, in the cut.

§ 18. *Vertebral column of Batrachia.*—Neither inter- nor dermo-neurals are present in any ganoccephalan or batrachian. In the former amphibious order the notochord persists, but with beginnings of the ossification of centrums: <sup>1</sup> in *Batrachia* it is converted into a series of separate centrums. These in the *Ichthyomorphs* are biconical, and deeply cupped at both ends, through the same arrest of ossification as in fishes: the development of the vertebra goes through the same piscine stage in the larvæ of the *Theriomorphs*, as indicated by the dotted lines *d*, fig. 42; in the mature quadrupedal stage of these *Batrachia*, ossification converts one terminal cup into a ball; which may be the front one, as in *Pipa*, or the hind one, as in *Rana*, and most frogs and toads. In the *Land-Salamander*, also, ossification goes to this stage, with the ball in front.



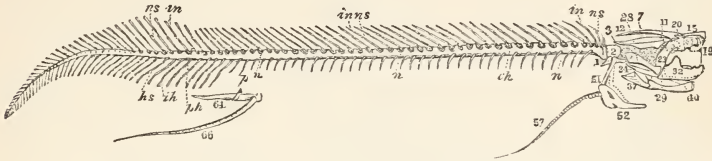
Endo- and exo-skeletal elements of a caudal vertebra of the *Plaice*, II.

<sup>1</sup> Lectures on Comp. Anat. p. 194, Fig. 84.



The Siren lacertina has between eighty and ninety trunk-vertebræ. They have many longitudinal ridges, the neural arch has coalesced with the centrum, the neural spine forms the highest ridge and bifurcates posteriorly to terminate upon the zygapophysis. A

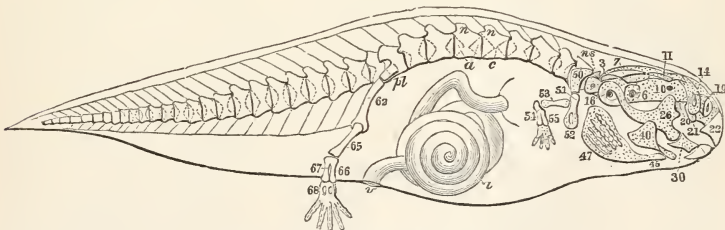
41



Skeleton of *Lepidosiren annectens*. XXXIII.

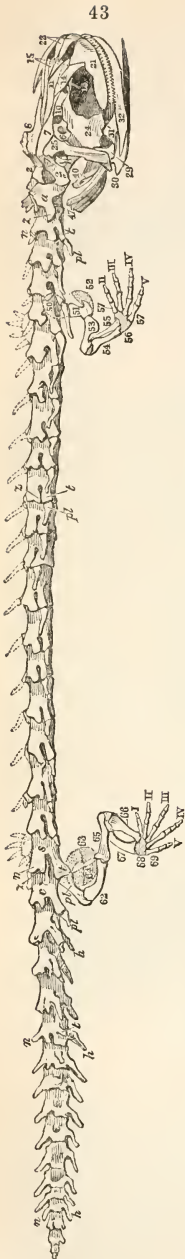
hypapophysial ridge forms, by defect of ossification on each side, the under part of the centrum. A parapophysial ridge extends from a short anterior parapophysis to the longer parapophysial part of the posterior transverse process. A diapophysial ridge extends above, and nearly parallel with the former, from the anterior zygapophysis to the diapophysial part of the posterior transverse process. Thence a third short ridge is continued to the posterior zygapophysis. The vacuities between these several ridges resemble those in the vertebræ of some fishes. The body of the atlas extends forward like a short odontoid process: short par- and di-apophysial plates are developed from each side of the atlas, which has also the posterior zygapophyses. In the second vertebra the par- and di-apophysial plates have united to form a compound

42



Skeleton of Tadpole of *Rana esculenta*

transverse process, which supports a short straight pleurapophysis. These elements are similarly developed from six or seven successive vertebræ. In the tail the vertebra is compressed and vertically extended by the bending down of the parapophysial plates to form two vertical walls, intercepting a hæmal canal. In the Proteus, which has about sixty trunk-vertebræ, the third to the ninth inclusive support short ribs, attached to the lower (parapophysial)



Skeleton of the Menopome  
*M. Alleghaniense*,  
or *Protonopsis*

half of the transverse process: they are wanting in the twenty-one following vertebræ, and reappear, well developed, in the thirty-first, where they form with cartilaginous hæmapophyses, a pelvic arch. In the Menopome, fig. 43, the second to the nineteenth vertebræ support short straight pleurapophyses, articulated to the ends of transverse processes formed by par- and diapophyses, which intercept by their terminal confluence an arterial canal. These processes, *t*, are enlarged in the twentieth vertebra, *s*, and a second rib-like piece, 62, the homotype of the second part of the scapula in fishes, is articulated to the short and thick rudimental rib, *pl*; the inferior or hæmal arch 63, 64, being cartilaginous. The segment thus completed by the hæmal arch, represents a so-called 'sacral' vertebra: the second division of its rib answers to the 'ilium,' 62, and the hæmal cartilage to the 'ischium,' or 'pubis.' Transverse processes *t*, progressively decreasing in length are developed from the six succeeding vertebræ. Bony pleurapophyses *pl*, are attached to the first of these, and cartilaginous rudiments of the same element to the three following. Hæmal arches are anchylosed to the under part of the centrum of the second to the twelfth caudal vertebra inclusive, and these become more compressed to the end of the tail, for the support of a vertical fin. The neural arches are broad, depressed, anchylosed to the centrum: they are complete to the fourteenth caudal vertebra. The body of the atlas presents an odontoid process between the two articular surfaces for the occipital condyles; it is deeply cupped behind, as are the succeeding vertebræ at both ends. This vertebra has neither di- nor pleurapophyses.

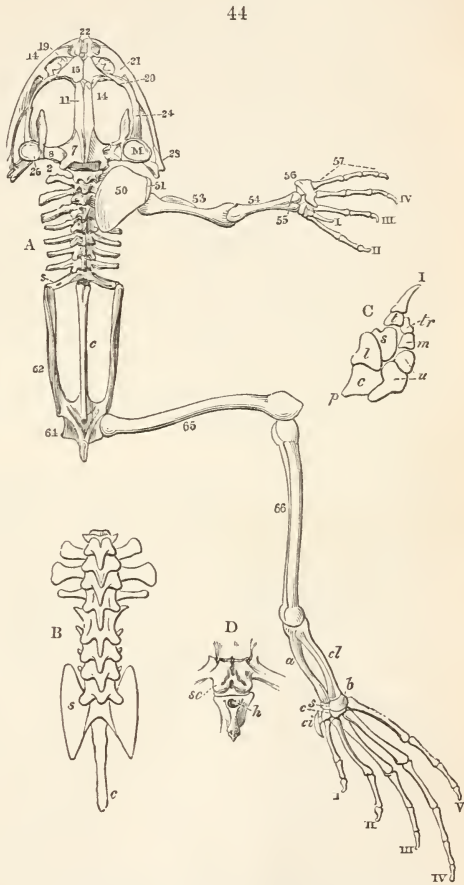
The skeleton of the Newt (*Triton*) resembles that of the Menopome in its general characters; the neural and hæmal spines are more produced in the long tail, supporting there the chief swimming organ of this aquatic batrachian. In one kind the ribs are more developed, occasioning the sub-

genus called *Pleurodeles*. In the land Salamander the backbone is strengthened by the ball-and-socket articulation of the trunk-vertebræ. Cuvier notices a curious inconstancy in the place of attachment of the pelvic arch, sometimes to the fifteenth, sometimes to the sixteenth, and in one instance suspended by the right pier to the sixteenth, by the left to the seventeenth, vertebra, in *Salamandra atra*.<sup>1</sup>

The ophiomorphous batrachia are remarkable for the multiplicity, the theriomorphous for the paucity, of distinct vertebræ in the trunk; these latter have the ball-and-socket articulation. The frog, fig. 44, A, has nine vertebræ and the coccygeal style *c*; but by coalescence of this with the sacrum, and of the atlas with the second vertebra, in the Surinam toad (*Pipa*), the number of distinct trunk-segments is in that species reduced to seven.

In *Rana boans* the atlas has no diapophyses; but they are present and of great length in the succeeding vertebræ

to the sacrum inclusive, where they are thick and support by their truncate ends two long rib-like bones, *ib.* A, 62, which expand at their distal ends, and unite there to two partially anchylosed bony plates, 64, which complete the hæmal arch of the ninth segment of the trunk. The superior development of this arch relates to the great size and strength of its appendages—



Skeleton of frog, A; vertebræ B and carpus C of toad.

<sup>1</sup> CLI. tom. v. pt. ii. p. 413.

the hinder extremities—in the tailless order, especially the frogs. In the seven vertebræ between the atlas and sacrum, two zygapophyses looking upward are developed from the fore part, and two looking downward from the back part of the neural arch; there is also a short spine.

In the Toad (*Bufo vulgaris*) the number of trunk-vertebræ, fig. 44, B, is the same as in the Frogs, but the diapophyses of the third and fourth vertebræ are relatively longer, those of the sacral vertebra, *s*, relatively shorter, broader, and expanded so as to overlap the ilia, which are shorter and more arched. In *Cystignathus pachypus* the sacral diapophyses are subcylindrical. In *Pipa* the diapophyses of the second and third vertebræ are of unusual length, and support semi-ossified, short, flattened pleurapophyses. The diapophyses of the four succeeding vertebræ are short and slender; those of the sacrum are more expanded than in the toad, and rest upon the anterior halves of the iliac bones. The coccygeal style shows, in most anourans, a simple anchylosed neural canal, and also a hæmal canal, as at *h*, D, fig. 44.

In the Ophiomorphs (*Ceciliæ*) the vertebræ, besides being very numerous, are biconcave.

§ 19. *Vertebral column of Ichthyopterygia*.—In an extinct order (*Ichthyopterygia*) of Dipnoal Reptiles, modified for marine life, but breathing air, the trunk-vertebræ were very numerous, very short, and biconcave; the centrums remained distinct from the neural and hæmal arches, and were ligamentously, not suturally, united thereto. In the *Ichthyosaurus communis*, fig. 105, there are about 140 vertebræ; in the anterior sixteen a short parapophysis is developed from the side of the centrum, and a diapophysis from the base of the neural arch; but this soon begins to project from the neurapophysial border of the centrum, and then from the side of the centrum below that border. It continues gradually to sink in position until, at about the fortieth vertebra, it blends with the parapophysis, which alone continues to represent a transverse process, as far as at about the eightieth vertebra,<sup>1</sup> where it disappears and the succeeding centrums become compressed, indicating the vertical position of the dermal tail-fin which they supported. The atlas and axis centrums become anchylosed by flat surfaces; but each supports its own neural arch. Between the lower part of the atlas and the occipital condyle is a wedge-shaped hypapophysis, representing the part called ‘body of the atlas’ in anthropotomy: a similar bone is

<sup>1</sup> A dislocation or fracture commonly occurred at this part between the death and final imbedding of the decomposing animal; CLXI.

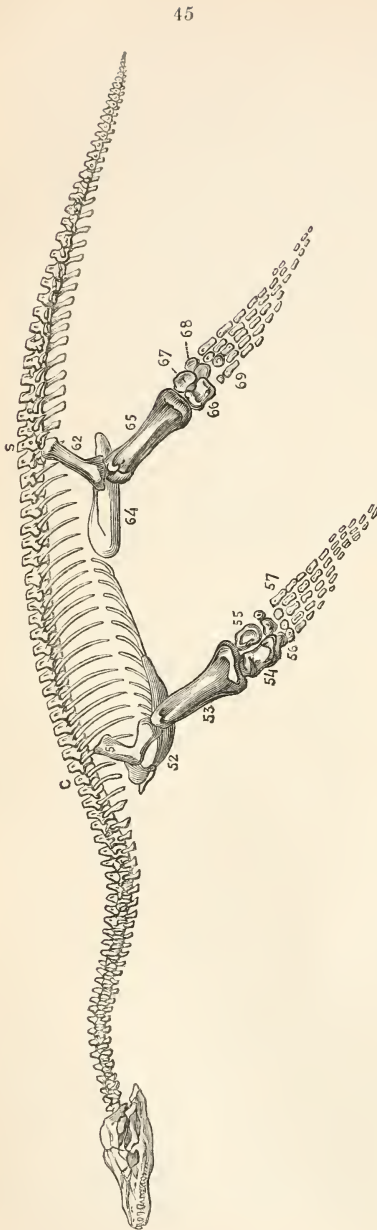


wedged between the atlas and axis, a third between this and the third vertebra; all tending to strengthen and stiffen the part of the vertebral column sustaining the skull, and adding to its power of displacing the water in the agile movements of this ancient predatory aquatic animal.<sup>1</sup> As in Fishes, also, the continuity of the broad occiput with the trunk was uninterrupted by any cervical constriction. The ribs commence at the second vertebra, but by a bifurcate head; and so continue, articulating with both par- and di-apophyses until the confluence of those processes, when they become single-headed. The ribs rapidly increase in length, which is greatest at the middle of the thoracic-abdominal cavity, and then gradually diminish to short and straight appendages, resembling detached transverse processes, in the tail. The longer ribs are grooved longitudinally; their lower ends are united to hæmapophyses, subdivided into two or three overlapping slender portions, the lowest articulating with a median transverse style, pointed at each end, representing the hæmal spine, and completing the hæmal arch in the abdomen. In the tail the hæmapophyses are simple, and attached by ligament, above to the centrum, and below to one another.

§ 20. *Vertebral column of Sauropterygia*.—In this extinct order of aquatic Reptiles the vertebral bodies had their terminal articular surfaces either flat or slightly concave, or with the middle of such cavity a little convex. In certain genera the neck-vertebræ were uncommonly numerous; this was remarkably so in the *Plesiosaurus*, fig. 45, in which those vertebræ consist of centrum, neural arch, and pleurapophyses. The latter are wanting in the first vertebra; but both this and the second have the hypapophyses. The cervical ribs are short, and expand at their free end. They articulate by a simple head to a shallow pit, which is rarely supported on a process, on the side of the centrum. The body of the atlas articulates with a large hypapophysis below, with the neurapophysis above, with the body of the axis behind, and with part of the occipital condyle in front; and all the articulations, save the last, may become obliterated by ankylosis. The hypapophysis forms the lower two-thirds, the neurapophysis contributes the upper and lateral parts, and the centrum forms the middle or bottom of the cup for the occipital condyle. The second hypapophysis becomes confluent with the inferior interspace between the bodies of the atlas and axis.<sup>2</sup> As the cervical vertebræ approach the dorsal, the costal pit gradually

<sup>1</sup> CLXV.<sup>2</sup> CLXVI.





Skeleton of Plesiosaurus. CLXIII.

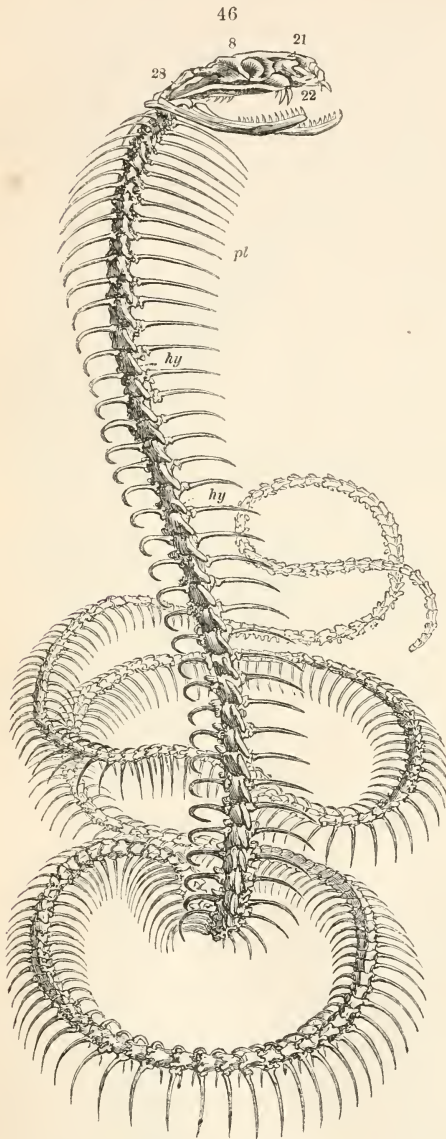
rises from the centrum to the neurapophysis. This takes place at the fortieth vertebra in the *Plesiosaurus homalospondylus* of the Whitby Lias, but, in the *Pl. dolichodeirus*, fig. 45, of the Dorsetshire Lias, at about the thirtieth, *c*. The dorsal region is arbitrarily commenced by the vertebra in which the costal surface begins to be supported on a diapophysis; this progressively increases in length in the second and third dorsal, continues as a transverse process to near the end of the trunk, and on the vertebra, *s*, between the iliac bones, 62, it subsides to the level of the neurapophysis. In the caudal vertebræ the costal surface gradually descends from the neurapophysis upon the side of the centrum; it is never divided by the longitudinal groove which, in most *Plesiosauri*, indents that surface in the cervical vertebræ. The neural arches are commonly unanchylosed with the centrum. The long and large spinous processes, in contact along the trunk and base of the neck, must have restricted the bending movements chiefly to the lateral directions. The pleurapophyses gain in length, and lose in terminal breadth, in the hinder cervicals; and become long and slender ribs in the dorsal region, curving outward and downward so as to encompass the upper two-

thirds of the thoracic-abdominal cavity. They decrease in length and curvature as they approach the tail, where they are reduced to short straight pieces, as in the neck, but are not terminally expanded; they cease to be developed near the end of the tail. The hæmapophyses in the abdominal region, are subdivided, and with the hæmal spine or median piece, form a kind of 'plastron' of transversely extended, slightly bent, median and lateral, overlapping bony bars, occupying the subabdominal space between the scapular, 52, and pelvic, 64, arches. In the tail the hæmapophyses are short and straight, and remain, as in the *Ichthyosaurus*, ununited both above and below. One Sauri-pterian genus, *Tanystropheus*, had the centrum, in certain vertebræ, so long and hollow as to simulate a limb-bone. In another genus, (*Pliosaurus*) they were as short, in the cervical region, as in the *Ichthyosaurus*. In a third genus (*Nothosaurus*) two vertebræ are recognised as sacral by their thick, straight, and convergent pleurapophyses, of which the first overlaps the second. In a fourth genus the wedge-shaped hypapophyses occur at the lower interspaces of the dorsal and lumbar vertebræ, whence its name, *Sphenosaurus*.

§ 21. *Vertebral column of Ophidia*.—Amongst existing Reptiles, the Serpents (*Ophidia*) surpass all others in the vast number of their vertebræ, which, with incomplete hæmal arches, compose the skeleton of the long, slender, limbless trunk, fig. 46.

In all these vertebræ the autogenous elements, except the pleurapophyses, fig. 46, *pl*, coalesce with one another, and the pleurapophyses become ankylosed to the diapophyses in the tail. There is no trace of suture between the neural arch, fig. 47, *ns*, *z*, and centrum, *c*. The outer substance of the vertebra is compact, with a smooth or polished surface. The vertebræ are 'procelian;' that is, they are articulated together by ball-and-socket joints, the socket being on the fore part of the centrum, fig. 47 A, where it forms a deep cup with its rim sharply defined; the cavity looking not directly forward, but a little downward, from the greater prominence of the upper border: the well-turned prominent ball terminates the back part of the centrum rather more obliquely, its aspect being backward and upward, fig. 47, *c*. The hypapophysis, *h*, is developed in different proportions from different vertebræ, but throughout the greater part of the trunk presents a considerable size in the cobra, 46, *hy*, and crotalus, figs. 47, 47 A, *h*: it is shorter in the python and boa. A vascular canal perforates the under surface of the centrum, and there are sometimes two or even three smaller foramina. In the

python a large, vertically oblong, but short diapophysis extends from the fore part of the side of the centrum obliquely backward:



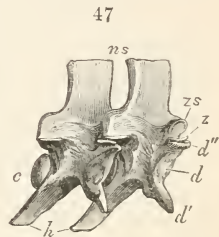
Skeleton of the cobra (*Naja tripudians*)

it is covered by the articular surface for the rib, is convex lengthwise and convex vertically at its upper half, but slightly concave at its lower half. In the rattlesnake the diapophysis develops a small, circumscribed, articular, tubercle, *ib. d*, for the 'vertebral rib' or pleurapophysis, *pl*; a parapophysis, *d'*, extends downward and forward below the level of the centrum; the anterior zygapophysis, *z*, is supported by a process, *ib. d''*, from the upper end of the diapophysis. The base of the neural arch swells outward from its confluence with the centrum, and develops from each angle a transversely-elongated zygapophysis; that from the anterior angle, *z*, looking upward, that from the posterior angle, *z'*, downward; both surfaces being flat, and almost horizontal, as in the Batrachians. The neural canal is narrow; the neural spine, *ns*, is of moderate height, about equal to its antero-posterior extent; it is compressed and truncate. A wedge-shaped process, 'zygosphene,' *zs*, is developed from the fore part of the

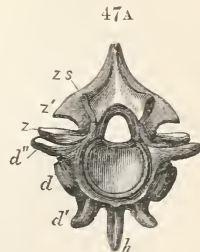
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base of the spine; the lower apex of the wedge being, as it were, cut off, and its sloping sides presenting two smooth, flat, articular surfaces. This wedge is received into a cavity, the 'zygantrum,' excavated in the posterior expansion of the neural arch, and having two smooth articular surfaces to which the zygosphenal surfaces are adapted. Thus the vertebræ of serpents articulate with each other by eight joints in addition to those of the cup and ball on the centrum; and interlock by parts reciprocally receiving and entering one another, like the joints called tenon-and-mortice in carpentry, fig. 47. In the caudal vertebræ, the hypapophysis is double, the transition being effected by its progressive bifurcation in the posterior abdominal vertebræ. The diapophyses become much longer in the caudal vertebræ, and support in the anterior ones short ribs which usually become anchylosed to their extremities.

The pleurapophyses or vertebral ribs have an oblong articular surface, concave above and almost flat below in the Python, with a tubercle developed from the upper part, and a rough surface excavated on the fore part of the expanded head for the insertion of the precostal ligament. They have a large medullary cavity, with dense but thin walls, and a fine cancellous structure at their articular ends. Their lower end supports a short cartilaginous hæmapophysis, which is attached to the broad and stiff abdominal scute. These scutes, alternately raised and depressed by muscles attached to the ribs and integument, aid in the gliding movements of serpents; and the ribs, like the legs in the centipede, subserve locomotion; but they have also accessory functions in relation to breathing and constriction. The anterior ribs in the cobra, fig. 46, *pl*, are unusually long, and are slightly bent; they can be folded back one upon another, and can be drawn forward, or erected, when they sustain a fold of integument, peculiarly coloured in some species — e.g., the spectacled cobra — and which has the effect of making this venomous snake more conspicuous at the moment when it is about to inflict its deadly bite. The ribs commence in the cobra, as in other serpents, at the third vertebra from the head.



Two vertebrae of the Rattlesnake  
(*Crotalus*)



Front view of a vertebra,  
Rattlesnake



The centrum of the first vertebra coalesces with that of the second, and its place is taken by an autogenous hypapophysis: this, in the python, is articulated by suture to the neurapophyses; it also presents a concave articular surface anteriorly for the lower part of the basioccipital tubercle, and a similar surface behind for the detached central part of the body of the atlas, or 'odontoid process of the axis.' The base of each neurapophysis has an antero-internal articular surface for the exoccipital tubercle, the middle one for the hypapophysis, and a postero-internal surface for the upper and lateral parts of the odontoid; they thus rest on both the separated parts of their proper centrum. The neurapophyses expand and arch over the neural canal, but meet without coalescing. There is no neural spine. Each neurapophysis develops from its upper and hinder border a short zygapophysis, and from its side a still shorter diapophysis. In the second vertebra, the odontoid presents a convex tubercle anteriorly, which fills up the articular cavity in the atlas for the occipital tubercle; below this is the surface for the hypapophysial part of the atlas, and above and behind it are the two surfaces for the atlantal neurapophyses. The whole posterior surface of the odontoid is ankylosed to the proper centrum of the axis, and in part to its hypapophysis. The neural arch of the axis develops a short ribless diapophysis from each side of its base; a thick sub-bifid zygapophysis from each side of the posterior margin; and a moderately long bent-back spine from its upper part. The centrum terminates in a ball behind, and below this sends downward and backward a long hypapophysis.

At the opposite extreme of the elongated body, two or three much simplified vertebræ are usually found blended together; they support the horny rings forming the warning rattle of the *Crotalus*. There is no sternum in true Ophidia.

The skeleton of the Python (*P. tigris*)<sup>1</sup> has 291 vertebræ, of which the 3rd to the 251st support movable ribs. The 74 anterior vertebræ develop hypapophyses. The skeleton of the *Boa constrictor*<sup>2</sup> has 305 vertebræ, a hypapophysis being developed from the 60 anterior ones. In the skeleton of a Rattle-snake (*Crotalus horridus*)<sup>3</sup> with 194 vertebræ, 168 support movable ribs, and all these develop hypapophyses, fig. 47, *h*, as long as the neural spines, *ns*. In the *Naja*, fig. 46, as many vertebræ have the lower process, but of less length. In the Rough Tree-snake (*Deirodon scaber*)<sup>4</sup> with 256 vertebræ, a hypapophysis projects

<sup>1</sup> XLIV. vol. i. No. 602, p. 123.

<sup>2</sup> *Ib.*, No. 630, p. 132.

<sup>3</sup> *Ib.*, No. 640, p. 135.

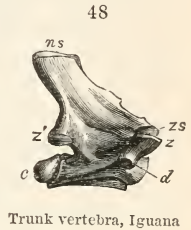
<sup>4</sup> *Ib.*, No. 638, p. 134.

from the 32 anterior ones, directed backward in the first ten, and forward in the last ten, where they are unusually long, and tipped with a coat of hard dentine; these perforate the œsophagus, and serve as teeth. The jaws are merely roughened by rudiments of teeth. The relation of this singular condition of the cervical hypapophyses and the modification of the dental system to the food of the *Deirodon* will be explained in the chapter on teeth.

§ 22. *Vertebral column of Lacertia.*—The anguine or snake-like reptiles, with fixed upper-jaws and a scapular arch, pass gradually, by other forms with rudiments of limbs (*Pseudopus*), to the slender-bodied long-tailed lacertians. The distinction is effected through the establishment of a costal arch in the trunk, completed by the addition of a hæmal spine (sternum) and hæmapophyses (sternal ribs) to the pleurapophyses or vertebral ribs, which are alone ossified in *Ophidia*.

The vertebræ of the trunk have the same procœlian character, i. e., with the cup anterior and the ball behind, fig. 48; the latter, *c*, being usually less prominent, more oblique, and more transversely oval than in serpents. The vertebræ also are commonly larger, and always fewer in number than in the typical *Ophidia*.

Those of the Iguanas retain the superadded articular surfaces of the zygosphene, fig. 48, *zs*, and zygantrum; but I have not met with these superadded processes in other lacertians. In the



49

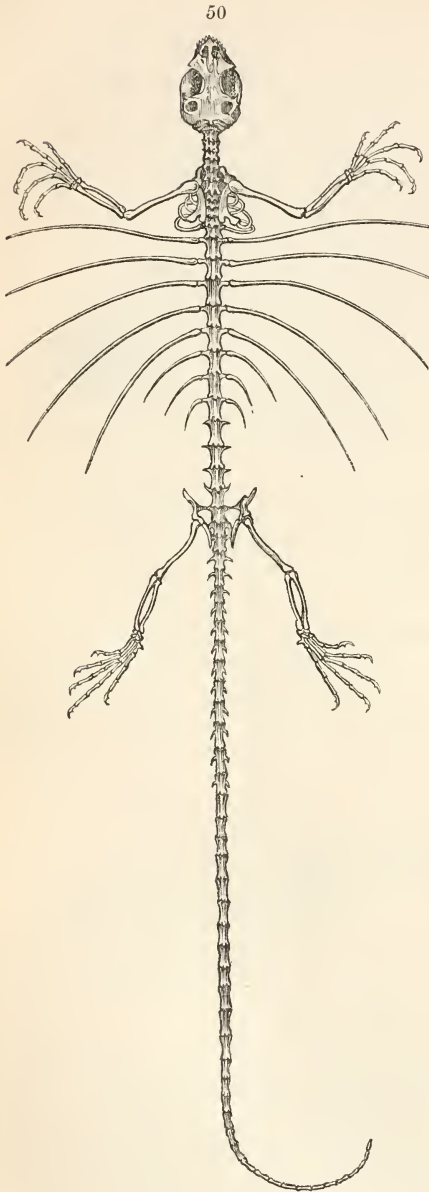


Fore part of skeleton of a Lizard

Geckos the vertebræ are, exceptionally, biconcave.<sup>1</sup> The ribs do not begin to be developed so near the head as in *Ophidia*. Not only the atlas and dentata, but the third vertebra, fig. 49, and sometimes, as in the Monitor (*Varanus*), the four following vertebræ, are devoid of pleurapophyses: when these first appear they

<sup>1</sup> See those of the subgenus *Rhynchocephalus*, XLIV. vol. i. No. 662, p. 142.

are short, as at *a*; but elongate in succeeding vertebræ, *b* to *e*;



Skeleton of *Draco volans*

and usually at the eighth, or ninth, fig. 49, *f*, 6, (*Lacerta*), from the head or tenth (*Varanus*), they are joined through the medium of ossified hæmapophyses to the sternum. Two (*Varanus*), three (*Chameleo*, *Iguana*), or four (*Cyclodus*), following vertebræ are similarly completed; and then the hæmapophyses are either united below without intervening sternum (*Chameleo*), or two or three of them are joined by a common cartilage to the cartilaginous end of the sternum. The hæmapophyses afterwards project freely, and are reduced to short appendages to the pleurapophyses. These also shorten, and sometimes suddenly, as, e. g., after the eighteenth vertebra in the Monitors (*Varanus*), in which they end at the twenty-eighth vertebra, as they began, viz., in the form of short straight appendages to the diapophyses.

The *Draco volans*, fig. 50, is so called on account of the wing-like expansions from the sides of its body, supported, like the hood of the cobra, by slender elongated ribs. In this little lizard there are twenty

vertebræ supporting movable ribs, which commence apparently

at the fifth. Those of the eighth vertebra first join the sternum, as do those of the ninth and tenth; the pleurapophyses of the eleventh vertebra suddenly acquire extreme length; those of the four following vertebræ are also long and slender; they extend outward and backward, and support the parachute formed by the broad lateral fold of the abdominal integuments. The pleurapophyses of the succeeding vertebræ rapidly shorten. The sacrum consists of two vertebræ. There are about fifty caudal vertebræ.

The semi-ossified sternum in the Iguana has a median groove and fissure, and readily separates into two lateral moieties. The long stem of the episternum covers the outer part of the groove, where it represents the 'keel' of the sternum in birds.

The two sacral vertebræ retain, in most Lacertians, the cup-and-ball joints; and in the Scincks, where they coalesce, the second presents a ball to the first caudal. Hæmapophyses are wanting in the first caudal, commence in the second, but are displaced to the interval between this and the third; they are confluent at their distal ends, and there produced into a spine: these 'chevron bones' are continued usually along two-thirds of the tail. In most of the caudal vertebræ the anterior third of the centrum is marked off by a line, just anterior to the diapophyses, where the tail snaps off, when a lizard escapes, leaving the part that has been seized in the hands of the baffled pursuer. The ossification of the centrum from two points, and their incomplete ankylosis has prospective relation to the liability of lizards to be caught by their long tail, and lends itself to their escape. The epiphysial line does not extend through the thin and brittle neural arch, which readily snaps when the two parts of the centrum to which it is ankylosed are separated. Lizards reproduce the lost tail; but the vertebral axis is never ossified in the new-formed part.

In the slow-worm (*Anguis*) there are 111 vertebræ, 61 of which, beginning at the fourth, support free ribs. The transverse processes of the tail are formed by short ankylosed pleurapophyses, which are bifurcate in the second and third caudals. The hypapophyses are, also, ankylosed to the centrum; but, instead of remaining distinct, as in true *Ophidia*, they unite at their lower ends and complete the hæmal arch. The vertebræ of the *Amphisbæna* have no neural spine.

The lacertian modifications of the atlas and axis<sup>1</sup> agree in the

<sup>1</sup> XLIV. vol. i. pp. 139—149.

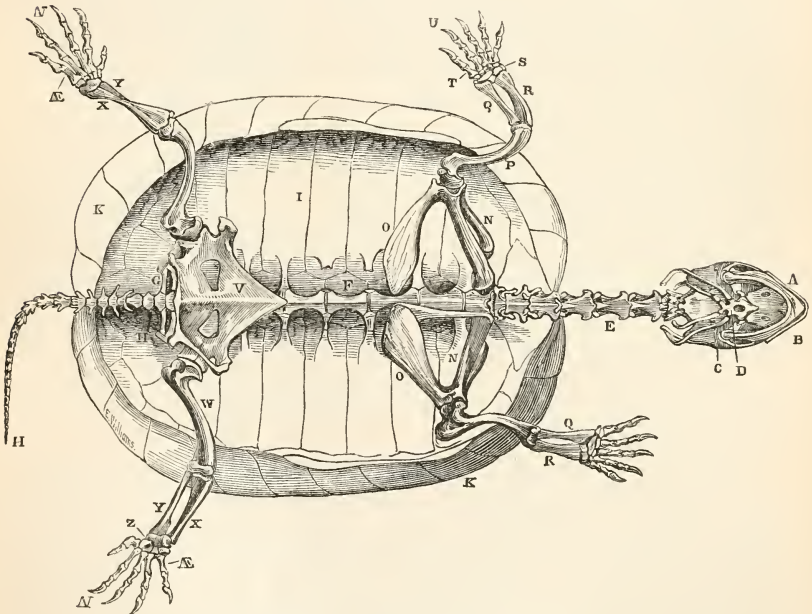


main with those in the *Python*. In *Istiurus* the cervical hypophyses are compressed, distinct, and articulated to the interspace between their own vertebra and the one in advance. The caudal vertebræ are remarkable for the great length of their neural spines.

In the Chameleon the ribs commence at the fourth vertebra, and those of the sixth are articulated by semiofified cartilages to the sternum, as are the three following pairs; in the next eight or ten pairs the long and slender cartilages meet and unite together at their extremities. There are two lumbar and three sacral vertebræ; the tail is long and prehensile. In the *Iguana tuberculata* twenty-one vertebræ, commencing with the fifth, support free ribs, and those of the ninth first join the sternum.

§ 23. *Vertebral column of Chelonia*.—This column is most ex-

51



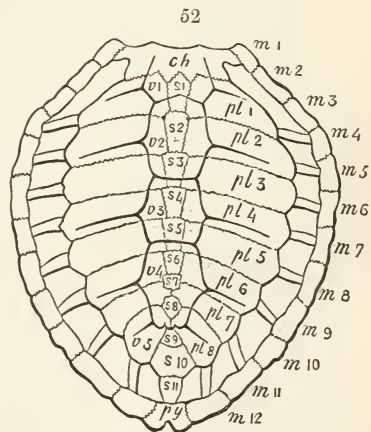
Skeleton of *Emys Europæa*. XXXVIII.

traordinary in those *Reptilia* to which, in the manifold modifications of the organic framework, has been given a portable abode, in compensation for inferior powers of locomotion and the want of defensive weapons.

The expanded thoracic-abdominal case, fig. 51, κ, κ, into which, in most Chelonians, the head, the tail, and the four extremities can be withdrawn, and in some of the species be there shut up by movable doors closely fitting both the anterior and posterior apertures—as, e. g., in the box-tortoises (*Cinosternon*, *Cistudo*)—has been the subject of many investigations; and not the least interesting result has been the discovery that this seemingly special and anomalous superaddition to the ordinary vertebrate structure is due, in a great degree to the modification of form and size, and, in a less degree, to a change of relative position, of ordinary elements of the vertebrate skeleton.

The natural dwelling-chamber of the *Chelonia* consists chiefly, and in the marine species (*Chelone*) and soft-turtles (*Trionyx*) solely, of the floor and the roof: side-walls of variable extent are added in the fresh-water species (*Emys*) and land-tortoises (*Testudo*). The whole consists chiefly of osseous ‘plates’ with superincumbent horny ‘scutes,’ except in *Trionyx* and *Sphargis*, in which these latter are wanting.

The roof, or ‘carapace,’ fig. 52, consists of a ‘median’ series of symmetrical plates, *ch*, *s* 1 to *s* 11, and of two ‘lateral’ series forming a pair, *pl* 1 to *pl* 8, the whole being surrounded by a circle of ‘marginal’ pieces, *m* 1 to *py*, completed anteriorly by *ch*, the first of the median series. Of the median series eight, *s* 1 to *s* 8, are attached to the spines of eight subjacent vertebræ: the lateral or parial plates, *pl* 1 to *pl* 8, are attached to, and more or less blended with, the ribs of the same vertebræ; and the ends of these ribs usually articulate by gomphosis with a corresponding number of the marginal pieces, of which, however, there may be from twenty-four to twenty-six, including the two median and symmetrical ones, *ch* and *py*. That these marginal pieces are the least essential parts of the carapace is shown, not only by their inconstant number, but by their partial or total absence in some of the soft-turtles (*Gymnopus*, *Sphargis*).



Carapace of the Loggerhead Turtle (*Chelone caouanna*)

The median pieces, *s* 1 to *s* 11, are called the 'neural' plates; the lateral pieces, *pl* 1 to *pl* 8, the 'costal' plates; the term 'marginal' is restricted to those peripheral pieces which form pairs, *m* 1 to *m* 12; the anterior symmetrical piece, *ch*, constant in all *Chelonia*, is called the 'nuchal' plate; the posterior symmetrical piece, *py*, which is wanting in all the *Trionycidæ*, is the 'pygal' plate. The neural arch, connate with the first neural plate, *s* 1, is supported partly by the centrum of the vertebra to which the first pair of free ribs is articulated, and which, therefore, is reckoned as the first dorsal vertebra: these ribs are small and slender, attached at both their extremities, the outer end abutting against the under part of the first pair of costal plates, which they help to sustain. The second to the ninth dorsal vertebræ inclusive, being those which are more immediately connected with the neural and costal plates, are the 'vertebræ of the carapace:' their characters, though not less artificial than those which distinguish the 'dorsal' or 'lumbar' vertebræ of other reptiles, are much more marked and constant. The eighth vertebra of the carapace is succeeded by one, which in some species (e. g. *Chelone caouanna*) supports a pair of short ribs, in others (*Trionyx*) none, and which is therefore reckoned a 'lumbar' vertebra; this is followed by two other vertebræ, with short and thickened ribs, abutting against the iliac bones and representing the 'sacrum,' fig. 51, G: as these three vertebræ are not immediately united with the ninth, tenth, and eleventh 'neural plates,' they have less claim than the first dorsal vertebra to be regarded as entering into the composition of the carapace.

The 'plastron,' fig. 53, or floor of the thoracic-abdominal chamber, consists, in all recent *Chelonia*, of nine pieces. The median and symmetrical piece, *s*, is the 'entosternal;' the four pairs, counted from before backward, are respectively, the 'episternals' (*es*), 'hyosternals' (*hs*), 'hyposternals' (*ps*), and 'xiphisternals' (*xs*).

In all the Chelonians, save the coriaceous (*Sphargis*) and soft turtles (*Trionycidæ*), the outer surface of the carapace is impressed by the horny scutes, commonly called 'tortoise-shell;' and these epidermal productions have received definite names in Zoological Treatises, their modifications being found of great use in characterising species. In fig. 52, *v* 1 is placed on the first 'vertebral scute' close to its union with the first and second 'costal scutes;' and *v* 2 to *v* 5 indicate the succeeding vertebral scutes, the outer angles of which are similarly wedged between the adjoining pairs of 'costal scutes:' beyond the costal scutes are a series of 'mar-

ginal scutes,' supported by the marginal plates, and crossing their sutures.

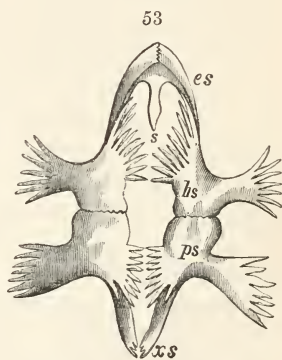
In the *Trionycidæ* the exterior surface of the carapace and plastron is remarkable for its rough vermicular or punctate sculpturing.

The median bony pieces of the carapace, fig. 52, *ch*, *s* 1 to *s* 11, have been regarded as lateral expansions of the summits of the neural spines; the medio-lateral pieces, *ib*. *pl* 1 to *pl* 8, as similar developements of the ribs; and the marginal pieces *ib*. *m* 1 to *m* 13, as the homologues of the sternal ribs. But the development of the carapace shows that ossification begins independently in a fibro-cartilaginous matrix of the corium in the first, *ch*, and some

of the last, *s* 9 to *s* 11, median plates, and extends from the summits of the neural spines into only eight of the intervening plates, *s* 1 to *s* 8: ossification also extends into the contiguous lateral plates, *pl* 1 to *pl* 8, in some *Chelonia*, not from the corresponding part of the subjacent ribs, but from points alternately nearer and farther from their heads,<sup>1</sup> showing that such extension of ossification into the corium is not a development of the tubercle of the rib, as has been supposed. Ossification commences independently in the corium

for all the marginal plates, *m* 1 to *py*; these never coalesce with the bones uniting the sternum with the vertebral ribs, are often more numerous, sometimes less numerous, than those ribs, and in a few species are wanting. Whence it is to be inferred that the expanded bones of the carapace, which are supported and impressed by the thick epidermal scutes called 'tortoise-shell,' are dermal ossifications, homologous with those which support the nuchal and dorsal epidermal scutes in the crocodile. Along the under surface of the costal plate the slender or proper portion of the rib may be traced, of its ordinary breadth to near the head, which liberates itself from the costal plate, as at 1, fig. 51, to articulate to the interspace of the two contiguous vertebræ, to the posterior of which such rib properly belongs.

In the 'plastron,' fig. 53, the entosternal, *s*, answers to the sternum in the crocodile: the parial pieces are 'hæmapophyses' or



Plastron of *Chelone caouanna*

<sup>1</sup> CLXII. p. 163, pl. xiii. fig. 4.



sternal ribs, connate in a more or less complete degree with dermal bony plates. There were five pairs in the extinct *Pleurosternon*.

In the marine Chelonians the dermal ossifications, fig. 52, *pl* 1 to 8, do not cover the whole of the intercostal spaces; the slender ribs project beyond them. In the fresh-water and land kinds they extend to the marginal plates and complete the bony roof, as in fig. 51. There is a similar difference in the degree of ossification of the 'plastron' between the genus *Chelone* and the genera *Emys* and *Testudo*.

In the *Chelonia* the true centrum of the atlas does not coalesce, as an 'odontoid' process, with that of the axis, and usually supports its own neural arch: the hypapophysis is proportionally reduced.<sup>1</sup> All the eight cervical vertebræ, fig. 51, E, are free, movable, and ribless: the fourth of these vertebræ has a much elongated centrum, which is convex at both ends: the eighth is short and broad, with the anterior surface of the body divided into two transversely elongated convexities, and the posterior part of the body forming a single convex surface divided into two lateral facets; the under part of the centrum is carinate; the neural arch, which is ankylosed to this centrum, is short, broad, obtuse, and overarched by the broad expanded nuchal plate. The first dorsal vertebra is also short and broad, with two short and thick pleurapophyses, articulated by one end to the expanded anterior part of the centrum, and united by suture at the other end to the succeeding pair of ribs. The head of each rib of the second pair is supported upon a strong trihedral neck, and articulated to the interspace of the first and second dorsal vertebræ: it is connate, at the part corresponding to the tubercle, with the first broad costal plate, which articulates by suture to the lateral margin of the first neural plate, and to portions of the nuchal and third neural plates: the connate rib, which is almost lost in the substance of the costal plate, is continued with it to the anterior and outer part of the carapace, where it resumes its subcylindrical form, and articulates with the second and third marginal pieces of the carapace. The neural arch of the second dorsal vertebra is shifted forwards to the interspace between its own centrum and that of the first dorsal vertebra. A similar disposition of the neural arch and of the ribs prevails in the third to the ninth dorsal vertebræ inclusive. The bony floor of the great abdominal box, or 'plastron,' is formed by the hæmapophyses and sternum connate with dermal osseous plates, forming, as in the turtle, nine pieces,

<sup>1</sup> CLXVII p. 435, pl. xiii.

but they are more ossified, and the hyo- and hypo-sternals unite suturally with the fourth, fifth, and sixth marginal plates, forming the side-walls of the bony chamber cut through in fig. 51. The junction between the hyo- and hypo-sternals admits of some yielding movement. The iliac bones abut against the pleurapophyses of the tenth, eleventh, and twelfth vertebræ, counting from the first dorsal vertebra. These three vertebræ form the sacrum: their pleurapophyses are unanchylosed, converge, and unite at their distal extremities to form the articular surface for the ilium. Beyond these the caudal vertebræ, *ib. H*, thirty-five in number in *Testudo elephantopus*, are free, with short, straight, and thick pleurapophyses, articulated to the sides of the anterior expanded portions of the centrums. They diminish to mere tubercles in the tenth caudal vertebra, and disappear in the remainder. The neural arches of the caudal vertebræ are flat above, and without spines.

§ 24. *Vertebral column of Crocodilia.*—In this order free pleurapophyses are developed from all the cervical vertebræ; that of the atlas, fig. 54, *a*, is attached to the hypapophysis; the neurapophyses rest, in part upon this element, in part upon the proper centrum, which coalesces with that of the axis: the neural spine of the atlas remains distinct, like that of the occiput, and is broad and flat. The centrum of the axis is flat in front, and convex behind: the neural arch, as in the succeeding vertebra, is completed by the connate spine. The pleurapophysis, *ib. b*, has a bifurcate head. With the exception of the two sacral vertebræ, which are flat at one end and concave at the other, and of the first caudal vertebra, which is convex at both ends, the bodies of all the vertebræ beyond the axis are concave in front and convex behind. The procœlian centrum of the third cervical is shorter but broader than the second; a parapophysis is developed from the side of the centrum, and a diapophysis from the base of the neural arch; the pleurapophysis is shorter, its fixed extremity is bifid, articulating to the two above-named processes; its free extremity expands, and its anterior angle is directed forward to abut against the inner surface of the extremity of the rib of both the axis and atlas, whilst its posterior prolongation overlaps the rib of the fourth vertebra. The same general characters and imbricated coadaptation of the ribs, not given in the diagram, 54, characterize the succeeding cervical vertebræ to the seventh inclusive, fig. 57, *p*, the hypapophysis progressively though slightly increasing in size. In the eighth cervical the rib, *h*, becomes elongated and slender; the anterior angle is almost or quite suppressed, and the posterior one more developed and produced

more downward, so as to form the body of the rib, which terminates, however, in a free point. In the ninth cervical, the rib, *i*, is increased in length, but is still what would be termed a 'false' or 'floating rib' in anthropotomy.

In the succeeding vertebra the pleurapophysis, fig. 54, *h*, articulates with a hæmapophysis, and the hæmal arch is completed by a hæmal spine; by which completion of the typical segment we distinguish the commencement of the series of dorsal vertebræ. With regard to the so-called 'perforation of the transverse process' this equally exists in the present vertebra, as in the cervicals; on the other hand, the cervical vertebræ equally show surfaces for the articulation of ribs. The typical characters of the segment, due to the completion of both neural and hæmal arches, are continued in some species of *Crocodylia* to the sixteenth, in some (*Crocodylus acutus*) to the eighteenth vertebra. In the *Crocodylus acutus* and the *Alligator lucius* the hæmapophysis of the eighth dorsal rib (seventeenth segment from the head) joins that of the antecedent vertebra. The pleurapophyses project freely outward, and become 'floating ribs' in the eighteenth, fig. 55, *b*, nineteenth, *ib. c*, and twentieth, *ib. d*, vertebræ, in which they become rapidly shorter, and in the last appear as mere appendages to the end of the long and broad diapophyses: but the hæmapophyses by no means disappear after the solution of their union with their pleurapophyses; they are essentially

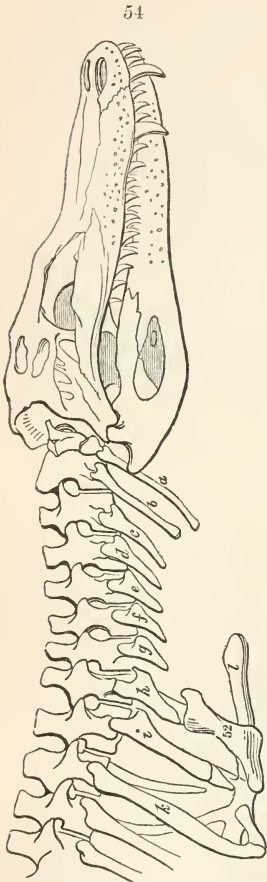


Diagram of anterior vertebræ,  
Crocodile. cc.

independent elements of the segment, and are accordingly continued, in pairs, fig. 55, 3, 4, 5, 6, 7, and 56, along the ventral surface of the abdomen of the *Crocodylia*, as far as their modified homotypes the pubic bones, *ib. 8*. They are more or less ossified, and are generally divided into two or three pieces. A short cartilaginous piece, an unossified part of the pleurapophysis, intervenes

between it and the hæmapophysis. A small cartilaginous appendage is attached to some of the ribs.

The lumbar vertebræ are those in which the diapophyses cease to support moveable pleurapophyses, although they are elongated by the coalesced rudiments of such, *ib. e, f, g, h*, which are distinct in the young Crocodile. The length and persistent individuality of more or fewer of these rudimental ribs determines the number of the dorsal and lumbar vertebræ respectively, and exemplifies the purely artificial character of the distinction. The number of vertebræ between the skull and the sacrum is twenty-four. In the skeleton of a Gavial, I have seen thirteen dorsal and two lumbar; in that of a *Crocodilus cataphractus* twelve dorsal and three lumbar; in those of a *Crocodilus acutus* and *Alligator lucius*, eleven dorsal and four lumbar, *fig. 57*, which is the most common number. Cuvier assigns five lumbar vertebræ to *Croc.*

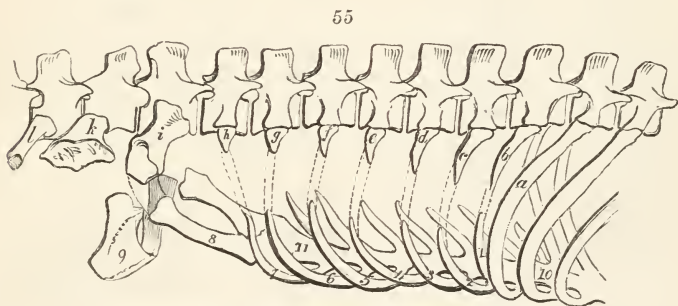


Diagram of posterior trunk-vertebræ, Crocodile. cc.

*biporcatus*. But these varieties in the development or coalescence of the stunted pleurapophysis are of no essential moment. The coalescence of the rib with the diapophysis obliterates of course the character of the 'costal articular surface,' which we have seen to be common to both dorsal and cervical vertebræ. The lumbar zygapophyses have their articular surfaces almost horizontal, and the diapophyses, if not longer, have their antero-posterior extent somewhat increased; they are much depressed, or flattened horizontally.

The sacral vertebræ, *fig. 57, s*, are very distinctly marked by the flatness of the coadapted ends of their centrums; there are never more than two such vertebræ in the *Crocodylia*, recent or extinct: in the first the anterior surface of the centrum is concave, in the second the posterior surface; the zygapophyses are not obliterated in either of these sacral vertebræ, so that the aspects of



their articular surface — upward in the anterior pair, downward in the posterior pair — determines at once the corresponding extremity of a detached sacral vertebra. The thick and strong transverse processes form another characteristic of these vertebræ ;

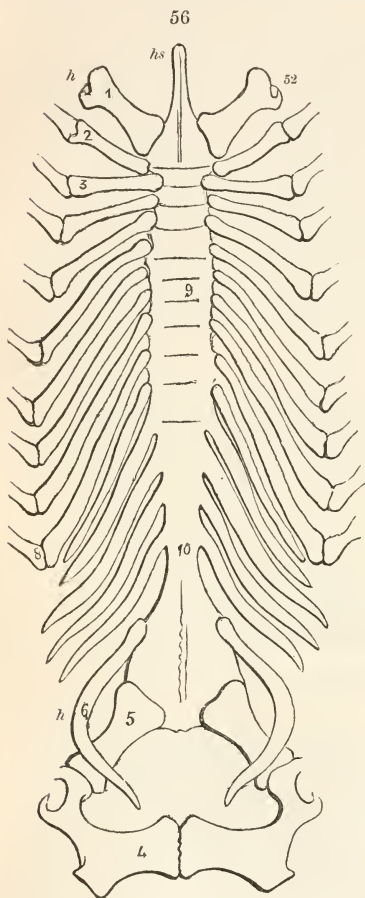


Diagram of the hæmal arches of the trunk, viewed from above. Crocodile. cc.

for a long period the suture near their base remains to show how large a proportion is formed by the pleurapophysis. This element, fig. 55, *i*, articulates more with the centrum than with the diapophysis developed from the neural arch; it terminates by a rough, truncate, expanded extremity, which almost or quite joins that of the similarly but more expanded rib, *ib. h*, of the other sacral vertebra. Against these extremities is applied a supplementary costal piece, serially homologous with the fibrous tract indicated by the dotted lines between *h* and 7, *g* and 6, fig. 55; but ossified, expanded, and interposing itself between the pleurapophyses and hæmapophyses of both sacral vertebræ, not of one only. This intermediate pleurapophysial part is called the 'ilium' fig. 57, 62: it is short, thick, very broad, and subtriangular, the lower truncated apex forming with the connected extremity of the hæmapophysis an articular cavity for the diverging appendage, called the 'hind leg.'

The hæmapophysis of the anterior sacral vertebra is called 'pubis,' fig. 55, 8, fig. 56, 5; it is moderately long and slender, but expanded and flattened at its lower extremity, which is directed forward toward that of its fellow, and joined to it through the intermedium of a broad, cartilaginous, hæmal spine, *ib. 10* and 11, completing the hæmal canal. The hæmapophysis of the second sacral, fig. 55, 9, fig. 56, 4, is broader, subdepressed, and subtriangular, expanding

as it approaches its fellow to complete the second pelvic hæmal arch. The size of these elements of the hæmal arch, and their distinctive shapes, have obtained for them, in anthropotomy, special names: their diverging appendage being developed into a potent locomotive member. The crocodile yields a clear view of the serial homologies of the hæmal elements along the trunk. In fig. 56, they are sketched as seen from the dorsal aspect. The hæmapophyses extend from *h* 1, 2, 3, to *h* 6, 5, 4: the hæmal spines, mostly confluent, are co-extensive from *hs* to 10, where they expand as a cartilage between 6 and 5. The pair of hæmapophyses, *h* 1, are called 'coracoids,' and bear the special number 52: the pair, 5, are the 'pubic bones'; the pair, 4, the 'ischia.' The hæmal spine, *hs*, is called 'episternum,' the succeeding more or less confluent spines, 9, form the 'sternum': in Man their abdominal continuation, not quitting the fibrous tissue-state, is called 'linea alba'; it becomes cartilage in the *Crocodylia*, ib. 10, and partly bony in old specimens. The abdominal hæmapophyses, represented by the 'intersectiones tendineæ musculi recti abdominis' of anthropotomy, are commonly ossified, each from two centres, in old *Crocodylia*.

The pleurapophysis is reduced to a transverse process in the first caudal vertebra, fig. 55, *l*; which, besides being biconvex, has no articular surface for the hæmapophyses: these elements reappear in the succeeding segments, detached, as in the lumbar series, from their pleurapophyses, but articulated to the centrum directly, fig. 7, with a backward displacement, to the interspace between their own and the succeeding vertebra, fig. 57, *h*. After the fourteenth caudal vertebra the transverse processes disappear, the centrum becomes compressed, and the neural and hæmal spines give adequate vertical extent to the long and strong natatory tail, to near its pointed termination.

The characters of the trunk-vertebræ of existing *Crocodylia*, especially their proœlian type, are those which their predecessors presented throughout all the tertiary series of deposits,<sup>1</sup> and by some species from cretaceous beds.<sup>2</sup> But in all the secondary series below the chalk, the *Crocodylia* present flattened or sub-concave vertebral surfaces; or, if the cup-and-ball structure be present, it shows reverse positions to the proœlian type, e. g. in the anterior trunk-vertebræ of the genus of oolitic Crocodylian, thence termed '*Streptospondylus*.' A similar 'opisthocœlian' modification is presented by the cervical and anterior dorsal vertebræ of the more gigantic *Cetiosaurus*; and, in a minor degree,

<sup>1</sup> CLXIII., part iii. p. 117, pls. 1 D, 3, 3 A.

<sup>2</sup> *Crocodylus basifissus*, CLXIV. p. 380.



huge terrestrial Dinosaurs, and other extinct groups with the same costal structure. The existing *Reptilia* are but a remnant of a once extensive and varied class of cold-blooded vertebrates, which, since the mesozoic epoch has been on the wane.<sup>1</sup>

§ 26. *Development of the skull.*— In reviewing the modifications of this part of the vertebral column in the *Hæmatocrya*, we retrace our steps to the lowest water-breathing forms, and recommence with the Dermopterous subclass.

Passing from the trunk to the head, we find in the Lancelet (*Branchiostoma*), fig. 23, that the cranium is not indicated by difference of size or structure of the rudimental vertebral column, but consists of the gradually contracting anterior termination of the neural canal, which retains its primitive fibro-membranous wall, *n, ob*, without any superaddition of parts, and is supported by the tapering end of the notochord, *ib. ch.* This part extends farther forward than the cranial end of the neural canal, indicating the non-developement of the prosencephalon and corresponding part of the cranial cavity. In fact, there is no ganglionic cerebral expansion whatever in this vermiform fish: the epencephalon or medulla oblongata is indicated by the origin of the trigeminal nerve, *ib. ob*, in advance of which the mesencephalic segment sends off the short optic nerve to the dark ocellus, *op*, and there terminates, somewhat obtusely, beneath what Dr. KÖLLIKER<sup>2</sup> has described as a ciliated olfactory capsule, *ib. ol.* The cranium of the Lancelet, therefore, may be said to be composed of the notochord and its membranous capsule, without the superaddition of cartilaginous or osseous coverings. But, as an appendage to the skull, may be described the jointed, cartilaginous, hæmal arch, *ib. h*, which extends from below the cranial end of the chorda dorsalis, downward and backward on each side of the orifice of the pharynx; this represents the labial arch of higher Myxinoids, and supports several pairs of the jointed slender oral filaments. It is the sole chondrified part of the skeleton in the *Branchiostoma*.

The cartilaginous tissue is superinduced upon the fibrous brain-sac in osseous fishes, in the following manner. The notochord advances as far as the pituitary sac, or ‘hypophysis cerebri,’ where it terminates in a point; cartilage is developed on each side, forming a thick ‘occipito-sphenoidal’<sup>3</sup> mass, which extends outward, and forms the earball or acoustic capsule. The cartilage rises a little way upon the lateral walls of the cranium, and is there insensibly lost in the primitive cranial membrane. At the

<sup>1</sup> CLXXX. p. 320.

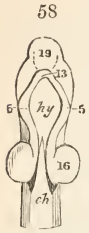
<sup>2</sup> XXXII. p. 32.

<sup>3</sup> *Plaque nuchale*, Vogt; *Knöcherner basis cranii*, Müller, XXI.



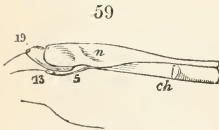
end of the notochord the basal cartilages, developed in continuations of its capsule, diverge, surround the pituitary vesicle, and meet in front of it, forming the 'sphenoidal arches,'<sup>1</sup> which join, or expand into the 'vomarine plate.'<sup>2</sup>

The immature Lamprey, called Sand-lance (*Ammocetes*), retains a like condition of the skull, fig. 58, to the second or third year. The occipital cartilages extend from the sides of the pointed end of the notochord, *ib. ch*, and expand into the acoustic capsules, *ib. 16*: the sphenoidal arches, *ib. 5*, encompass the pituitary or hypophysial space, *hy*, now closed by a membrano-cartilaginous plate, and unite anteriorly to form a small vomarine plate, *ib. 13*, in front of which is the single undivided nasal capsule, *ib. 19*. The now expanded cerebral end of the neural canal, fig. 59, *n*, is still defended by fibrous membrane only; but is divided from the vomarine plate, *ib. 13*, by a backward extension of the nasal sac, *ib. 19*, to the pituitary vesicle.



Base of skull,  
*Ammocete*,  
Müller

In the Myxine the acoustic capsules are approximated at the base of the skull; the sphenoidal arches are longer, and unite with the palatine plate and arches, from which are sent off the labial cartilaginous processes supporting the buccal tentacles homologous with those in the Lancelet. In the long hypophysial interspace of the sphenoidal arches a more or less firm cartilaginous plate is developed, from which a slender median process is continued forward to the vomarine or palatine plate, which supports the nasal capsule; another process extends backward to the occipital cartilage. Other processes are also sent off from the sides, which form a complex system of peculiarly Myxinoid cartilages.<sup>3</sup>



Side view of skull, *Ammocete*,  
Müller

In the mature Lamprey (*Petromyzon*), fig. 60, the occipital cartilage is continued backward, in the form of two slender processes, *c*, upon the under part of the notochord, *ch*, into the cervical region. The hypophysial space, *hy*, in front of the occipital cartilage, remains permanently open, but has been converted into the posterior aperture of the naso-palatine canal. The sphenoidal arches, *5*, are very short, approximated towards the middle line; and the vomarine cartilage, *13*, is brought back closer to the sphenoidal arches. Two cartilaginous arches, *24*,

<sup>1</sup> *Anses latérales*, Vogt; *Flügel-forsätze basis cranii*, Müller.

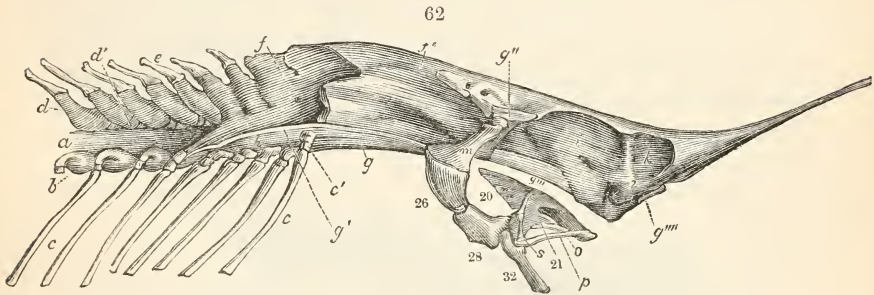
<sup>2</sup> *Plaque faciale*, Vogt; *Gaumenplatte*, Müller.

<sup>3</sup> XXI.



proceeds in a special direction, to stamp the species with its own distinctive and peculiar character: in the Branchiostoma by the articulated cartilaginous labial arch and its numerous filaments; and in the proper Myxinoids and Lampreys by the formation of the complex system of lateral and labial cartilages; or by the modification of the palatine, maxillary, and hyoid rudiments, in relation to the suctorial function of the mouth.

In the Sturgeon (*Acipenser*) fig. 62, the growth of cartilage has inclosed the whole of the brain-case, *f*, *g*, and blended with its walls the ear-capsules: in advance of this it develops protective cavities for the now well-developed eyes and double nasal sacs: the orbit, *i*, being divided from the nostril, *k*, by the ridge, 2, and both supported by a 'vomarine' basis, *g'''*: beyond which the cranium is continued forward as a long pointed rostrum. The cartilaginous pedicle suspending the palato-maxillary apparatus is



Fore part of endoskeleton, Sturgeon

divided into three pieces; the epitympanic, ib. *m*, the mesotympanic, ib. *n*, and the hypotympanic, ib. 26. The latter supports the palatine vault, 20, with which the pterygoids, *se*, are confluent; the maxillary, 21, the premaxillary bone, 22, the labial cartilage, 74, and the mandible, 32. All these parts of the edentulous suctorial mouth are very small in proportion to the size of the head and entire fish; and they are the only ossified parts of the endoskeleton. The premaxillary is a subtriangular plate, joined by ligament to its fellow, trenchant anteriorly, and extending in an arched form to the mandible. The mandible, 32, articulates by a concavity to the pterygoid and premaxillary, and consists of a single piece, united to its fellow by a ligamentous symphysis.

The mouth of the Sturgeon opens upon the under surface of the head, and is protruded and retracted chiefly by the move-

ments of the tympanic pedicle, which swings, like a pendulum, from its point of suspension to the post-orbital process, fig. 29, *g''*. The hyoid arch is also small and simple in the Sturgeon. The epi-hyal is short, and attached to near the upper end of the hypotympanic. The cerato-hyal, fig. 62, 40, of thrice the length, is expanded above, and is attached by ligament extending from that part to near the joint of the lower jaw. The basi-hyal is a short subcubical piece: it gives attachment anteriorly to cerato-hyals, and posteriorly to the anterior basi-branchial and hypo-branchial cartilages.

The three first branchial arches consist of hypo-branchials, progressively decreasing in size, of cerato-branchials, epi-branchials, and pharyngo-branchials: the fourth arch consists of cerato-branchials and epi-branchials: the fifth arch of cerato-branchials only. The branchial cavity is closed by an opercular dermal scale, *d*, 35, supported by the expanded tympanic cartilage, *m*, fig. 62.

The cartilaginous representative of the par-occipital projects backward from each angle of the occiput. A triangular supra-scapular cartilage, fig. 62, 50, has the angles of its base slightly produced, one being articulated to the end of the par-occipital, the other to the ex-occipital region. To the apex is attached the scapulo-coracoid arch, *ib.* 51, 52. The coracoid cartilage expands as it descends, sends inward and forward a broad wedge-shaped plate, and presents a large perforation at its thick posterior part, answering probably to the perforated ulna of osseous Fishes, here confluent with the arch. The pectoral fin is articulated to the under part of this perforated projection: the coracoid terminates by a broad thin plate beneath the pericardium, where it is joined by strong aponeurosis to that of the opposite coracoid.

Special development proceeds further in the skull of the singular Acipenseroid, called 'paddle-fish' (*Planirostra Spatula*). It is remarkable for the rostral prolongation of the nasal and vomerine bones, the rostrum being flattened horizontally and expanded like the mandibles of a Spoonbill. The sides of the rostrum are strengthened by a reticulate disposition of bony matter in the form of stars, the rays of which anastomose. The upper part of the cranium is less perfectly chondrified than in the Sturgeon. There is a long vacuity between the frontal, parietal, postfrontal and mastoid bones: the tympanic pedicle is a simple elongated piece of bone expanded at both ends. The mandibular and hyoidean arches are suspended by a short cartilage



to the end of the tympanic bone : the palatines are extremely small. The premaxillary and maxillary bones seem to have coalesced ; they expand as they extend backward to become attached to the cartilage supporting the mandibular arch. The slightly ossified pterygoids run parallel with them along the inner sides to the same part. The articular and dentary pieces of the lower jaw have coalesced, but there is a trace of a slender splenial piece on the inner side of the mandible. All the bones of the mouth are edentulous, but the membrane covering the extremities of the upper and lower jaw is roughened by extremely minute denticles in the recent fish. The ceratohyals are partially ossified : the rest of the hyoidean arch is cartilaginous. A branchiostegal appendage in the form of an irregular elongated flattened bone, resolved posteriorly into osseous fibres, extends from each side of the commencement of the hyoidean arch. A similar but larger opercular appendage extends backward from the extremity of the tympanic pedicle.

§ 27. *Skull of Plagiostomi.*—The more or less cartilaginous skull of the Plagiostomous fishes might be histologically regarded as the transitional step from the Cyclostomous to the Osseous fishes ; but, morphologically, it offers a different, apparently simpler type ; and one which, through the progress of developement in the direct vertebrate route, more nearly approximates to the cranial organisation in the Batrachia. The Monk-fish (*Squatina*,—an intermediate form between the Sharks and Rays,) affords a good and typical example of the essential characters of the plagiostomous skull. The cranial end of the notochord and its capsule are converted into firm granular cartilage ; extending forward so as to constitute an oblong flattened plate forming the whole basis cranii. The posterior margin of this ‘occipito-sphenoidal’ plate supports two convex condyles, for articulation with the body and parapophyses of the axis. The body of the atlas has coalesced with the basi-occipital, as is indicated by its slender but separate neural arch. The lateral margins of the basal cartilage have two notches, the intervening prominence representing the primitive sphenoidal arch, here filled up and sending off a rudimental pterygoid process outwards. Just anterior to the median ridge there is a small fossa, (in the young *Squatina* a foramen,) the last trace of the pituitary canal : the basal cartilage then expands to form the lower border of the groove which receives the palatine process or point of suspension of the palato-maxillary arch, in front of which it contracts to form the vomerine base of the cranium. The cranial cavity is not moulded on the brain, but is of larger size ; it

communicates by means of the nervous and vascular foramina with the acoustic chamber in the thick lateral wall: this insulation of the labyrinth is common to the Plagiostomes. The cranial cavity is closed by membrane anteriorly. The foramina for the fifth pair of nerves mark the 'alisphenoidal' portion of the endo-cartilage: those for the optic nerves the 'orbitosphenoidal' part: the 'prefrontal' portion is marked by the olfactory foramina, and their articulation with the palatine part of the maxillary arch.

The exterior of the skull is variously and singularly modified in different Sharks and Rays, the developement proceeding from the advanced cartilaginous stage just described, to establish peculiar plagiostomous characters, and to adapt the individual to its special sphere of existence.

The same general confluence of cartilage, which pervades the protecting walls of the brain-case, characterises the appended arches of the cranium. A single strong suspensory pedicle, fig. 30, *c*, articulated to the side of the skull beneath the posterior angular (mastoid) process, has the hyoidean, and partly the mandibular,<sup>1</sup> arches attached to its lower end, the former, *d*, by a close joint, the latter by two ligaments. The maxillary arch, in *Squatina*, is suspended by a ligament from its ascending or palatal process, to the notch between the vomerine and the anterior supracranial cartilaginous plate. From this point the jaw is continued in one direction forward and inward, completing the arch, *ib. e*, by meeting its fellow, to which it has a close ligamentous junction; and in the opposite direction, backward and outward, as a coalesced diverging appendage to the outer side of the tympanic pedicle, where it forms the more immediate articulation for the lower jaw, like the hypotympanic continuation of the upper maxillary bone in the Batrachia, fig. 71, *e*. Each lateral half or ramus of the mandible, fig. 30, *d*, consists of a single cartilage, the two being united together at the symphysis by ligament.

Two slender labial cartilages, *ib. f*, are developed on each side the maxillary, and one, *g*, on each side the mandibular arch; which complete the sides of the mouth. These cartilages Cuvier regarded as rudiments, respectively, of the maxillary and dentary bones, the dentigerous maxillary arch as the palatine bones, and the mandibular arch as the articular piece of the lower jaw: but both palatines and articulares co-exist with labial cartilages, like those of *Squatina*, in a Brazilian Torpedo

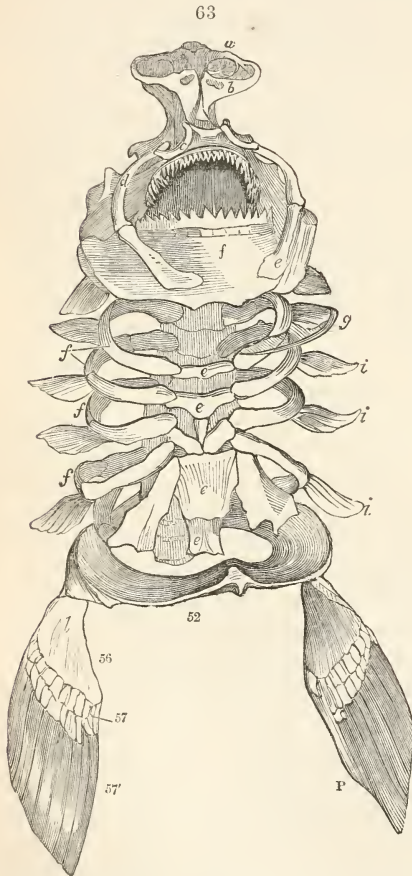
<sup>1</sup> Throughout this work the term 'mandible' is applied to the lower jaw, and the inverted cranial arch which that jaw completes is called 'mandibular:' the arch formed by the upper jaw is called 'maxillary.'

(*Narcine*), and at the same time with distinct pterygoid cartilages.<sup>1</sup>

Four or five short cartilaginous rays diverge from the posterior margin of the tympanic pedicle, *ib. c*, and support a membrane answering to the opercular flap in Osseous fishes; in their ultimate homology these rays are the skeleton of the diverging appendage or limb of the tympano-mandibular arch.

The hyoid arch in *Squatina*, as in most other Plagiostomes, consists of two long and strong cerato-hyals, and a median flattened symmetrical piece,

the basi-hyal. Six short cartilaginous rays extend outwards from the back part of the cornua, supporting the outer membranous wall of the branchial sac: these answer to the branchiostegal rays in osseous fishes, and support the diverging appendage or limb of the hyoidean arch. But the fold of integument in which they project is not liberated, and is continuous with that supported by the opercular rays from the tympanic pedicle. Five branchial arches, *fig. 30*, 1, 2, 3, 4, 5, succeed the hyoidean; but are suspended, as in the Lamprey, from the sides of the anterior vertebræ of the trunk. In the Sea-hound (*Scymnus licha*), *fig. 63*, the ceratobranchials, *f, f*, and basibranchials, *e, e*, are shown, with the framework of the gills, *g, i*. Behind these arches is the scapulo-coracoid arc, *52*, united by cartilaginous confluence at the mid-line, not by ligament as in the Sturgeon.



Skull with branchial and scapular arches, *Scymnus*. XLIII.

pulo-coracoid arc, *52*, united by cartilaginous confluence at the mid-line, not by ligament as in the Sturgeon.

<sup>1</sup> XXI. 1835, pl. v. figs. 3 & 4. It may be questioned whether the detached plate, called palatine by Dr. Henle, be not rather the entopterygoid.

The *Cestracion*, so interesting from its early introduction into the seas of this planet, is not so far advanced in cranial development as is the more modern *Squatina*. In the existing species of the Australian seas (*Cestracion Phillipi*), the cartilaginous basioccipital retains a deep conical excavation, adapted to a corresponding one in the atlas, which cavity is consolidated by cartilage in the *Squatina*; the original place of the extended anterior end of the chorda, along the middle of the posterior half of the basicranial cartilage, continues membranous, and the pituitary perforation is permanently closed by membrane only; the basal cartilage expands anterior to this, and comes into close connection with the maxillary arch, and is thence continued forward, contracting to a point between the nasal capsules, which meet at the middle line above the symphysis of the upper jaw. The proper cranial cartilage is thinner than in the *Squatina*; the anterior or pineal fontanelle forms an extended membranous tract on the upper part of the cranium; the vertical ridges, which rise from the sides of this tract, extend forward and outward to support the nasal sacs, and are continued backward, interrupted by a notch filled by membrane, to the posterior angular processes, which overhang the joint of the maxillo-hyoidean pedicle. The maxillary and mandibular arches are as simple as in *Squatina*, but much stronger, since they support a series of massive grinding teeth, as well as pointed ones, or laniaries. The rami of the lower jaw are confluent at the symphysis.

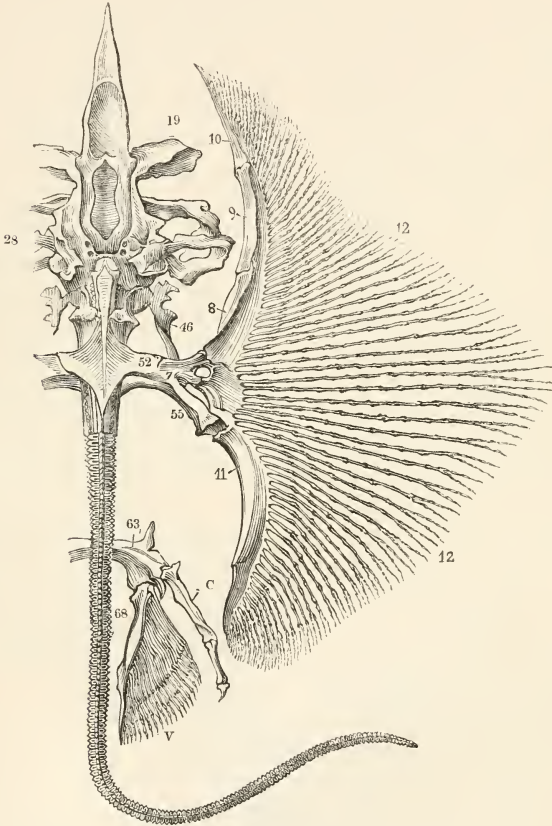
The Skates and Rays have the skull movably articulated, as in *Squatina*, by two basilar condyles and an intervening space, to the axis. The skull is flat and broad; the upper wall membranous for a greater or less extent, fig. 64, except in *Narcine*, where it is closed by cartilage. The anterior or vomerine part forms a long pyramidal rostrum, to which are usually articulated cartilages connecting its extremities with the anterior angles of the enormously developed pectoral fin, ib. 12: in the space between the skull and those fins, the *Torpedo* carries its electric batteries. The tympanic pedicles, are short and thick; the maxillary and mandibular arches long and wide, stretching transversely across the under part of the head.

In the ordinary Sharks the forward prolongation of the cranial cavity gives a quite anterior position, and almost vertical plane, to the fontanelle: three columnar rostral cartilages are produced, two from above, and one from between the nasal cavities, which processes converge and coalesce to form the framework of a kind of cut-water, at the fore-part of the skull. In the place of articular



condyles, processes extend backward from each side of the occipital foramen and clasp, as it were, the bodies of three or four anterior vertebræ of the trunk. The pterygoidean arches extend outward, in *Carcharias*, from the base of the cranium, but, as in embryo osseous fishes, are confluent therewith at both ends. The maxillary arch, suspended near its closed anterior extremity to

61

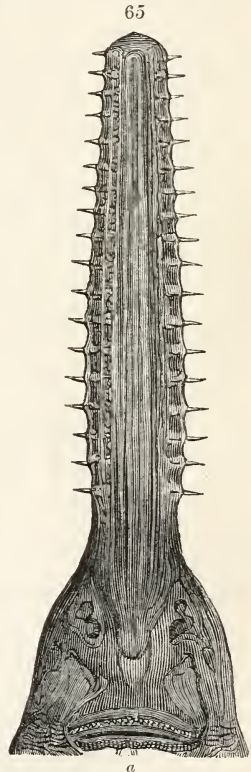
Skate (*Raia batis*)

the vomerine part of the base of the skull, is thence extended backward to the articulation of the lower jaw. A simple cartilaginous pedicle forms the upper part (pleurapophysis) of the mandibular arch, which is completed below by the lower jaw. A few cartilaginous rays diverge outward and backward from the pedicle, and support a small opercular flap or fin. The hyoid

arch consists of a basihyoid and two simple ceratohyoid cartilages; the stylohyal is ligamentous, as in the *Squatina*. Short cartilaginous rays diverge from the ceratohyal to support the branchiostegal membrane, or hyoid fin. The scapular arch, which we shall find normally articulated with the occiput in osseous fishes, is attached thereto, at a little distance behind the head, by ligament and muscles in the Sharks, fig. 30, 51: from this arch, also, cartilaginous rays, *ib. k, l*, immediately diverge for the support of a radiated appendage or fin—the homotype of the tympanic or opercular fin.

The capsules of the special organs of sense are all cartilaginous: that of the ear is involved in the lateral walls of the cranium; that of the eye is articulated by a cartilaginous pedicle with the orbit; and that of the nose, figs. 30 and 63, *b*, is overarched by the nasal processes of the epicranial cartilage, *ib. a*, and is completed below by membrane. At the summit of the occiput in *Carcharias* and some other sharks may be seen two closely approximated oval ‘fenestræ,’ which lead to the acoustic labyrinth, and are covered by skin in the recent fish.

Amongst the stranger forms in which special development radiates, in diverging from that stage of the common vertebrate route attained by the Plagiostomes, may be noticed the lateral transverse elongations of the orbital processes, supporting the eyeballs at their extremity, and giving the peculiar form to the skull of certain Sharks, thence called ‘Hammer-headed’ (*Zygæna*). In the ‘Saw-fish’ (*Pristis*), the rostrum, fig. 65, is produced into a long, flat, plate, having a row of tooth-like bodies implanted in sockets along each margin. The walls of these sockets and the midpart of the rostrum are ossified.



Mouth and rostrum of Saw-fish (*Pristis*).

The proper jaws and teeth *a* have the usual inferior position in the Sharks. In the Eagle-ray (*Myliobates*) a cartilage is attached to the anterior prolonged angle of the great pectoral fin, and connects it with the fore part of the cranial (internasal) cartilage; it supports a number of branched and jointed cartilaginous rays,

which project forward, and are connected at the middle line with a like series from the opposite side of the head; they may be regarded as partial dismemberments of the great pectorals; and in *Rhinoptera Braziliensis* their supporting cartilage is directly continued from that of the pectoral fins, though it is closely attached to the fore part of the head. These form what Müller has termed 'cranial fins;' but the parts more properly meriting that name are the opercular and branchiostegal appendages of the tympanic and hyoidean arches.

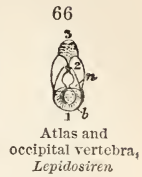
§ 28. *Skull of Protopteri*.—Thus far we have seen that the base of the skull is first formed by the anterior prolongation of the notochord and the expansion therefrom of its capsule; and that the cranial cavity results from the extension of the outer layer of that membrane over the anterior end of the nervous axis. We saw next the superaddition of special capsules for the organs of sense; and the cartilaginous tissue developed in the notochordal sheath at the base and sides of the cranium, according to a pattern common to the lowest and to the embryos of the higher vertebrata. We saw the cartilaginous tissue acquiring a firmer texture, hardened by superficial osseous grains, or tesseræ, mounting higher upon the lateral and upper walls of the cranium, and at length entirely defending it: and we then also recognised the maxillary, mandibular, and hyoidean arches, established in a firm cartilaginous material, and on a recognisable ichthyic type.

We have now to trace the course and the forms under which the osseous material is superadded to, or substituted for, the primitive cartilaginous material of the skull; and the remarkable *Lepidosiren*, whose organisation was first made known as in the generic form called *Protopterus*,<sup>1</sup> offers a transitional step, in the shape and structure of its skull, between the gristly and the bony cold-blooded vertebrates.

In the *Lepidosiren*, ossification of the cranial end of the notochord extends along the under and lateral part of its sheath, backward to beneath the atlas, fig. 41, 1, the posterior slightly expanded end of this ossified part supporting, as in *Squatina*, the neurapophyses of the atlas, fig. 66, *n*, the bases of which expand and meet above the notochord and below the spinal canal. Ossification of the notochordal sheath commencing at its under part, *ib. b*, ascends upon the sides of the notochord as it advances forward, and encloses it above, where it supports the medulla oblongata, and the lateral bony plates (neurapophyses)

<sup>1</sup> XXXIII.

called exoccipitals, *ib.* 2; leaving behind a wide oblique concavity lodging the anterior unossified end of the notochord, which does not extend further upon the basis cranii. The exoccipitals, *ib.* 2, 2, expand as they ascend and converge to meet above the 'foramen magnum' which they complete. A small mass of cartilage connects their upper ends with each other, and with the overhanging backwardly projecting point of the frontoccipital spine, *ib.* 3. This cartilaginous mass answers to the base of the superoccipital in better ossified fishes: a similar cartilage connects the exoccipitals with the occipital spine in the *Tetrodon*.

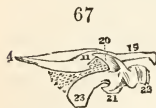


We clearly perceive in the *Lepidosiren* that ossification, advancing on the common cartilaginous mould of the piscine skull, has marked out the neurapophyses and centrum of the posterior cranial vertebra. The occipital pleurapophyses, called 'scapulæ,' *fig.* 41, 51, appear as strong, bony, styliform appendages, articulated by a synovial capsule and joint, one on each side, to the ex- and basi-occipitals. To the pleurapophyses are attached the upper extremities of the hæmapophyses (coracoids, *fig.* 41, 52) which unite together below, and thus complete the hæmal arch of the occipital vertebra, here unusually developed in relation to its office of protecting the heart and pericardium. The coracoids belong to the same category of vertebral elements as the sternal ribs which protect the heart in higher Vertebrata. The hæmal arch of the occipital vertebra of the *Lepidosiren* supports a filiform appendage, *ib.* 57; it is the key to the homology of the anterior or upper limbs of the higher Vertebrata.

In the second (parietal) and third (frontal) cranial vertebræ, ossification extends along the basal and along the spinal elements, but not into the neurapophysial or lateral elements; these remain cartilaginous in continuation with the cartilage surrounding the internal ear. The basal ossification, representing at its posterior end the body of the atlas, then the basioccipital, expands as it advances along the base of the skull in the situation of the sphenoids, constituting the floor of the cerebral chamber, supporting the medulla oblongata, the hypophysis, the crura and lobes of the cerebrum, and terminating a little in advance of the olfactory lobes by a broad transverse margin, bounding a triangular space left between it and the converging palatine arches, which space is filled by the persistent 'vomarine' cartilage. The sides of the basicranial plate bend down to abut against the bases of the pterygoid plates. In this expansion of the basisphenoid the



Lepidosiren resembles the Plagiostomes. Two ridges rise from the upper surface of the basioccipito-sphenoidal plate, near its outer margin, and support the cartilaginous lateral walls of the cranium. The cranial cavity is defended above by a longitudinal bony roof, fig. 67, 11, nearly coextensive with the bony floor beneath: the roof commences behind by the spine or point which overhangs the exoccipitals, gradually expands as it advances, resting upon the cartilaginous walls of the cranium, is then suddenly contracted, and is united anteriorly by fibrous ligament to the ascending process of the palato-maxillary arch, 20, and to the base of the naso-premaxillary plate, 15. A strong sharp crest or spine rises from above the whole of the middle line of the cranial roof-bone, which may be regarded as representing the mid-frontal, the parietal, and superoccipital bones, or, in more general terms, the neural spines of the three cranial vertebræ: but this supracranial bone not only covers the medulla oblongata, cerebellum, optic lobes, pineal sac, and cerebral hemispheres, but also the olfactory lobes. The lateral cartilaginous walls of the cranium are continued forward from the acoustic capsule between the basal and superior osseous plates: the part perforated by the fifth pair of nerves, and protecting the side of the optic lobes, represents the 'alisphenoid': the next portion in advance, protecting the sides of the cerebral hemispheres and perforated by the optic nerve, answers to the orbitosphenoid: and the cartilage terminates by a 'prefrontal' part which is perforated by the olfactory nerve, and which abuts laterally against the ascending or palatine process of the maxillary arch.



67  
Cranial spines and  
upper jaw of *Lepi-*  
*dosiren*

The extension of the lateral cartilages of the cranium forward and downward to form the articulation for the lower jaw, is like that in the *Chimæra* and batrachian larva, fig. 69A, *e*; but ossification has co-extended along two tracts, which converge as they descend, one, fig. 41, 28, from above and behind to the outer, the other, *ib.* 23, from before to the inner, side of the cartilaginous mandibular joint, which these bony plates strengthen and support like the backs of a book. The posterior of these is the tympanic, the anterior one the pterygoid, which is confluent with the palato-maxillary bone, the dentigerous part of which extends outward, downward, and backward, fig. 67, 21, but does not reach, as in the Sharks and Rays, the mandibular joint. From the upper part of the palato-maxillary a compressed sharp process, *ib.* 20, ascends obliquely backward, and terminates in a point: the inner side of this process is closely attached by ligament to the fore and outer part of the frontal portion of the

epicranial bone, ib. 11; the outer side of the process is excavated for the reception of the outer and anterior process of the super-temporal bone. This bone, fig. 41, 12, in connection with the ascending process of the maxillary, ib. 20, forms the upper part of the orbit, and behind this connection it sends out the post-orbital process, beyond which it extends backward, freely overhanging the fronto-occipital, and gradually decreasing to a point, and giving attachment to the anterior end of the great dorso-lateral muscles of the trunk. This bone is flat above like a scale, and from its superficial position might be classed with the dermal skeleton: the strong temporal muscle is attached to the two surfaces, divided by the ridge on its inferior part: it is movable up and down upon its anterior ligamentous union. It represents the postorbital and supratemporal bones in *Ganocephala*.

Each ramus of the lower jaw is composed of an articular, ib. 29, and a dentary, ib. 32, piece, the latter anchylosed together at the symphysis, and completing the tympano-mandibular arch. The articular piece is a simple slender plate, strengthening the outer part of the articular concavity of the jaw, and closing the outer groove of the dentary, along which it is continued forward to near the symphysis, where it ends in a point. The articular trochlea is formed by the persistent cartilage. The dentary piece has the notched and trenchant dentinal plate anchylosed to it, and sends up a strong coronoid process. Serial homology guides in the determination of the special one of the part of the upper jaw to which the dentary is opposed. Behind the tympanic is the preopercular, fig. 41, 34. The ceratohyal, 40, is suspended to the petrosal cartilage close behind the tympanic pedicle; it joins its fellow below without the intervention of a basihyal: it supports a branchiostegal ray, 37.

In the *Ganocephala* the head was connected by ligament, as in the *Protopteri*, to the vertebral column of the trunk, and chiefly by the basioccipital part. The temporal vacuities were more completely roofed over by bone, including the postorbital and supertemporal ossifications.

§ 29. *Skull of Batrachia*.—In modern members of this order the ossification of the skull, like its chondrification in *Plagiostomi*, is simplified, or so continuous as to indicate but obscurely its essentially segmental character: and this condition will be noticed before entering upon the description of the complex and instructive osteology of the head in the more specially developed and divergent cold-blooded Vertebrates, called ‘bony fishes.’

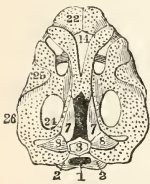
In *Batrachia* the plagiostomous articulation of the head to the

trunk by a pair of condyles, fig. 72, *e, e*, is resumed. The chief steps in the developement of the batrachian skull will be premised before entering upon the various modifications. In the larva of the frog, fig. 42, the outer layer of the notochordal capsule expands at the fore part of that vertebral basis to enclose the brain, and its appendages, the sense-organs. The cartilage therein developed, fig. 68, as the head expands, forms an occipito-petrosal mass, fig. 42, 16, including laterally the ear-capsules; it bifurcates anteriorly into the 'sphenoidal arches,' which reunite in front of an oblong hypophysial space to form a broad prefronto-vomerine mass. The occipito-petrosal cartilage sends out on each side a thick 'mastotympanic' process, which bifurcates; the division directed forward and inward fig. 42, 26, is the 'pterygoid;' that passing forward and downward is the 'hypotympanic.' To the back part is attached the hyoid cartilage, ib. 40: to the end is attached the 'mandibular' cartilage, ib. 30, fig. 69A, *d*, also called 'Meckel's process.' The subsequent ossification begins partly in the cartilage, partly in the persistent notochordal membrane: the first may be called 'chondrogenous,' the second 'sclerogenous' bones: some are disposed to regard the first only as 'endoskeletal,' the latter as 'exoskeletal.'

To the first category belong the neurapophyses of the occiput, exoccipitals, figs. 43 and 68, 2; each of which developes a 'zygapophysis' or condyle, fig. 73, *e*, for the atlas, fig. 43, *a*: any petrosal ossification upon the ear-capsule is a growth from the exoccipital and from the alisphenoid, ib. 6: the expanded disc of the 'columella' or 'stapes' is a distinct ossicle, between 2 and 25, fig. 43; as is also the 'hypotympanic' articulation, ib. 29, for the mandible, 30, 32. The neurapophyses of the third segment, 'orbitosphenoid,' figs. 42 and 43, 10, perforated by the optic nerves, are ossified in the cartilaginous basis, as are those of the fourth segment (prefrontals), figs. 42, 44, 68, 14, perforated by the olfactory nerves; whilst those of the second segment, 'alisphenoids,' ib. 6, perforated by the trigeminal, longer remain gristly. All the chondrogenous elements are thick bones.

From the membranous basis of the skull are developed the following bones, which are more or less lamelliform. The basioccipito-sphenoidal plate, fig. 73, *m*, forms the base of the skull from the condyles to the vomerine cartilage. The mastotympanic, fig. 43, 25, fig. 44, 8, 25, fig. 68, 8, extends from the mastoid cartilage, where it is broadest, to the outside of the

68



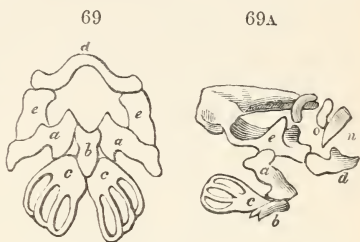
Incipient ossification  
of the skull. Larva  
of Frog (*Rana*)

hypotympanic, fig. 43, 29. The parietals, *ib.*, 44 and 68, 7, and afterwards the frontals, *ib.* *ib.*, 11, progressively cover the 'fontanelle' above, as the basioccipito-sphenoid covers the hypophysial vacuity below. An antorbital plate, fig. 72, *b*, extends from the frontal to the maxillary. The premaxillaries, at first beak-shaped, figs. 42, 22, and 69A, *n*, expand transversely as the mouth widens to form its fore-part, fig. 71, *n*: external to the premaxillary pedicles begins the ossification of the turbinals. The 'pterygoid plate,' fig. 43, 24, extends to the inner side of the hypotympanic, 29, and forward to the 'palatine' bone, and the bifid dentigerous 'vomarine' plate, fig. 73, *l*, *l*. From the membrane covering

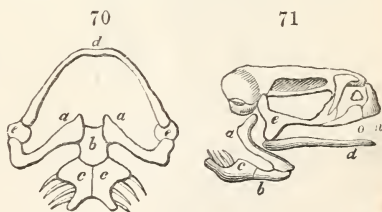
'Meckel's cartilage,' figs. 69A and 70, *d*, are exclusively developed the mandibular elements, the 'angular,' fig. 43, 30, and 'dentary,' *ib.* 32, being the chief; there is also a 'splenial,' which in some perennibranchiate Batrachia supports teeth. As the mandible, fig. 71, *d*, lengthens, the tympanic, *ib.* *e*, shortens and becomes more vertical, and the hyoid arch, *ib.* *a*, shifts its attachment to the petrosal, close behind, but distinct from, the tympanic.

In the *Lepidosiren* the ali- and orbito-sphenoids and the hypotympanic remain cartilaginous; premaxillaries are represented by their ascending or facial parts coalesced into a single plate, supporting the two prehensile teeth. The postorbito-supertemporals, fig. 41, 12, are 'dermal' or scleral bones, overlapping the fronto-parietals. They are not present in modern Batrachia.

In the *Axolotl* (*Axolotes marmoratus*), the basioccipital is represented by the posterior part of the common broad and flat basi-cranial bone. The exoccipitals are separated below by this process, and above by a cartilaginous representative of the superoccipital. Each exoccipital develops a small, almost flattened condyle, anterior to which it is perforated by the eighth pair of nerves; it articulates above with the parietal and mastotympanic, and is separated from the alisphenoid by the large cartilaginous petrosal, to which a small discoid representative of the stapes is attached,



Hyo-branchial frame, skull, Tadpole. CXXXIX.



Hyo-branchial frame, skull, older Tadpole. CXXXI.

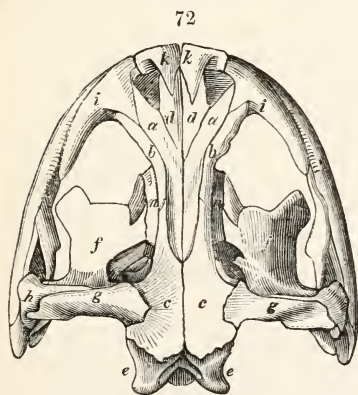


closing the homologue of the 'fenestra ovalis.' The basi-sphenoidal portion of the basicranial plate sends out an angular process on each side, which supports the alisphenoid. The surfaces of the alisphenoid are directed forward and backward, instead of from side to side, and it constitutes chiefly the anterior parietes of the otocrane; the inner and anterior border is notched by the great trigeminal nerve. The parietals are long and broad, divided by the sagittal suture, and impressed at the posterior and outer angle by the anterior attachment of the great dorsal trunk-muscles. The masto-tympanic is articulated to this part of the parietal and to the exoccipital; it includes all the divisions of the pedicle save the lowest, 'hypotympanic,' which affords the articulation to the mandible. The orbitosphenoids are divided by an unossified tract of some extent from the alisphenoids, and articulate above with the extremity of the parietal, the frontal and prefrontal bones. There are neither paroccipitals nor postfrontals. The vomerine portion of the basicranial plate is chiefly cartilaginous. The turbinals are very small, and separated from each other by the junction of the premaxillaries with the frontals. The bone extending from the frontal to the maxillary in front of the orbit may be termed 'antorbital;' the ossification which extends therefrom, in higher Batrachians, takes the situation of the facial plate of the prefrontal, of the nasal, and of the lacrymal. The pedicles ('apophyse montante,' Cuvier,) of the premaxillaries are long and narrow. The small maxillary is attached to the antorbital, to the palatine, and to the premaxillary; the end of the bone extends freely backward as in the Menopome, fig. 43, 21. The alveolar border of both premaxillaries and maxillaries supports a single row of small equal and sharp-pointed denticles. Two bones attached to the anterior and outer part of the basicranial bone, and which may be regarded either as vomerine or palatal, support each a narrow rasp-like group of minute denticles, which are continued backward upon the beginning of the pterygoids; the pterygoids continued from these bones and from the sides of the basicranial bone expand as they extend backward and apply themselves to the inner side of the tympanic pedicle. The nasal meatus has its posterior termination between the beginning of the pterygoid and the end of the maxillary bones. Besides the ordinary row of denticles upon the dentary piece of the lower jaw, there is a second shorter series upon the splenial piece.

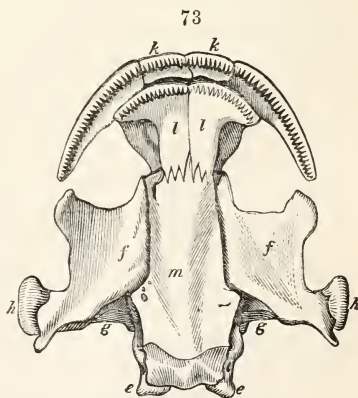
In the Menobranch (*Menobranchus lateralis*) the occipital condyles are transversely oblong, convex vertically, concave transversely,

developed from the exoccipitals, which are separated above and below, as in the Axolotl: each exoccipital forms the posterior half of the otocrane, is perforated by the nervus vagus, and articulates above with the parietal and masto-tympanic. The basisphenoid is very broad and flat: the alisphenoids bound the fore part of the otocrane, transmit the trigeminal nerve, and abut against the tympanic pedicle in its course backward to the mastoid. The parietals are divided by the sagittal suture and develop a small ridge there posteriorly: each parietal sends down a process in front of the alisphenoid which rests upon the pterygoid, representing the so-called 'columella' in Lizards. There are no maxillary bones. The alveolar border of the premaxillaries, which support a single row of long and slender teeth, ten in number in each bone, terminates in a point projecting freely outward and backward. The vomero-palatine bones unite together anteriorly, but diverge posteriorly, where they give attachment by their outer margin to the pterygoids.

The two foregoing are examples of the Ichthyomorphs which retain the gills, and thence are termed 'perennibranchiate.' The Menopome, figs. 43, 72, and 73, represents a later phase of larval



Upper view of skull of the Menopome. CXXXIX.



Under view of the skull.

life, the gills being absorbed and only the branchial slits remaining. In fig. 72, *e e* are exoccipitals, each developing a condyle; *c c*, parietals; *g g* mastotympanics; *h* hypotympanic; *a a*, frontals, *b b*, antorbital; *d d*, nasals; *n*, orbitosphenoid; *k k*, premaxillaries; *i i*, maxillaries; *f f*, pterygoids. In fig. 73, *m* is the basioccipito-sphenoidal; *e e*, exoccipitals; *g g*, mastotympanics; *h h*, hypotympanics; *f f*, pterygoids; *l l*, vomers; *k k*, premaxillaries.

In the Frog (*Rana*) when the metamorphosis is complete, the

exoccipitals have coalesced with the superoccipital above, and with the basioccipito-sphenoidal plate below; this latter, fig. 98 A, sends out on each side a process to form the floor of the otocrane, and its forward extension is long and narrow: the tympanic develops a frame for the large ear-drum, fig. 44, N: the stapes, now columelliform, stretches from that membrane to the foramen of the labyrinth. 'Meckel's cartilage,' figs. 69 and 71, *d*, contributes nothing to the bony conductor of sonorous vibrations which becomes subdivided into a chain of ossicles in *Mammalia*. The hypotympanic, fig. 44, 28, sends forward a process to the end of the maxillary, thus articulating, as in the Plagiostomes, with both upper and lower jaws. The essential or neurapophysial parts of the prefrontals encompass the prosencephalon, and coalesce to form a ring of bone, like the exoccipitals: it is the 'os en ceinture' of Cuvier,<sup>1</sup> part of which appears at the upper surface of the cranium, fig. 44, 14, between the frontals and antorbitals, *ib.* 15, which here, and still more in the Toad, assume the character of nasals connate with lacrymals. Between these and the premaxillaries are the small bony parts of the olfactory sacs, usually described as 'nasal bones.' The orbital and temporal fossæ form one wide common vacuity on each side the cranium: it is divided from the nostril by the junction of the maxillary, *ib.* 21, with the naso-lacrymal bone: the premaxillaries, *ib.* 22, are small bones, with a well-marked facial and buccal portion. The palatines, fig. 98, A, are transversely extended: the divided vomer is dentigerous: the pterygoid, *ib.* 24, sends out three rays for the sphenoidal, tympanic, and palato-maxillary connections respectively. The mandible is edentulous. The hyoid arch with its branchial appendages has changed its connections as well as shape. In the tadpole, with the fully-developed gills, the cartilage representing the stylo- and cerato-hyals, figs. 69 and 69A, *a*, is short and thick, and attached to the back of the tympanic pedicle, *ib.* *e*, to the end of which is articulated the mandible, *ib.* *d*. The ceratohyals are connected below to a median piece, *ib.* *b*, which may represent both the basihyal and basibranchial: it directly supports the hypobranchials *c*, *c*, to which the ceratobranchials, or branchial arches are attached. As the gills wither, the stylo-ceratohyals, figs. 70 and 71, *a*, lengthen, attenuate, and acquire an independent attachment to the petrosal; the basi- and hypo-branchials, fig. 74, *c*, *c*, coalesce into a single cartilaginous plate, with the 'basihyal,' *ib.* *b*; and the ceratobranchials are reduced to a single pair, which represent the so-called 'posterior cornua' of the hyoid.

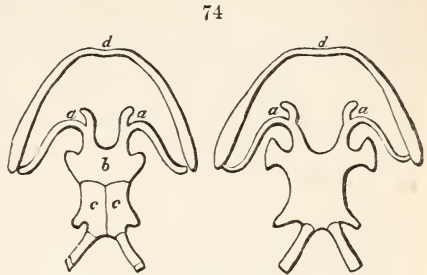
<sup>1</sup> CXXXIX. tom v. pt. 2, p. 389, pls. xxiv.—xxvii., well illustrate the osteology of the Batrachia.

The scapular arch, fig. 42, 50, 51, retrogrades, like the hyoid, from its primitive position in the larva.

Cuvier, at the conclusion of his description of the batrachian skull, remarks, 'This skull does not accord with the theory of the three, four, or seven vertebræ, or even of one (cranial) vertebra, any more than it does with that of the identity in the number of bones' (in different animals).<sup>1</sup>

At the same time he determines the special homology of the twenty-six bones, exclusive of the mandible and hyoid apparatus, and assigns to them the same names,—and as regards the majority, correctly,—which those bones bear in the rest of the vertebrate province. We have been led, therefore, to look for some higher law within which that of the special conformity may be included.

In many instances of trunk-vertebræ, the neurapophyses meet below, as well as above the neural axis, their bases being extended towards each other so as to interpose between that axis and the vertebral centrum. This condition is repeated by the exoccipitals which form the neural arch of the epencephalon, and encompass it, in *Batrachia*, giving passage to its chief pair of nerves and developing articular processes for the succeeding vertebra. The two pairs of neurapophyses in advance, retain the more ordinary relations of these elements, the more expanded mes- and pros-encephala having their bony ring or arch completed by a centrum below and a spine above. One neurapophysis (alisphenoid) transmits the trigeminal nerve, the other (orbitosphenoid) the optic nerve: the fourth or anterior neural arch ('os en ceinture' and 'ethmoïde' of Cuvier) encompasses the foremost segment of the brain as the exoccipitals do the hindmost; and they give passage to the olfactory nerves. Ossification of this ring of bone begins in its lateral halves: the essential relations and functions being those which characterise the bones which in bony fishes will be described as 'prefrontals.' Beneath, and supporting them, is a pair of bones which may be regarded as a mesially divided 'centrum' (vomer): and above is a pair of bones which may be



Hyobranchial frame, *Rana paradoxa*. CXXXIX.

<sup>1</sup> CXXXIX. 'Ce crane ne s'accorde pas plus avec la théorie des trois, des quatre, ou des sept vertèbres, même avec celle d'une vertèbre, qu'avec celle de l'identité de nombre des os,' vol. v. pt. ii. p. 391.



regarded as a mesially divided neural spine (nasal). Thus may be discerned four cranial segments having the essential characters and relations of the neural arch of the type vertebra. The upper, 22, and lower, 30, jaws, the hyoid, 40, and scapulocoracoid, 50-52, fig. 42, constitute four inverted arches; but their vertebral relations will be better understood in the composition of the skull in bony fishes.

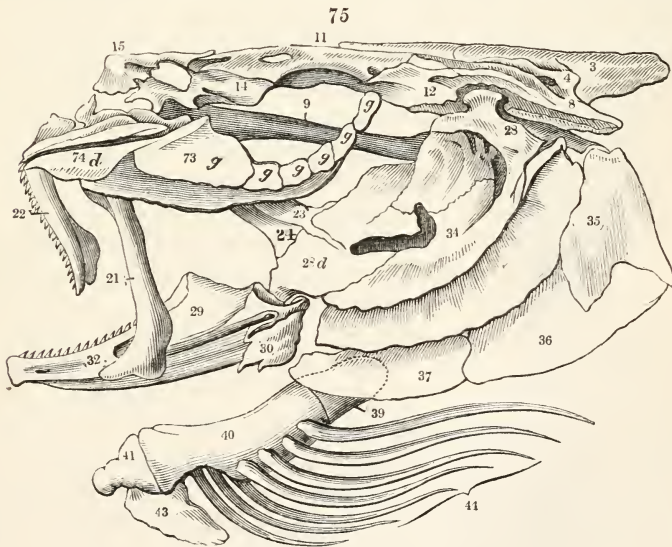
§ 30. *Skull of Osseous Fishes.*—The head is larger in proportion to the trunk in fishes than in other vertebrate classes; it is usually in form of a cone, figs. 34, 38, whose base is vertical, directed backward, and joined at once to the trunk, and whose sides are three in number, one superior, and two lateral and inferior. The cone is shorter or longer, more or less compressed or squeezed from side to side, more or less depressed or flattened from above downward, with a sharper or blunter apex, in different species. The base of the skull is perforated by the hole, called ‘foramen magnum,’ for the exit of the spinal marrow; the apex is more or less widely and deeply cleft transversely by the aperture of the mouth; the eye-sockets or ‘orbits,’ ib. 17, are lateral, large, and usually with a free and wide intercommunication in the skeleton; the two vertical fissures behind are called ‘gill-slits,’ or branchial or opercular apertures; and there is a mechanism like a door, ib., 35, 36, 37, for opening and closing them. The mouth receives not only the food, but also the streams of water for respiration, which escape by the gill-slits. The head contains not only the brain and organs of sense, but likewise the heart and breathing organs. The inferior or ‘hamal’ arches are greatly developed accordingly, and their diverging appendages support membranes that can act upon the surrounding fluid, and are more or less employed in locomotion: one pair of these appendages, ib. P, 55, 56, answers, in fact, to the fore-limbs in higher animals; and their sustaining arch, ib. 51, 52, in many fishes, also supports the homologues of the hind-limbs, v, 70. Thus brain and sense-organs, jaws and tongue, heart and gills, arms and legs, may all belong to the head; and the disproportionate size of the skull, and its firm attachment to the trunk, required by these functions, are precisely the conditions most favourable for facilitating the course of the fish through its native element.

It may well be conceived, then, that more bones enter into the formation of the skull in fishes than in any other animals; and the composition of this skull has been rightly deemed the most difficult problem in Comparative Anatomy. ‘It is truly remarkable,’ writes the gifted Oken, to whom we owe the first clue to its solution, ‘what it costs to solve any one problem in Philosophical

Anatomy. Without knowing the *what*, the *how*, and the *why*, one may stand, not for hours or days, but weeks, before a fish's skull, and our contemplation will be little more than a vacant stare at its complex stalactitic form.'

To show *what* the bones are that enter into the composition of the skull of the fish; *how*, or according to what law, they are there arranged; and *why*, or to what end, they are modified, so as to deviate from that law or archetype, will next be our aim. These points, rightly understood, yield the key to the composition of the skull in all vertebrata, and they cannot be omitted without detriment to the main end of the most elementary essay on the skeletons of animals. The comprehension of the description will be facilitated by reference to figs. 75—85; and still more if the reader have at hand the skull of any large fish.

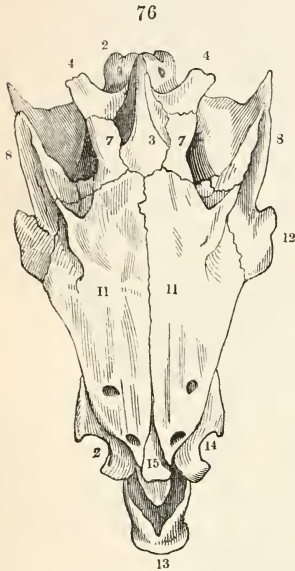
In the Cod (*Gadus morrhua*, L. fig. 75), e. g., it may be observed, in the first place, that most of the bones are, more or less, like



Skull of Cod (*Morrhua vulgaris*), Cuv.

large scales; have what, in anatomy, is called the 'squamous' character and mode of union, being flattened, thinned off at the edge, and overlapping one another; and one sees that, though the skull, as a whole, has less freedom of movement on the trunk, more of the component bones enjoy independent movements. Before we proceed to pull apart the bones, it may be well to remark, that the principal cavities, formed by their coadaptation, are the 'cranium,'

lodging the brain and the organs of hearing; the 'orbital,' and 'nasal' chambers; the 'buccal' and 'branchial' canals. Some of these cavities are not well defined. The exterior of the skull is traversed by five longitudinal crests, intercepting four channels which lodge the beginnings of the great muscles of the upper half of the trunk. The median crest is developed from the superoccipital, figs. 75, 76, 3, and sometimes also from the frontal, fig. 75, 11: the lateral crest is formed by the parietal, fig. 76, 7, and paroccipital, ib. 4: the external crest by the postfrontal, ib. 12, and mastoid, ib. 8. The lower border of the orbit, fig. 75, *g, g*, projects freely downward. The hind border of the operculum is produced into spines in some species, fig. 82.

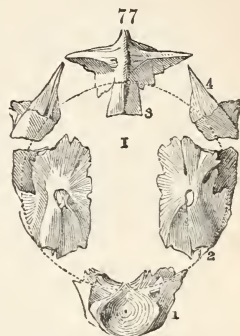


Upper surface of cranium, Perch  
(*Perca fluviatilis*)

In the analysis of the fish's skull it is best to begin at the back part; for the segments of the skeleton deviate most from the archetype as they recede in position toward the two extremes of the body. After a little practice one succeeds in detaching the bones which form the back part or base of the conical skull, and which immediately precede and join those of the trunk; we thus obtain a 'segment' or 'vertebra' of the skull. If we next proceed to separate a little the bones composing this segment, we find those that were most closely interlocked to be in number and arrangement as follows:—

Two single and symmetrical bones, and two pairs of unsymmetrical bones, forming a circle; or, if the lower symmetrical bone, which is the largest, be regarded as the base, the other five form an arch supported by it, of which the upper symmetrical bone is the key-stone, fig. 77. This answers to the 'neural' arch of the typical vertebra: the base-bone is the 'centrum,' 1; the pair of bones, which articulated with its upper surface and protected the hind division of the brain, form the 'neurapophyses,' 2; the smaller pair of bones, projecting outward, like transverse processes, are the 'diapophyses,' 4; the symmetrical bone completing the arch, and terminating above in a long crest or spine, is the 'neural spine,' 3. It will be observed that the centrum is concave at that surface which articulates with

the centrum of the first vertebra of the trunk: the opposite surface is also concave, but expanded and very irregular, in order to effect a much firmer union with the centrum of the next cranial segment in advance — great strength and fixity being required in this part of the skeleton, instead of the mobility and elasticity which is needed in the vertebral column of the trunk. It may be also observed that the ‘neurapophyses’ are perforated, like most of those in the trunk, for the passage of nerves; that the diapophyses give attachment to the bones which form the great inferior or hæmal arch; and that the neural spine retains much of the shape of the parts so called in the trunk. Nevertheless, the elements of the neural arch of this hindmost segment of the skull



Disarticulated epencephalic arch,  
viewed from behind: Cod  
(*Morrhua vulgaris*)

have undergone so much development and modification of shape, that they have received special names, and have been enumerated as so many distinct and particular bones. The centrum, 1, is called ‘basioccipital;’ the neurapophyses, 2, ‘exoccipitals;’ the neural spine, 3, ‘superoccipital;’ the diapophyses, 4, ‘paroccipitals.’ In the human skeleton all those parts are blended together into a mass, which is called the ‘occipital bone.’ In Philosophical Anatomy it is the ‘epencephalic arch,’ because it surrounds the hindmost segment of the brain called ‘epencephalon.’

The entire segment, here disarticulated, is called the ‘occipital vertebra,’ and in it we have next to notice the widely-expanded inferior or hæmal arch, fig. 81, 50, II. This consists of three pairs of bones. The first pair are bifurcate, and have two points of attachment to the neural arch, the lower prong, answering to what is called the ‘head of the rib,’ abutting upon the neurapophysis; the upper prong, answering to the ‘tubercle of the rib,’ articulating to the diapophysis. The second pair of bones are long and slender, and represent the body of the rib. The first and second piece together answer to the element called ‘pleurapophysis;’ the third pair of bones are the ‘hæmapophyses;’ these support diverging appendages consisting of many bones and rays. The special names of the above elements of the hæmal arch of the occipital vertebra are, from above downwards, ‘suprascapula,’ 50; ‘scapula,’ 51; ‘coracoid,’ 52. The inverted arch, so formed, encompasses, supports, and protects the heart or centre of the hæmal system; it is called the ‘scapular arch.’ There

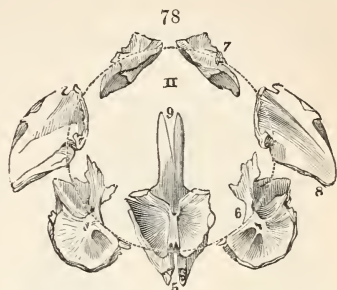


are cold-blooded animals—the gymnothorax and slow-worm, e. g.—in which this arch supports no appendage; there are others—Lepidosiren and Protopterus, fig. 41, 52—in which it supports an appendage in the form of a single many-jointed ray, ib. 57. In other fishes, the number of rays progressively increase, until, in those called ‘rays’ *par excellence*, fig. 64, they exceed a hundred in number, and are of great length, forming the chief and most conspicuous parts of the fish. The more common condition of the appendage in question is that exhibited in the Cod, fig. 34. So developed, it is called in Ichthyology the ‘pectoral fin,’ ib. p: otherwise and variously modified in higher animals, the same part becomes a fore-leg, a wing, an arm and hand.

Proceeding to the next segment, in advance, in the Cod-fish’s skull, we find that the bone which articulated with the centrum of the occipital segment is continued forward beneath a great proportion of the skull. In quadrupeds, however, the corresponding part of the base of the skull is occupied by two bones; and if the single long bone in the fish be sawn across at the part where the natural suture exists in the beast, we have then little difficulty in disarticulating and bringing away with it a series of bones similar in number and arrangement to those of the occipital segment.

In the skeletons of most animals the centrums of two or more segments become, in certain parts of the body, confluent, or they may be connate; they form, in fact, one bone, like that, e. g., which human anatomists call ‘sacrum.’ By the term ‘confluent’ is meant the cohesion or blending together of two bones which were originally separate; by ‘connate,’ that the ossification of the common fibrous or cartilaginous bases of two bones proceeds from one point or centre, and so converts such bases into one bone: this is the case, e. g., in the radius and ulna of the frog, and in its tibia and fibula. In both instances they are to the eye a single bone; but the mind, transcending the senses, recognises such single bone as being essentially two. In like manner it recognises the ‘occipital bone’ of man as essentially four bones; but these have become ‘confluent,’ and were not ‘connate.’ The centrums of the two middle segments of the fish’s skull are connate, and the little violence above recommended is requisite to detach the penultimate segment of the skull. When detached, the bones of it are seen to be so arranged as to form a neural and a hæmal arch. In the neural arch, fig. 78, the centrum, neurapophyses, diapophyses, and neural spine are distinct: moreover, the neural spine in the Cod, and many other fishes, is bifid, or split at the median line. The centrum is called ‘basiphœnoid,’ 5;

the neurapophysis, 'alisphenoid,' 6; the neural spine, 'parietal,' 7; and the diapophysis, 'mastoid,' 8. The alisphenoids protect the sides of the optic lobes, and the rest of the penultimate segment of the brain called 'mesencephalon;' the mastoids project outward and backward as strong transverse processes, and give attachment to the piers of the great inverted hæmal arch. Before noticing its structure, I may remark that, in the recent Cod-fish, the case, partly gristly, partly bony, which contains the organ of hearing, is wedged between the last and penultimate neural arches of the skull. The extent to which the ear-case is ossified varies in different fishes, but the bone is always developed in the outer-wall of the case. In the Cod it is unusually large, and is called 'petrosal,' fig. 81, 16; in the Perch, fig. 84, 16, and Carp, fig. 83, 16, it is smaller: it forms no part of the segmented neuroskeleton. In the acoustic organ which it contributes to enclose, there is a body as hard as shell, like half a split almond: it is the 'otolite,' fig. 81, 16.



Disarticulated mesencephalic arch, viewed from behind; Cod (*Morrhua vulgaris*)

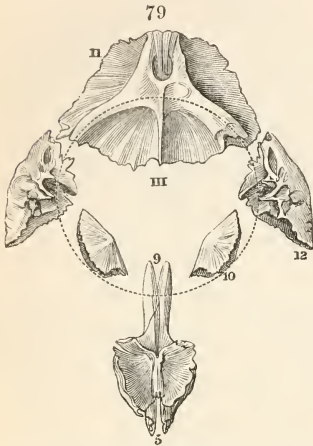
The hæmal arch consists of a pleurapophysis and a hæmapophysis on each side, and a hæmal spine; the pleurapophysis is in two parts, the upper one called 'stylohyal,' ib. 38; the lower one called 'epihyal,' ib. 39; the hæmapophysis is called 'ceratohyal,' ib. 40. The hæmal spine is subdivided into four stumpy bones, called collectively 'basihyal,' ib. 41; and which, in most fishes, support a bone directed forward, entering the substance of the tongue, called 'glossohyal,' ib. 42; and another bone directed backward, called 'urohyal,' ib. 43.

The ceratohyal part of the hæmapophysis supports an appendage, or rudimental limb, called 'branchiostegal,' fig. 81, 44, answering to the pectoral fin diverging from the hæmal arch, in the adjoining occipital segment.

The penultimate segment of the skull above described is called the 'parietal vertebra;' the neural arch is called 'mesencephalic;' and the hæmal arch is called 'hyoidean' in reference to its supporting and subserving the movements of the tongue.

The next segment, or the second of the skull, counting backward, can be detached from the foremost segment without dividing any bone. It is then seen to consist, like the third and fourth

segments, of two arches and a common centre; but the constituent bones have been subject to more extreme modifications. The centrum, called 'presphenoid,' fig. 79, 9, is produced far forward, slightly expanding; the neurapophyses, called 'orbito-



Disarticulated prosencephalic arch, Cod  
(*Morrhua vulgaris*)

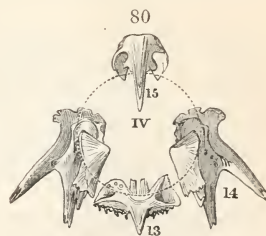
sphenoids,' ib. 10, are small semi-oval plates, protecting the sides of the cerebrum; the neural spine, or key-bone of the arch, called 'frontal,' ib. 11, is enormously expanded, but in the Cod is single; the diapophyses, called 'post-frontals,' ib. 12, project outward from the hinder angles of the frontal, and give attachment to the piers of the inverted hæmal arch. The first bone of this arch is common in Fishes to it and to that of the last described vertebra, being the bone called 'epitympanic,' fig. 81, 25; this modification is called for by the necessity of consentaneous movements of the two inverted arches, in

connection with the deglutition and course of the streams of water required for the branchial respiration. The hæmal arch of the present segment—enormously developed—is plainly divided primarily on each side into a pleurapophysis and hæmapophysis; for these elements are joined together by a movable articulation, whilst the bones into which they are subdivided are suturally interlocked together. The pleurapophysis is so subdivided into four pieces; the upper one, articulating with the postfrontal and mastoid—the diapophyses of the two middle segments of the skull—is called 'epitympanic,' ib. 25; the hindmost of the two middle pieces is the 'mesotympanic,' ib. 26; the foremost of the two middle pieces is the 'pretympanic,' ib. 27; the lower piece is the hypotympanic, ib. 28; this presents a joint-surface, convex in one way, concave in the other, called a 'ginglymoid condyle,' for the hæmapophysis, or lower division of the arch. In most air-breathing vertebrates—the Serpent, fig. 97, e.g.—the pleurapophysis resumes its normal simplicity, and is a single bone, 28, which is called the 'tympanic;' in the eel-tribe, as in the Batrachia, figs. 43, 72, *g, h*, it is in two pieces. The greater subdivision, in more actively breathing Fishes, of the tympanic pedicle, gives it additional elasticity, and by their overlapping, interlocking junction, greater resistance against fracture; and

these qualities seem to have been required in consequence of the presence of a complex and largely developed diverging appendage, which forms the framework of the principal flap or door, called 'operculum,' figs. 81, 84, 34-37, that opens and closes the branchial fissures on each side. The appendage in question consists of four bones; the one articulated to the tympanic pedicle is called 'preopercular,' ib. 34; the other three are, counting downward, the 'opercular,' ib. 35; the 'subopercular,' ib. 36; the 'interopercular,' ib. 37. The hæmapophysis is subdivided into two, three, or more pieces, in different fishes, suturally interlocked together; the most common division is into two subequal parts, one presenting the concavo-convex joint to the pleurapophysis, and called 'articular,' ib. 29; the other, bifurcated behind to receive the point of 29, and joining its fellow at the opposite end, to complete the hæmal arch: it supports a number of the hard bodies called 'teeth,' and hence it has been termed the 'dentary,' ib. 32. In the Cod there is a small separate bone, below the joint of the articular, forming an angle there, and called the 'angular piece,' fig. 75, 30.

In consequence of this extreme modification, in relation to the offices of seizing and acting upon the food, the pair of hæmapophyses of the present segment of the skull have received the name of 'lower jaw,' or 'mandible' (*mandibula*). The hæmal arch is, hence, called 'mandibular:' the neural arch 'prosencephalic:' the entire segment is called the 'frontal vertebra.'

The first segment, forming the anterior extremity of the neuroskeleton, like most peripheral parts, is that which has undergone the most extreme modifications. The obvious arrangement, nevertheless, of its constituent bones, when viewed from behind, after its detachment from the second segment, affords one of the most conclusive proofs of the principle of adherence to common type which governs all the segments of the neuroskeleton, whatever offices they may be modified to fulfil. The neural arch, fig. 80, is plainly manifested, but is now reduced to its essential elements—viz., the centrum, the neurapophyses, and the neural spine. The centrum is expanded anteriorly, where it usually supports some teeth on its under surface in fishes; it is called the 'vomer,' ib. 13. The neurapophyses are notched (in the Cod), or perforated (in the Sword-fish), by the crura or prolongations of the brain, which expand into its anterior division, called rhinencephalon, or

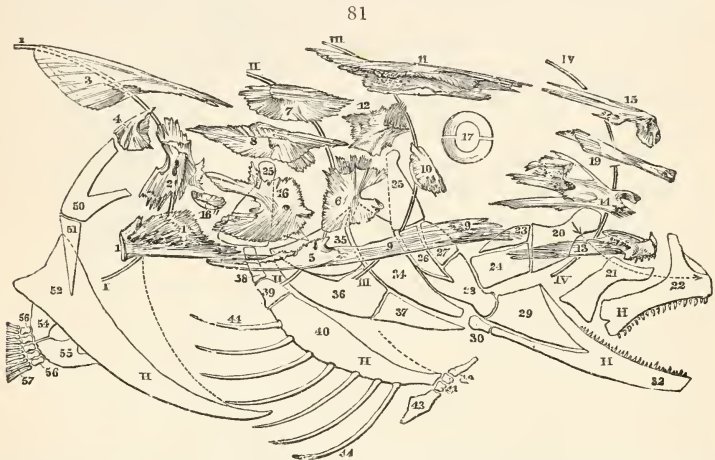


Disarticulated rhinencephalic arch,  
Cod (*Morrhua vulgaris*)



‘olfactory lobes’; the special name of such neuropophysis is ‘pre-frontal,’ *ib.* 14. The neural spine is usually single, sometimes cleft along the middle; it is the ‘nasal,’ *ib.* 15.

The hæmal arch, *fig.* 81, 20–22, II, is drawn forward, so that its apex, as well as its piers, are joined to the centrum (vomer), and usually also to the neural spine (nasal), closing up anteriorly the neural canal. The pleurapophyses are simple, short, sending backward an expanded plate; they are called ‘palatines,’ *ib.* and *fig.* 84, 20. The hæmapophyses are simple, and their essential part, intervening between the pleurapophysis and hæmal spine, is



Side view of cranial vertebrae and sense-capsules; the hæmal arches, II, III, in outline, *Cod (Morrhua vulgaris)*

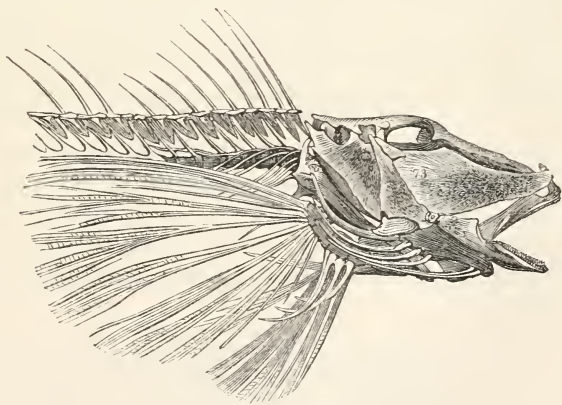
short and thick; but they send a long process backward; this element is called ‘maxillary,’ *ib.* 21. The hæmal spine, cleft at the middle line, sends one process upward of varying length in different fishes, and a second downward and backward, and its under surface is beset with teeth in most fishes: it is called ‘premaxillary,’ *ib.* 22. Each pleurapophysis supports a ‘diverging appendage,’ consisting commonly of two bones: the outer one, which fixes the present hæmal arch to the succeeding one, is called ‘pterygoid,’ *figs.* 75, 81, 24; the inner one is the ‘entopterygoid,’ *ib.* 23. The entire segment is called the ‘nasal vertebra;’ its neural arch is the ‘rhinencephalic;’ its hæmal arch, forming what is termed the upper jaw (*maxilla*), is called the ‘maxillary’ arch and appendages.

On reviewing the arrangement of the bones of the foregoing segments, one cannot but be struck by the strength of the arches which protect and encompass the brain, and by the efficiency of that

arrangement which provides such an arch for each primary division of the brain; and a sentiment of admiration naturally arises on examining the firm interlocking of the extended sutural surfaces, and especially of those uniting the proper elements of the arch with the buttresses wedged in between the piers and keystone, and to which buttresses (diapophyses) the larger hæmal arches are suspended.

In addition to the parts of the neuroskeleton, the bones of the head include the ossified part of the ear-capsule, 'petrosal,' fig. 81, 16, already mentioned; an ossified part of the eye-capsule, commonly in two pieces, 'sclerotals,' ib. 17; and an ossified part of the capsule of the organ of smell, 'turbinal,' ib. 19. Another assemblage of splanchnoskeletal bones support the gills, and are in the form of slender bony hoops, called 'branchial arches,' fig. 85, 48, 49. They are partly supported by the hyoidean arch. Amongst the bones of the muco-dermal system, may be noticed those that circumscribe the lower part of the orbit, fig. 75, *g, g*; of which the anterior, ib. 73, is pretty constant in the vertebrate series, and is called 'lacrymal.' In fishes they are called 'suborbitals,' and are occasionally present in great numbers, as, e. g., in the Tunny, or developed to enormous size as in the Gurnard, fig. 82, and allied fishes, thence called 'mail-checked.' A similar

82



Fore part of the skeleton of the Gurnard (*Trigla Lyra*)

series of bones called 'supertemporals' sometimes overarches the temporal fossa.

At the outset of the study of Osteology it is essential to know well the numerous bones in the head of a fish, and to fix in the memory their arrangement and names. The latter, as we have

seen, are of two kinds, as regards the bones of the neuroskeleton: the one kind is 'general,' indicative of the relation of the skull-bones to the typical segment, and which names they bear in common with the same elements in the segments of the trunk; the other kind is 'special,' and bestowed on account of the particular development and shape of such elements, as they are modified in the head for particular functions. A great proportion of the bones in the head of a fish exist in a very similar state of connection and arrangement in the heads of other vertebrates, up to and including man himself. No method could be less conducive to a true and philosophical comprehension of the vertebrate skeleton than the beginning its study in man — the most modified of all vertebrate forms, and that which recedes furthest from the common pattern. Through an inevitable ignorance of that pattern, the bones in Anthropotomy are indicated only by special names more or less relating to the particular forms these bones happen to bear in man; such names, when applied to the tallying bones in lower animals, losing that significance, and becoming arbitrary signs. Owing to the frequent modification by confluence of the human bones, collections of them, so united, have received a single name, as, e. g. 'occipital,' 'temporal,' &c.; whilst their constituents, which are usually distinct vertebral elements, have received no names, or are defined as processes, e. g. 'condyloid process of the occipital bone,' 'styloid process of the temporal bone,' 'petrous portion of the temporal bone,' &c. The classification, moreover, of the bones of the head in Human Anatomy, viz. into those of the cranium and those of the face, is artificial or special, and consequently defective. Many bones which essentially belong to the skull are wholly omitted in such classification.

In regard to the archetype skeleton, fishes, which were the first forms of vertebrate life introduced into this planet, deviate the least therefrom; and according to the foregoing analysis of the bones of the head, it follows that such bones are primarily divisible into those of—

The Neuroskeleton;  
 The Splanchnoskeleton;  
 The Dermoskeleton.

The neuroskeletal bones are arranged in four segments, called

The Occipital vertebra;  
 The Parietal vertebra;  
 The Frontal vertebra;  
 The Nasal vertebra.

Each segment consists of a 'neural' and a 'hæmal' arch.  
(Fig. 81, N, II.) The neural arches are—

- N I. Epencephalic arch (bones Nos. 1, 2, 3, 4);
- N II. Mesencephalic arch (5, 6, 7, 8);
- N III. Prosencephalic arch (9, 10, 11, 12);
- N IV. Rhinencephalic arch (13, 14, 15).

The hæmal arches are—

- H I. Scapular arch (50-52);
- H II. Hyoidean arch (38-43);
- H III. Mandibular arch (28-32);
- H IV. Maxillary arch (20-22).

The diverging appendages of the hæmal arches are—

1. The Pectoral (54-57);
2. The Branchiostegal (44);
3. The Opercular (34-37);
4. The Pterygoid (23-24).

The bones or parts of the splanchnoskeleton which are intercalated with or attached to the arches of the true vertebral segments, are—

- The Petrosal (16) or ear-capsule, with the otolite, 16'';
- The Sclerotol (17) or eye-capsule;
- The Turbinal (19) or nose-capsule;
- The Branchial arches (45-49);
- The Teeth.

The bones of the dermoskeleton are—

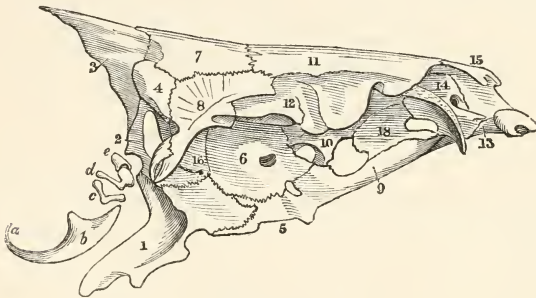
- The Supratemporals (74);
- The Postorbitals (72);
- The Superorbitals (71);
- The Suborbitals (73);
- The Labials (75), and others which will be pointed out in certain ganoid fishes.

Such appears to be the natural classification of the parts which constitute the complex skull of Osseous Fishes.



The term 'cranium' might well be applied to the four neural arches collectively, figs. 76, 83; but would exclude some bones called 'cranial,' and include some called 'facial,' in Human Anatomy. In a side view of the naturally connected bones of those arches, such as is shown in the Carp, fig. 83, the upper part of the cranium is formed by the neural spines called superoccipital 3, parietal 7, frontal 11, and nasal 15; the lower part by the centrums called basioccipital 1, basisphenoid 5, presphenoid 9, and vomer 13: the side-walls by the neurapophyses called exoccipital 2, alisphenoid 6, orbitosphenoid 10, and prefrontal 14. Between 2 and 6 is intercalated the petrosal 16: between the fore part of 9 and 10 is the 'interorbital 18,' which is an inconstant ossification in fishes. The outstanding or transverse processes are the paroccipital 4, the mastoid 8, and the postfrontal 12.

83

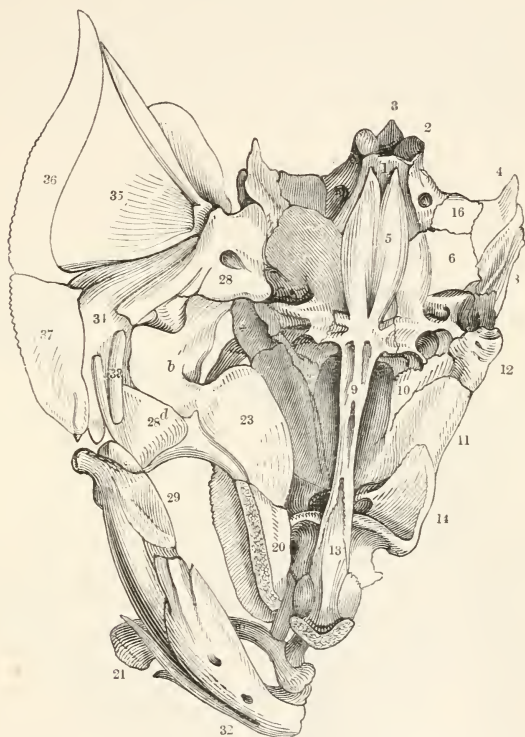


Cranium of a Carp.

In the Carp the parietals meet and unite upon the vertex by a 'sagittal' suture: in most osseous fishes, as in the Cod and Perch, figs. 76, 77, they are separated by the junction of the superoccipital, 3, with the very large frontals, 11, 11. At the base of the skull may be seen, in the Perch, fig. 84, the basioccipital 1, the articular processes of the exoccipitals 2, and the spine-shaped end of the superoccipital 3. The paroccipital 4, is separated below from the exoccipital by the petrosal 16. The basi-presphenoid, 5 and 9, carries forward the bodies of the vertebræ to the vomer 13, which is expanded and dentigerous anteriorly, as the bodies of the cervical vertebræ support teeth in the *Deirodon* (p. 57). The alisphenoids 6, the orbitosphenoids 10, and the prefrontals 14, are attached to the sides of the basal elements; more externally are seen the frontal 11, postfrontal 12, mastoid 8, and paroccipital 4. On the left side are shown the palatine 20, the entopterygoid

23, and external to it the pterygoid abutting upon the hypotympanic, 28 *d*: between this and the epitympanic, 28, are the mesotympanic, 38, and the pretympanic *b*. The preopercular, 34, runs parallel with, strengthens, and connects together the divisions

84



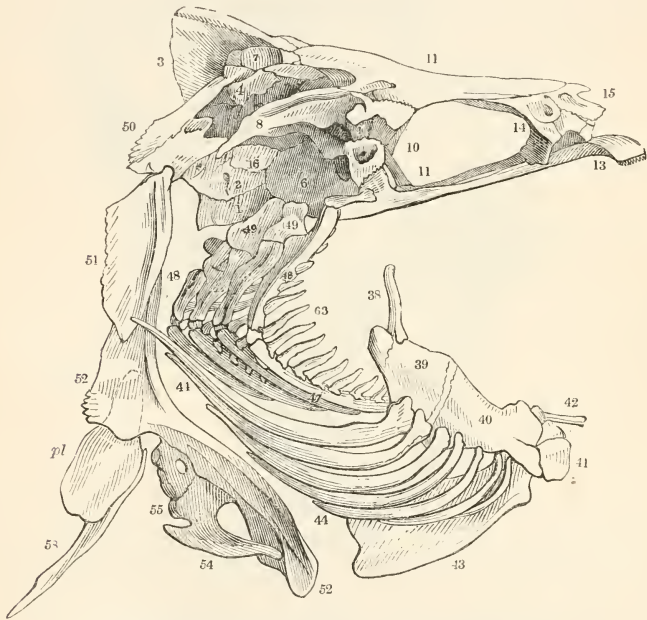
Base of the skull with left side of mandibular arch and its opercular appendage, Perch (*Perca fluviatilis*)

of the tympanic pedicle: it supports the opercular, 35, the subopercular, 36, and the interopercular, 37. In the mandibular ramus the articular is marked 29, and the dentary 32. The free end of the maxillary is seen at 21.

In fig. 85 the maxillary and mandibular arches and appendages are removed, the stylohyal, 38, having been detached from the epitympanic. It resumes its normal attachment to its segment when the special branchial apparatus becomes abrogated, as in the advanced batrachian, fig. 71, in which we saw the change of position, as contrasted with the earlier piscine condition of the larva, fig. 69 A. In the complex and ossified hyoidean arch of

fishes we find, after the stylohyal 33, the epihyal 39, the ceratohyal 40, and basihyal 41; to which may be articulated a glossohyal 42, and a urohyal 43: this is a large compressed lamelliform bone in the Perch. Seven branchiostegal rays, 44, are articulated to the epi- and cerato-hyals. Four branchial arches are attached to the base of the cranium. The first consists of the ceratobranchial, 47, and epibranchial, 48, elements: both of which support a series of processes, 63, directed towards the cavity of the mouth and defending the entry to the branchial fissures. The second and third arches are connected above by the pharyngo-

85



Hyobranchial and scapular arches, Perch (*Perca fluviatilis*)

branchial elements, 49, to the cranium; and these elements usually support teeth. The gills are attached to grooves on the outer side of the epi- and cerato-branchials; the arches being closed below by the 'basibranchials' which are attached to the hyoid. The suprascapula, 50, is attached by its lower branch to the basioccipital, and by its upper one to the paroccipital, 4. The scapula, 51, supports the coracoid, 52, to which the clavicle, 58, is attached, the relative position of which to the coracoid becomes changed as the scapular arch is detached from its natural con-

nection and displaced backward. The humeral segment of the fore limb is rarely developed in fishes; the radius, 54, and ulna, 55, are directly articulated with the coracoid, and are commonly much more broad than long.

Some of the special characters and modifications of the bones of the head will next be briefly noticed.

The articular cup for the atlas varies from the deep conical excavation seen, fig. 77, 1, in the Cod, to the almost flat surface in the Halibut; it is rare to find, as in the Pipe-fish (*Fistularia*), the basioccipital presenting a convex surface for articulation with the body of the atlas; or to find this centrum confluent with the basioccipital, as in *Polypterus*. In many fishes the under part of the basioccipital is expanded and excavated; in the Carp, the under part is produced into a broad triangular plate, fig. 83, 1, which supports the large upper pharyngeal grinding tooth; in the ganoid *Lepidosteus*, the basioccipital develops two plates from its upper and outer angles, which complete the foramen magnum and support the exoccipitals above. The exoccipitals, fig. 77, 2, are perforated for the passage of the nervi vagi, sometimes for the first spinal or hypoglossal nerve; the foramina being unusually large in the Carp tribe, fig. 83, 2, where they relate also to the connection of the air-bladder with the organ of hearing, by means of the ossicles, *a*, *b*, *c*, *d*, and *e*.

In some fishes, e.g. *Perca*, fig. 84, 2, the exoccipitals send backward articular processes modified to allow a slight movement upon the anterior articular processes of the atlas. Like the neurapophyses of the trunk in some fishes (e.g. *Lepidosiren*, *Thynnus*, *Xiphias*), the bases of the exoccipitals expand, and meet upon the upper surface of the basioccipital, and immediately support the medulla oblongata.

The superoccipital, fig. 77, 3, usually sends upward and backward a strong compressed spine from the whole extent of the middle line, and a transverse 'superoccipital' ridge outwards from each side of the base of the spine, to the external angles of the bone. In most fishes this bone advances forward and joins the frontal, pushing aside, as it were, the parietals, as in fig. 76, 3; in *Balistes* the produced part of the superoccipital is even wedged into the hinder half of the frontal suture. In the Carp, on the contrary, the anterior angle of the superoccipital is truncated, forming the base of the triangle, and is articulated by a lamboidal suture to the parietal bones, fig. 83, 7, which here meet at the mid-line of the skull, and the upper part of the occipital spine is low and flattened. The superoccipital is also separated



from the frontal by the parietals, in the Salmonoid, Clupeoid, Murænoïd, and most ganoid fishes; and is itself divided, in *Amia* and *Lepidosteus*, by a median suture; these modifications tell strongly against extending the homology of the superoccipital with the supernumerary 'interparietal' bone of Mammals, beyond the anteriorly produced interparietal portion; which, however, is not developed from a separate centre in Fishes.

When the skull is much compressed the occipital spine is usually very lofty, as in the Opah-fish and *Argyreosus*, fig. 38: in the Light-horseman fish (*Ephippus*) it expands above its origin into a thick crest of bone, giving the skull the appearance of a helmet; but in low flattened skulls the spine is much reduced, projecting merely backward, as in the Pike and Salmon, and being sometimes obsolete, as in the Remora. In a few instances, the broad posterior part of the superoccipital articulates with the neural arch and spine of the atlas, and sometimes, on the other hand, e.g. in the Halibut, the entire bone is pushed by the paroccipitals upon the upper surface of the skull, where it manifests the loss of symmetry by the absence of the expanded plate on the left side of the spine.

In broad and depressed skulls the paroccipital,<sup>1</sup> fig. 76, 4, forms a strong crest, and exceeds the exoccipital in size; in narrow and deep skulls the proportions of these bones are commonly reversed, and the paroccipitals sometimes disappear. In the Shad, the paroccipitals unite with the mastoids almost as in the Chelonia; and in *Polyprion* they are connate with the exoccipitals as in batrachian and crocodilian Reptiles. In *Synodus*, *Callichthys*, and *Heterobranchus*, the paroccipital is visible only at the back part, not at the upper part, of the skull. The inner surface of the paroccipital, like that of the exoccipital, is excavated for the lodgment of part of the posterior and external semicircular canal of the enormous internal organ of hearing in Fishes. The outer projecting process supports the upper fork of the first piece of the scapular arch; sometimes, as in *Ephippus*, by a distinct articular cavity. The neural parts of the occipital vertebra are those which are commonly in Fishes the most completely ossified at the expense of their primitive cartilaginous bases; and, in *Polypterus*, they become ankylosed into one piece, like the occipital bone of Anthropotomy, the superoccipital being as little developed as in *Protopterus*.

<sup>1</sup> The paroccipitals are not to be confounded with the dermal bone called 'epiotic' by Professor Huxley, in his reproduction of Müller's figure of the head of *Polypterus*, in the Government Publication, (CLXVIII.) p. 22, fig. 16.

The *basisphenoid* (figs. 78 and 84, 5) is usually bifurcate posteriorly, and more or less expanded beneath the cranial cavity; it is then continued forward (sometimes after sending out a pair of lateral processes, as in the Perch, more commonly without such processes) along the base of the interorbital space to near the fore part of the roof of the mouth: its posterior extremity is joined by a squamose suture, as in *Diodon*, to the basioccipital; or, more commonly, as in the Cod, is firmly wedged by a kind of double gomphosis into the basioccipital; its expanded part supports the petrosals and alisphenoids: the presphenoidal prolongation (figs. 83 and 84, 9) articulates with the orbitosphenoids and the ethmoid, 18, when this is ossified; and it terminates forward by a cavity receiving the pointed end of the vomer, fig. 84, 13. It is this portion of the basi-pre-sphenoid which manifests the loss of symmetry in the flat fishes (*Pleuronectidæ*), being twisted up to one side of the skull. The basi-pre-sphenoid varies in form with that of the head in general, being longest and narrowest in long and narrow skulls, and the converse. The whole of its upper surface is commonly rough for articulation with the petrosals and alisphenoids; rarely does any portion enter into the direct formation of the cranial cavity, and then, e. g. in the Cod, a small surface may support the pituitary sac. When it enters more largely into the formation of the floor of the cranial cavity, it usually sends upward a little process on each side; or, as in *Fistularia*, a transverse ridge. The basisphenoid is smooth below, where it is usually flattened or convex, but sometimes is produced downward in the form of a median ridge, and sometimes is perforated for the lodgment of certain muscles of the eyeball. In the Polypterus both ali- and orbito-sphenoids are ankylosed to the basi-pre-sphenoid, and the result is a bone that answers to the major part of the 'os sphenoides' of Anthropotomy. As two large and important hæmal arches of the head are suspended from the parapophyses of the second and third cranial vertebræ, this seems to be the condition of the fixation and coalescence of the bodies of those vertebræ in all Fishes.

In some, e. g. Perch and Carp, the base of each alisphenoid rises above the basisphenoid, and then sends inward a horizontal plate, which, meeting that of the opposite alisphenoid, forms the immediate support of the mesencephalon, and at the same time the roof of a canal, excavated in the basisphenoid, and which traverses the base of the skull, below the cranial cavity, from before backwards, opening behind at the under part of the basi-occipital; this subcranial canal exists in the Salmonoids, Sparoids,

Scomberoids, and is very remarkable in most fishes with lofty compressed skulls, as the *Ephippus*. In them it resembles, but is not homologous with, the posterior prolongation of the nasal passages in the Crocodiles, and it lodges some of the muscles of the eyeball. The form of the alisphenoids is influenced by that of the skull; when this is low and flat, their antero-posterior exceeds their vertical extent; in deep and compressed skulls they are narrow and high plates; in ordinary shaped skulls they present either a sub-circular form, and are perforated, as in the Carp, fig. 83, 6, or are reniform, the anterior border being deeply notched, as in the Cod, fig. 81, 6; they form a more definite and fixed proportion of the lateral parietes of the skull than do the petrosals, *ib.* 16, which are interposed between them and the exoccipitals; and they have their essential function in sustaining and protecting the sides of the mesencephalon, and in affording exit to the second and third divisions of the fifth pair of nerves. The alisphenoid articulates in the Cod with the petrosal posteriorly, with the orbitosphenoid anteriorly, and with the mastoid and postfrontal above. Where the alisphenoids have a greater relative size, as in the Perch, and where the less constant petrosal decreases or disappears, their connections are more extensive; they then reach the exoccipitals, and sometimes even join a small part of the basioccipital. In the incompletely ossified skulls of some fishes, e. g. the Pike and the Salmon tribe, the basal and lateral cranial bones are lined by cartilage, which forms the medium of union between them, especially the lateral ones: in better ossified fishes, e. g. the Cod, the union of the alisphenoids is by suture, partly dentated, partly squamous. In the Cod the second and third divisions of the trigeminal nerve pass out of the cranium by the anterior notch; in some other fishes they escape by foramina in the alisphenoid: a part of the vestibule and the anterior semicircular canal of the acoustic labyrinth usually encroach upon its inner concavity, whence some have deemed it to be the petrous bone. The chief variety in the parietals, figs. 76 and 83 7, has been noted in connection with the superoccipital, *ib.* 3.

In some fishes the parietal is perforated by the 'nervus lateralis,' which supplies the vertical fins. The left parietal is broader than the right in the Halibut and some other flat fishes (*Pleuronectidæ*).

The process for the attachment of the great trunk-muscles is developed from the outer margin of the mastoid, figs. 83, 85, 8; the inner side of this bone is expanded, and enters slightly into the formation of the walls of the cranial, or rather of the acoustic

cavity; its inner, usually cartilaginous, surface lodging part of one of the semicircular canals. It is wedged into the interspace of the ex- and par-occipitals, the petrosal, the alisphenoid, the parietal, the frontal, and postfrontal bones. The projecting process lodges above the chief mucous canal of the head, and below affords attachment to the epitympanic, or upper piece of the bony pedicle from which the mandibular, hyoid, and opercular bones are suspended.

The *orbitosphenoids*, figs. 83, 85, 10, are osseous plates usually of a square shape, sometimes semicircular or semielliptic, as in the Cod; larger in the *Malacopteri*, fig. 83, 10; very small in most *Acanthopteri*; and sometimes represented by a descending plate of the frontal, as in the Garpike, or by unossified cartilage, as in mail-cheeked fishes. In the Carp their bases meet, like those of the alisphenoids, above the sphenoid: when osseous matter is developed in the interorbital septum the orbitosphenoids are articulated by their under and anterior part to that bone or bones, fig. 83, 10.<sup>1</sup> The olfactory nerves pass forward by the superior interspace of the orbitosphenoids and the optic nerves escape by their inferior interspace, or by a direct perforation; and the essential functions of the orbitosphenoids relate to the protection of the sides of the cerebrum or prosencephalon, and to the transmission of the optic nerves. The orbitosphenoids frequently bound or complete the foramen ovale.

Although the *frontal* always enters into the formation of the cranial cavity, its major part forms the roof of the orbits, which accessory function is the chief condition of the great expanse of this neural spine in fishes. Single, and sending up a median crest in the Cod, the Eplippus, and some other fishes, the frontal is more commonly divided along the median line, the divisions having the form of long and broad subtriangular plates, fig. 76, 11, 11; narrower in the lofty compressed skulls, smaller in those with large orbits, and becoming greatly expanded in the fishes with small and deep-set eyes. Each frontal sends up its own crest in the Tunny,<sup>2</sup> the interspace leading to a foramen, penetrating the cranial cavity in front of the single occipital spine: a larger fontanelle exists in the Cobitis and some Siluroids between the frontal and parietal bones. In the Salamandroid fishes (e. g. *Polypterus*) each frontal sends down a vertical longitudinal plate,

<sup>1</sup> The specially developed interorbital septum, or 'cranial æthmoid' of Cuvier in the Bream and Carp, misled Bojanus into the belief that it was the body of the prosencephalic vertebra (vertebra optica).—*Isis*, 1818, p. 502.

<sup>2</sup> Reminding one of the double spine of the neural arch of the atlas in *Tetrodon*.



which rests directly upon the presphenoid, and intercepts a canal along which the olfactory 'crura' are continued forward to the prefrontals: the lateral parietes of this canal thus form not only a complete, but a double bony partition between the orbits. In the Shad a corresponding descending plate takes the place of the orbitosphenoid. In most Acanthopteri an olfactory groove is formed by short vertical descending plates from the under surface of the frontal. The midfrontal is single in the *Pleuronectidæ*, but has undergone more modification than any of the preceding bones in connection with the general distortion and loss of symmetry of the head: in the Halibut the right posterior angle is truncated, and the rest of that side scooped out, as it were, to form the large orbit of the right side: the left side of the bone retains its normal form: a median crest, a continuation of that upon the superoccipital, divides the two sides.

The *postfrontals*, figs. 75, 76, 83, 12, 12, obviously belong to the same category of vertebral pieces as the mastoids, whose prominent crest they partly underlie and complete, lending their aid in the formation of the single (e. g. Cod, Salmon), or double, (e. g. Pike) articular cavities for the tympanic pedicle: like the mastoids they are ossified in and from the primitive cranial cartilage; and their inner surface is expanded, but this less frequently enters into the formation of the cranial cavity: they form the posterior boundary of the orbit; are articulated below to the orbitosphenoid and alisphenoid, above to the frontal, and by their posterior and upper surfaces to the mastoid.

The *vomer*, figs. 83, 84, 13, is wedged into the under part of the presphenoid; its antero-lateral angles are articulated to the prefrontals; its upper surface supports the nasal bone, sometimes immediately, sometimes by an intervening ethmoidal cartilage. The palatine bones abut against the expanded anterior part of the vomer, the under side of which commonly supports teeth. The left ala of the anterior end of the vomer is chiefly developed in the Halibut and other flat fishes. In the *Lepidosteus*, the vomer is divided into two, as in *Batrachia*, by a median cleft. Although its posterior end joins obliquely to the under part of the presphenoid, it is not, therefore, less a continuation of the basicranial series than is the postsphenoid, which joins in a similar manner with the basioccipital.

The *prefrontals* defend and support the olfactory prolongations of the cerebral axis, give passage to these so-called 'olfactory nerves,' bound the orbits anteriorly, form the surface of attachment or suspension for the palatine bones, and through these for the

palato-maxillary arch: they rest below upon the presphenoid and vomer, support above the fore part of the frontal and the back part of the nasal bones, and, by their outer or facial extension, give attachment to the large antorbital or lacrymal bone. They are ossified in and from pre-existing cranial cartilage.

Such are the essential characters of the bones which Cuvier has called 'frontaux antérieures'<sup>1</sup> in Fishes, and to which I apply the name of 'prefrontal' in all classes of Vertebrate animals. In the Cyprinoids, and most Halecoids, the prefrontals form part of an interorbital septum. When anchylosis begins to prevail in the cranial bones of Fishes, the prefrontals manifest their essential relationship to the vomerine and nasal bones by becoming confluent with them: thus we recognise the prefrontals in the confluent parts of the nasal vertebra of the Conger, by the external groove conducting the olfactory nerves to the nasal capsules, and by the inferior process from which the palatine bone is suspended.<sup>2</sup> In the *Muræna*, also, the prefrontals are plainly confluent with the nasal, 15, bone, and form the well marked articular surfaces for the palato-maxillary bone. In some fishes a process of the prefrontal circumscribes the foramen by which the olfactory 'crus' finally emerges from the anterior prolongation of the cranio-vertebral canal. In the Carp this part of the brain traverses a deep notch on the inner side of the prefrontal, fig. 83, 14. In the Cod the palatine arch is chiefly but not wholly suspended to the prefrontals. The right prefrontal is the smallest in the unsymmetrical skulls of the flat-fishes.

The *nasal bone* is usually single, and terminates forward in a thick obtuse extremity. The anterior end of the nasal is deepest in those Fishes which have a small maxillary arch suspended from the cranial axis by vertical palatines, and which have a large

<sup>1</sup> 'Deux *frontaux antérieures*, qui donnent passage aux nerfs olfactifs, ferment les orbites en avant, s'appuyent sur le sphénoïde et le vomer, et donnent attache par une faeette de leur borde inférieure aux palatins.'—*Leçons d'Anat. Comp.* ii. 1837, p. 606. Compare this enunciation of the essential characters of the anterior frontals with Cuvier's descriptions of the bones to which he applies that name in other classes, and with the variable determinations of the same bones by other anatomists—*le lacrymal*, Geoffroy and Spix; *lamina cribrosa ossis ethmoïdei* of Bojanus; *seitliche reichbeine*, Meekel, Wagner. Without at present entering into the respective merits or demerits of these determinations, I shall only state that the prefrontals, under whatever names they are described, are essentially the neurapophyses of the nasal vertebra, and that the failure in the attempt to determine the special homologies of these bones may, in every case, be traced to the non-appreciation of their true general homology.

<sup>2</sup> In the Conger, Cuvier<sup>1</sup> recognises the prefrontals as persistent cartilages.

<sup>1</sup> Op. cit. (xiii.), ii. p. 235.

basiscranial canal. In some fishes, as the *Salmonidæ*, the nasal is broad but not deep: in *Istiophorus* it is long and narrow: in the *Discoboles* and *Lophobranchii* it is a short vertical compressed plate: it is altogether absent in the *Lophius*, or is represented here, as in the *Diodon*, by a fibrous membrane, retaining the primitive histological condition of the skeleton. In the Flying Gurnard the nasal has no immediate connection with the vomer; but this is a rare exception. In most fishes the nasal cavity is more completely divided by the nasal bone into two distinct lateral fossæ than in any other class of Vertebrates.

In *Amia*, *Lepidosteus*, *Polypterus*, and many extinct ganoid Fishes the nasal is divided at the median line. The horn-like projection from the fore part of the skull of the *Naseus unicornis* is formed chiefly by a process of the frontal bone, to the under part of which a small nasal is articulated.

The turbinals, or osseous capsules of the nose, are situated at the sides or above the nasal: the premaxillary and the maxillary bones are usually attached to its extremity through the medium of a symmetrical cartilage which is articulated with the fore part of the nasal bone, and extends forward to the interspace of the upper ends of the premaxillaries. This 'prenasal' cartilage often forms a septum between the two 'ossa turbinata:': it is partially ossified in the Carp.

The sense-capsules are so intercalated with the neural arches, which are modified to form cavities for their reception, that the demonstration of the skull will be best facilitated by describing them before we proceed to the hæmal arches of the cranial vertebræ.

Acoustic capsule, or *petrosal*, figs. 81, 83, 85, 16.

We have seen that the first developed cartilage upon the primitive membranous wall of the skull forms a special protecting envelope for the labyrinth, which alone constitutes the organ of hearing in Fishes (*Ammocetes*, fig. 58, 16). In the progressive accumulation of cartilaginous tissue upon the base and sides of the cranium, the ear-capsule loses its individuality, and becomes buried in the common thick basilateral parietes of the cranium. It is blended with that persistent cartilaginous part of the skull in the *Lepidosiren*; but, in the better ossified Fishes, when the osseous centres of the neurapophyses of the cranial vertebræ begin to be established in that cartilaginous basis, a distinct bone is likewise, in most cases, developed for the more express defence of the labyrinth. Since, however, functions are less specialised, less confined to the particular organ ultimately destined for their

performance in the lower than in the higher classes, we find in Fishes several bones taking part with the special acoustic capsule in the lodgment of the labyrinth; and it is only in the higher Vertebrates that the capsule, under the name of the 'petrous bone,' entirely and exclusively envelopes the labyrinth. Its ossification commences later than that of the cranial neurapophyses, in the series of Osseous Fishes: there are species (e. g. Pike) in which, after the exoccipitals, alisphenoids, and orbitosphenoids have received their destined amount of ossification, the petrosal still remains in the cartilaginous state: it is small in the Carp, fig. 83, 16, and Bream; in the Perch, figs. 84, 85, 16, it is more developed; it is somewhat larger in the flat-fish (e. g. Halibut); and in the Cod, fig. 81, 16, attains an equal size with the alisphenoid, ib. 6, which it resembles in form, except that the notched margin is posterior. Here it forms the posterior lateral wall of the cranium; articulates below with the basioccipital 1, and basisphenoid, above with the mastoid 8, and paroccipital 4, behind with the exoccipital 2, and before with the alisphenoid 6: it supports the cochlear division of the labyrinth containing the otolites. The cavity called 'otocrane' lodging the petrosal with the rest of the ear-capsule, is formed, on each side, by the exoccipital, paroccipital 4, alisphenoid 6, mastoid 8, and postfrontal 4: it is sometimes closed externally, but opens widely into the cranial cavity.

The optic capsule, or *sclerotal*, fig. 81, 17, like the acoustic capsule, is cartilaginous in Plagiostomes, and also in the semi-osseous fishes, as in most Ganoids, the Lepidosiren, the Lophius, the Lophobranchs and Plectognathes. In better ossified fishes it is bony, and commonly consists of two hollow hemispheroid pieces, each with two opposite emarginations; the inner ones circumscribing the hole, (analogous to the meatus internus of the petrosal), for the entry of the nerves and vessels to the essential parts of the organ of vision; and the outer or anterior emarginations supporting the cornea. As this part of the skeleton of the head retains its primitive fibro-membranous condition in Man, it is called 'the sclerotic coat of the eye;' and the osseous plates developed in it in Birds, many Reptiles, and Fishes, are termed 'sclerotic bones.' It bears, however, the same essential relation to the vascular and nervous parts of the organ of sight, which the petrous bone does to those parts of the organ of hearing, and which the turbinal bones do to the organ of smell: the persistent independence of the eye-capsule, which has led to its being commonly overlooked as part of the skeleton, relates to the requisite mobility and free suspension of the organ of vision. In



the Cartilaginous Fishes, however, it is articulated by means of a pedicle with the orbitosphenoid. The osseous cavity or 'orbit' lodging the eyeball is formed by the presphenoid, orbitosphenoid, frontal 11, postfrontal 4, prefrontal 14, and palatine 20, bones: it opens widely outwards, where it is, often, further circumscribed by the chain of suborbital scale-bones below, and, but less frequently, by a superorbital bone above. The bony orbits in most fishes communicate freely together, or rather with that narrow prolongation of the cranial cavity lodging the olfactory crura: but, in many *Malacopteri*, e. g. the Shads and *Erythrinus*, the *Citharinus* and *Hydrocyon*, the *Synbranchus*, and the genus *Cyprinus*, fig. 83, an osseous septum, 18, divides the orbits. In the *Amia*, *Lepidosteus* and *Polypterus* the orbits are divided by a double septum, forming the proper walls of the olfactory prolongation of the cranium, as is the case in the *Batrachia*.

The olfactory capsules, or *turbinals*, fig. 81, 19, are lodged in a cavity called 'nasal,' bounded by a variable number of bones, of which the vomer, ib. 13, the prefrontals, ib. 14, and the nasals, ib. 15, are the most constant: in many bony fishes the nasal chamber is closed behind by cartilage, which partly forms the interorbital septum; but in which, in some species, a slender symmetrical bifurcate (Perch) or subquadrate ossicle is developed; in the Cyprinoid (fig. 83, 18) and Siluroid Fishes, it articulates below to the presphenoid, behind and above to the orbitosphenoids, and above and before to the frontals and prefrontals, forming the chief part of the interorbital septum. The capsules of the terminal pituitary expansion of the organ of smell are cartilaginous in the Plagiostomes, Chimæroids, in most Ganoids, and in the Lepidosiren. They form a single tube, with interrupted cartilaginous parietes, like a trachea, in several of the Cyclostomes. The turbinals are developed for the more immediate support of each olfactory capsule, in osseous fishes; they are generally thin, more or less elongated, and coiled scales; situated at the sides of the nasal bone and of the ascending processes of the premaxillaries; usually free, but in the Gurnards articulated with the prefrontals and nasal, and in the Cock-fish (*Argyreiosus*) suspended above the nasal bone, from the anterior prominence of the frontal spine.

The palato-maxillary arch, fig. 81, 20, 21, 22, II, presents a simple and intelligible condition in the Lepidosiren and Plagiostomous fishes; in all it is completed or closed at one point only, viz., where the premaxillaries meet or coalesce, fig. 67, 22. The palatine bones are the piers of this inverted arch, and their points of suspension are their attachments to the prefrontals, the vomerine, and the

nasal bones. The arch is completed by the maxillary and premaxillary bones, the symphysis of the latter forming its apex; and it is inclined forward, nearly or quite parallel with the base of the skull; which, in most fishes, extends to the apex of the arch, and in some far beyond it, being usually more or less closely attached to it. In air-breathing Vertebrates the arch is more dependent, circumscribing below the nasal or respiratory canal. The pterygoid bones project backward and outward as the appendages of the palato-maxillary arch, *ib.* 23. Both maxillary and intermaxillary bones tend by their peculiar developement and independent movement in bony fishes to project freely outward, downward, and backward. We find, at least, that the general form, position, and attachments of the single and simple palato-maxillary arch, in the *Lepidosiren* or *Cestracion*, are represented in most osseous fishes, by their several detached bones, the names of which have been just mentioned.

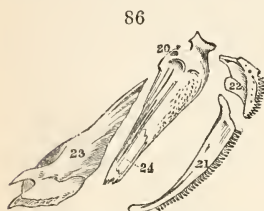
The *palatine* (pleurapophysis of nasal vertebra, *figs.* 81, 84, 20) is an inequilateral triangular bone, thick and strong at its upper part, which sends off two processes: one is the essential point of suspension of the palato-maxillary arch, and articulates with the prefrontal and vomer at their point of union; the other is convex, and passes forward to be articulated to a concavity in the superior maxillary, to which, in all Fishes, it affords a more or less moveable joint. In the Parrot-fishes and *Diodons* the articulation is quite analogous to that of the mandible below with the tympanic pedicle. In the *Lepidosteus*, *Amia*, and most *Ganoids*, it is by a suture. In the *Shad* the palatine articulates with the premaxillary as well as the maxillary. In the *Mormyrus* the palatines meet, and unite together at the median line. The posterior border is joined to the entopterygoid, *fig.* 84, 23, and its outer angle to the pterygoid. The palatine contributes to form the floor of the orbit and the roof of the mouth; in many fishes it supports teeth, but is edentulous in the *Cod*. It varies much in form in different species; is slender and elongated in the wide-mouthed voracious fishes as the *Pike*, and is short and broad in the broad-headed, small-mouthed fishes.

The *maxillary* (*hæmapophysis* of nasal vertebra, *fig.* 81, 21) is usually a small edentulous bone,<sup>1</sup> concealed in a fold of the skin between the palatine and premaxillary: it lies, in the *Cod*, *fig.* 75, 21, posterior to and parallel with the premaxillary, 22, which it resembles in form, but is longer and thinner in most osseous fishes:

<sup>1</sup> The *Os mystaceum* of ichthyotomists.

the upper, usually bifurcate, end of the maxillary, forms a socket on which the ascending or nasal process of the premaxillary glides; a posterior tubercle at this end is attached to the palatine, and ligaments connect the same expanded end to the nasal, the turbinal, the vomer, and the premaxillary: the lower and hinder expanded end of the bone is attached by strong elastic ligament, in which a labial gristle is commonly developed, to the lower jaw.

In the Salmon and Herring tribe, the Sudis, fig. 86, 21, *Amia*, and most Ganoids, the maxillary supports teeth. In the *Plectognathi* (Globe-fish and File-fish), the maxillaries coalesce wholly or in part with the premaxillaries. In the *Lepidosteus* the contrary condition prevails: the premaxillary and maxillary bones constitute, indeed, a single dentigerous arch or border of the upper jaw, as in fig. 86, but are subdivided into many bony pieces, a condition which seems to



Disarticulated bones of palato-maxillary arch (*Arapaima gigas*)

have prevailed in some of the ancient extinct ganoid fishes. In the *Polypterus* the maxillary is large and undivided on each side; it supports teeth, and sends inward a palatine plate to join the vomer and the palatine bone; thus acquiring a fixed position and all the normal features of the bone in higher animals. The maxillary bone is very diminutive in the Siluroid fishes, and appears, with the premaxillary, to be entirely wanting in certain Eels (*Muraenidae*).

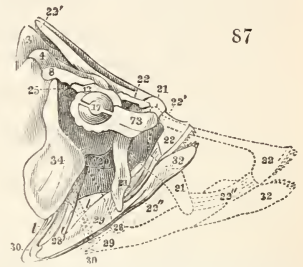
The *premaxillary* (hæmal spine of nasal vertebra, figs. 75, 81, 22), one of a symmetrical pair in the Cod and most other osseous fishes, is moderately long and slender, slightly curved, expanded and notched at both extremities: the anterior end is bent upward, forming the nasal process, and is attached by lax ligaments to the nasal bone and prenasal cartilage, to the palatine, and to the anterior ends of the maxillary bones. The premaxillaries are movably connected to each other by their anterior ends; the nasal processes are separated by the prenasal cartilage, the lower or outer branches project freely downward and outward, fig. 75, 22: the labial border of each premaxillary is beset with teeth, whilst the maxillary bone is quite edentulous in most osseous fishes, as in the Cod, ib. 21. In *Diodon* the premaxillaries and their lamellated dental apparatus coalesce and constitute a single symmetrical beak-shaped bone: the premaxillary is also single in *Mormyrus*. The confluent premaxillaries constitute the sword-like anterior prolongation of the snout in *Xiphias*, and are firmly

and immovably articulated with the prenasal and maxillary bones, in both the Sword-fish and the Garpike. The premaxillaries are commonly more extended in the transverse than in the vertical direction; but there are many examples in Fishes where their development is equal in both directions. The vertical extension, which forms the nasal branch of the premaxillary, is of unusual length in the fishes with protractile snouts, as, for example, in the Picarels (*Menidæ*), the Dories (*Zeus*), and in certain Wrasses, as *Coricus*, and especially the *Epibulus*, or *Sparus insidiator* of Pallas, fig. 87, 22. In this fish the nasal branch of the inter-

maxillary, ib. 22', plays in a groove on the upper surface of the skull, and reaches as far back as the occiput when the mouth is retracted. The descending or maxillary branch is attached by a ligament, ib. 22'', longer than itself, to the lower end of the maxillary bone, ib. 21, and consequently draws forward that bone, together with the lower jaw, to which the same end of the maxillary is attached by liga-

ment, when the long nasal branch of the premaxillary glides forward out of the epicranial groove. The protractile action is further favoured by a peculiar modification of the hypotympanic, ib. 28, which, by its great length and movable articulation at both ends, cooperates with the long premaxillary in the sudden projection of the mouth, by which this fish seizes the small, agile, aquatic insects that constitute its prey. In the *Lophius* the nasal processes of the premaxillaries enter a groove in the frontal: in the *Uranoscopus* they also reach the frontal, playing upon the small nasal bone and pressing it down, as it were, upon the vomer. In the *Dactylopterus* they penetrate between the nasal and the vomer, and play in the cavity of the rhinencephalic arch.

The diverging appendage of the palato-maxillary arch consists, in Fishes, of the pterygoid and entopterygoid bones, which, as they are the least important parts of the arch, so are they the least constant: they are wanting, for example, in the *Synodon*, *Platystacus*, *Hydrocyon*, and *Lophius*; are connate with, or indistinguishable from, the palatine in most Salmonoids and Eels; whilst in the *Muræna* a single bone, the pterygoid, exists, but is disconnected with the maxillary arch. Most Fishes, however, present, as in the Cod, the two bones above named. The entopterygoid is edentulous in the Perch, fig. 84, 23, Cod, and most



Mechanism of protraction and retraction of the mouth (*Epibulus insidiator*)



other fishes, but is richly beset with teeth in the *Arapaima gigas*. It principally constitutes the floor of the orbit, its breadth depending much upon the depth of that cavity; it sometimes is joined by its median margin to the vomer and presphenoid, as in the Cod-tribe, Carp-tribe, and Flat-fishes; and to the basisphenoid in *Lepidosteus*, *Erythrinus*, and *Polypterus*, and then divides the orbit from the mouth; but more commonly a vacuity here exists in the bony skull, filled up only by mucous membrane in the recent fish; in *Upeneus*, *Polyprion*, and *Cheilinis*, for example, the entopterygoid does not join the basisphenoid.

The pterygoid forms in the Cod, fig. 75, 24, an inequilateral triangular plate, but more elongated than the palatine, with which it is dovetailed anteriorly; it becomes thicker towards its posterior end, which is truncated and firmly ingrained with the anterior border of the hypotympanic; its lower border is smooth, thickened, and concave; edentulous in the Cod, but more frequently supporting teeth, as in the Perch. The pterygoid and palatine appear to form one bone in the great Sudis, (*Arapaima gigas*, fig. 86, 20, 24): and they are confluent in the Eel tribe.

The ten bones of which the palato-maxillary arch is composed in Osseous fishes are, in the Cod and most other species, so disposed, in relation to the peculiar movements of the mouth, as to appear like three parallel and independent arches, successively attached behind one another, by their keystones, to the fore part of the axis of the skull, and with their piers or crura suspended freely downward and outward, fig. 75, 22, 21, except those of the last or pterygo-palatine arch, ib. 23, 24, which abut against the tympanic pedicles. The simplification or confluence of the two first of these spurious arches is effected in the Salmonoid Fishes, Sudis, fig. 86, &c., by the shortening of the premaxillary, and by the mode of its attachment to the maxillary, which now forms the larger part of the border of the mouth and supports teeth: the maxillaries are brought into close articulation with the palatines in the Plectognathes, and the consolidation of the whole series into its normal unity is effected in the Lepidosiren. The palatines form the true bases of the inverted arch at their points of attachment to the prefrontals; the premaxillaries constitute the true apex, at their mutual junction or symphysis; the approximation of which to the anterior end of the axis of the skull is rendered possible in fishes, by the absence of any air-passage or nasal canal; the pterygoids are the diverging appendages of the arch; but are attached posteriorly to strengthen the pedicle supporting the lower jaw, and combine its movements with those of

the upper jaw ; just as the bony appendages of one costal arch in Birds associate its movements with those of the next.

*Tympano-mandibular arch*, fig. 81, H, 25—32.—This presents its true inverted or hæmal character ; its apex or key-stone formed by the symphysial junction of the lower jaw hanging downwards freely, below the vertebral axis of the skull. The piers, or points of suspension, of the arch, are formed by the *epitympans* : each epitympanic is articulated to both the postfrontal, 12, and the mastoid, 8, and is divided artificially in fig. 81 ; its articular surface is formed in the Cod by a single elongated condyle, fig. 75, 28 ; in many other fishes by a double condyle, one for each of the above-named cranial parapophyses, fig. 84, 28. In the Diodon the upper border of the epitympanic is articulated by a deeply indented suture to the frontal, the postfrontal and mastoid bones : its posterior margin supports, as in many other fishes, a circular articular surface for the opercular bone, fig. 84, 35. Below the condyle, the epitympanic in the Cod, fig. 75, becomes compressed laterally, but is much expanded from before backward. The almost constant bifurcation of both ends of the epitympanic in osseous fishes, for articulation with two cranial parapophyses above, and suspending two inverted arches below, make it appear like a coalescence of the uppermost pieces of both those arches. In most fishes the lower end is bifid, and supports both the mandibular and the hyoidean arches ; the stylohyoid, fig. 81, 38, being attached near the junction of the epitympanic with the mesotympanic. The contiguous ribs of the Chelonia are immovably connected together to ensure fixity and strength to the carapace : the bulky apparatus suspended from the parietal and frontal vertebræ of osseous fishes demanded the additional strength in the supporting axis which is gained by the confluence of their bodies, and also by that of the proximal pieces of the pleurapophyses by which the two hæmal arches are suspended from those vertebræ. The anterior division of the epitympanic piece articulates with the preopercular, fig. 75, 34, the mesotympanic, fig. 81, 26, and pretympanic, ib. 27 ; the posterior division is again bifurcate in the Cod, supporting part of the preopercular and part of the opercular bone. A strong crest projects from its outer surface in this and many other fishes. The epitympanic is simple at both ends in the Carp tribe.

The *mesotympanic*, figs. 81, 26, 84, 38, is a slender, compressed, slightly curved, elongated bone, articulated by its upper part or base to the epitympanic and preopercular ; by its lower end to the inner side of the hypotympanic, reaching almost to the mandibular

trochlea; and by its anterior border to the pretympanic. *ib. b.* The mesotympanic is confluent with the epitympanic in the Siluroid, the Murænid, and some other fishes; but does not join the epitympanic in the *Lepidosteus*, being in that fish supported by the preopercular.

The *pretympanic*, *figs. 81, 27, 84, b*, is an oblong bony scale, with the posterior margin thickened and grooved for the reception of the fore part of the mesotympanic and the upper and fore part of the hypotympanic. It is confluent with the hypotympanic in the Conger and *Muræna*: it does not join either this or the mesotympanic in the *Lepidosteus*.

The *hypotympanic*, *figs. 81, 28, 75 and 84, 2sd*, is a triangular plate of bone, like the epitympanic reversed, bearing the articular convex trochlea for the lower jaw upon its inferior apex and with a straight base. The posterior margin of the hypotympanic is grooved for the reception of part of the preopercular, *ib. 34*, its inner side is excavated for the insertion of the pointed end of the mesotympanic, and the anterior angle is wedged between the pretympanic and the pterygoid, *24*, and is firmly united to the latter; the trochlea is slightly concave transversely, convex in a greater degree from before backwards. The Sly-bream (*Epibulus*, *Cuv.*), presents the most remarkable modification of the hypotympanic, *fig. 87, 28*; it is much elongated and slender, carrying the lower jaw at an unusual distance from the base of the skull, and it is itself movably connected at its upper end with the mesotympanic. Thus, in the extensive protractile and retractile movements of the mouth, the under jaw swings backward and forward on its long pedicle, as on a pendulum; the lower jaw being further supported or steadied in those movements by a long ligament, extending from the preoperculum to its angular piece, *ib. l, 30*.

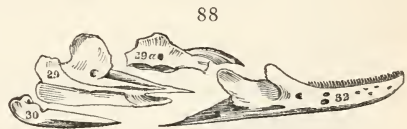
By the confluence of the meso- and epi-tympanics, and of the pre- and hypo-tympanics, in the Eel tribe, the suspensory pedicle of the lower jaw is reduced to two pieces, as in *Batrachia*. In the *Lepidosiren* it is represented, as we have seen, by a single osseous piece; but this I regard as the homologue of only the lower half of the pedicle in the *Muræna*, *viz.* the confluent pre- and hypo-tympanic pieces. This progressive simplification, or diminution of the multiplied centres of ossification of the tympanic pedicle of Fishes, even within the limits of the class, has mainly weighed with me in rejecting the Cuvierian view of its special homologies; according to which, not only the squamotemporal bone and the malar bone of higher animals, but also the 'symplectic'—a peculiar ichthyic bone—are superadded to the 'tympanic' or quadrate bone of Reptiles and Birds, in the formation of the

suspensory pedicle of the under jaw of Fishes. Ascending to the higher generalisations of homology, we see in the tympanic pedicle a serial repetition of the palatine bone; and, in both, the ribs or pleurapophyses of contiguous vertebræ specially modified for the masticatory functions of the arches they support.

The mandible, figs. 81, 84, 29, 32, is the lower portion of the arch, being articulated to the hypotympanics above, and closed by a ligamentous union or bony symphysis with its fellow at its lower end. The term 'ramus' is applied in Anthropotomy to each half of the mandible, and each ramus consists of two, three, or more pieces in different fishes. Most commonly it consists of two pieces, one (hæmapophysis proper, 29,) articulated to the suspensory pedicle, and edentulous, analogous to the maxillary; and the other (hæmal spine, 32,) completing the arch, and commonly supporting teeth, like the premaxillary. In the Cod, and some other fishes, a third small piece is superadded, at the angle of the posterior piece, fig. 75, 30. The dentary, 32, is deeply excavated, and receives a cylindrical cartilage, the remnant of the embryonal hæmal arch, fig. 69 A, d, and the vessels and nerves of the teeth. The Sudis, fig. 88, the Polypterus, and Amia, have the splint-like plate along the inner surface of the ramus, called 'splenial:' it supports teeth and develops a coronoid process. In both Sudis and Lepidosteus there is superadded a small bony piece, ib. 29 a, answering to the surangular in Reptiles.

The *Diverging Appendage* of the tympano-mandibular arch consists of the bones which support the gill-cover, a kind of short and broad fin, the movements of which regulate the passage of the currents through the branchial cavity, opening and closing the branchial aperture on each side of the head. The first of these 'opercular' bones is the preopercular, fig. 75, 34, which is usually the longest in the vertical direction. In the Gurnards, or 'mailed-checked' Fishes, fig. 82, the preopercular is articulated with the enormously developed suborbital scale bone, 73.

Three bones usually constitute the second series of this appendage: the upper one is commonly the largest and of a triangular form, thin and with radiated lines like a scale: it is the opercular, figs. 75, 84, 35: in the Cod it is principally connected with the posterior margin of the preopercular, and below with the subopercular, ib. 36; but it has usually, also, a partial attachment to the outer angle of the epitympanic, fig. 84; and is some-



Lower jaw, (*Arapaima gigas*)



times (*Diodon*, *Lophius*, *Anguilla*) exclusively suspended therefrom. In the *Lophius piscatorius* the opercular is a long and strong bone suspended vertically from the convex epitympanic condyle, and with a long and slender fin-ray proceeding from the back part of that joint. The subopercular forms the chief part of the opercular fin by its long backwardly produced lower angle. The subopercular bone in the Conger is soon reduced to a mere ray, which curves backwards and upwards like one of the branchiostegals. The opercular itself, though shorter and retaining more of its laminated form, also shows plainly, by its length and curvature in the Eels, its essential nature as a metamorphosed ray of the tympanic fin. We have seen that all the framework of this fin had the form of rays in the Plagiostomes. In *Muraena* the small opercular bones articulate only to the under half of the tympanic pedicle. The subopercular is wanting in the Shad. The lowermost bone, called the interopercular, figs. 75, 84, 37, is articulated to the preopercular above, to the subopercular behind, and usually to the back part of the mandible; it is attached, also, in the Cod, by ligament to the ceratohyoid in front. The interopercular and preopercular are the parts of the appendage which are most elongated in the peculiarly lengthened head of the *Fistularia*.

The third inverted arch of the skull is the 'hyoidean,' fig. 81, 38-41, and is suspended, in Osseous Fishes, through the medium of the epitympanic bone, 25, to the mastoid, 8; showing it to be the hæmal arch of the parietal vertebra. The first portion of the arch, stylohyal, fig. 85, 38, is a slender styloform bone, which is attached at the upper end by ligament to the inner side of the epitympanic, close to its junction with the mesotympanic, and at the lower end to the apex of a triangular plate of bone, which forms the upper portion of the 'great cornu.' I apply to this second piece, which is pretty constant in fishes, the name of epihyal, ib. 39: the third longer and stronger piece is the ceratohyal, ib. 40. The keystone or body of the inverted hyoid arch is formed by two small subcubical bones on each side, the basihyals, ib. 41. These complete the bony arch in some fishes: in most others there is a median styloform ossicle, extended forward from the basihyal symphysis into the substance of the tongue, called the glosso-hyal, ib. 42; and another symmetrical, but usually triangular, compressed bone, which expands as it extends backwards, in the middle line, from the basihyals; this is the urohyal, ib. and fig. 75, 43. It is connected with the symphysis of the coracoids, which closes below the fourth of the cranial inverted arches, and it thus forms the isthmus which

separates below the two branchial apertures. In the Conger the hyoidean arch is simplified by the persistent ligamentous state of the stylohyal, and by the confluence of the basihyals with the ceratohyals; a long glossohyal is articulated to the upper part of the ligamentous symphysis, and a long compressed urohyal to the under part of the same junction of the hyoid arch. The glossohyal is wanting in the *Muraenophis*.

The *Diverging Appendage* of the hyoidean arch retains the form of simple, elongated, slender, slightly curved rays, articulated to depressions in the outer and posterior margins of the epi- and cerato-hyals: they are called 'branchiostegals,' or gill-cover rays, fig. 85, 44, because they support the membrane which closes externally the branchial chamber. The number of these rays varies, and their presence is not constant even in the bony Fishes: there are but three broad and flat rays in the Carp; whilst the clupeoid *Elops* has more than thirty rays in each gill-cover: the most common number is seven, as in the Cod, fig. 75, 44. They are of enormous length in the Angler, and serve to support the membrane which is developed to form a great receptacle on each side of the head of that singular fish.

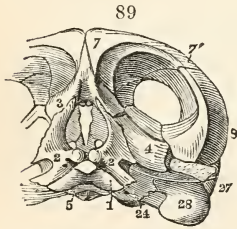
The fourth cranial inverted arch, fig. 81, 50—52, II, is that which is attached to the paroccipital; or to the paroccipital and mastoid; or, as in the Cod, to the paroccipital and petrosal; or as in the Perch, fig. 85, 50, and Shad, to the paroccipital and basioccipital: thus either wholly or in part to the parapophysis of the occipital vertebra, of which it is essentially the hæmal arch; it is usually termed the 'scapular arch.' In the Eel tribe, where it is very feebly developed, and sometimes devoid of any diverging appendage, it is loosely suspended behind the skull; and in the Plagiostomes, fig. 30, 51, 52, it is not directly attached to its proper vertebra, the occiput, but is removed further back, where we shall usually find it displaced in higher Vertebrates, in order to allow of greater freedom to the movements of the head.

The superior piece of the arch, 'supra-scapular,' figs. 81, 85, 50, is bifurcate in the Cod, or consists of two short columnar bones, attached anteriorly, the one to the paroccipital, the other and shorter piece to the petrosal, and coalescing posteriorly at an acute angle, to form a slightly expanded disk, from which the second piece of the arch is suspended vertically. This piece, called 'scapula,' ib. 51, is a slender, straight bone, terminating in a point below, and mortised into a groove on the upper and outer side of the lower and principal bone of the scapular arch. The

suprascapula and scapula together represent the rib or pleurapophysis of the occipital vertebra; they are always confluent in the Siluroids. The lower bone 'coracoid,' ib. 52, completes the arch. In the Cod its pointed upper extremity projects behind the scapula; the middle part develops backward a broad plate giving attachment to the radiated appendage of the arch: the lower end bends inward and forward gradually decreasing to a point, which is usually connected to that of the opposite coracoid by ligament, and also to the urohyal. In the Siluridæ the coracoids expand below, and are united together by a dentated suture. In all Fishes they support and defend the heart, and form the frame or 'sill' against which the opercular and branchiostegal doors shut in closing the branchial cavity: they also give attachment to the aponeurotic diaphragm dividing the pericardial from the abdominal cavity.

The bones of the head being in completest number, departing least from the vertebral pattern, and susceptible of the most intelligible definitions in the class of Fishes, afford the best basis for determining their homologies and fixing their nomenclature in the higher vertebrate series.

§ 31. *Skull of Chelonia.* If the back part of the skull of a

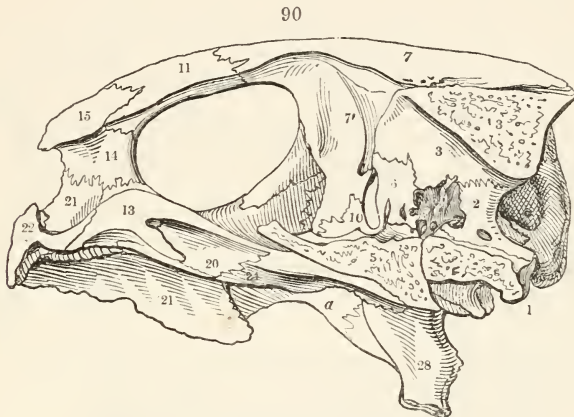


Back view of cranium, Turtle

Turtle (*Chelone*, fig. 89) be compared with that of a Cod, fig. 77, it will be seen that the lowest bone, 1, offers an articular surface for the centrum of the atlas, passes forward, expanding, to articulate with the basisphenoid, supports the 'medulla oblongata,' and is suturally articulated above to the pair of bones, fig. 89, 2, 2, which protect the sides of the epencephalon. These, moreover, transmit the hypoglossal and

vagal nerves, develop each an articulation for the neurapophyses of the atlas, and converge above to support the keystone of the arch, 3. We have, thus, unmistakable characters of the basi-ex- and super-occipitals; there is also a bone, 4, wedged between the ex- 2, and super- 3, occipitals mesially, and joined laterally to the mastoid, 8: excavated on its inner surface by the postero-external semicircular canal, and produced on its outer surface for the insertion of the 'biventer cervicis' and 'complexus'; it is the homologue of the paroccipital ('occipitale externe,' Cuvier), and bears the same general relation to the hindmost vertebral segment of the skull which the mastoid, 8, does to the next segment in advance.

In fig. 90, the centrum 1, neurapophyses 2, and neural spine 3, of the epencephalic arch, are seen from their inner or cranial surface: with the increasing bulk of the brain, the spine, 3, begins to expand laterally, and take a greater share in roofing over the hinder part or epencephalon: the parapophysis, 4, is excluded in this view. The gristly capsule of the ear-organ fills up the otocrane formed by the bones, 2, 3, 5, and 6; and extends outward and backward to enter the basal cavity of 4, the par-



Section of cranium, Turtle (*Chelone mydas*)

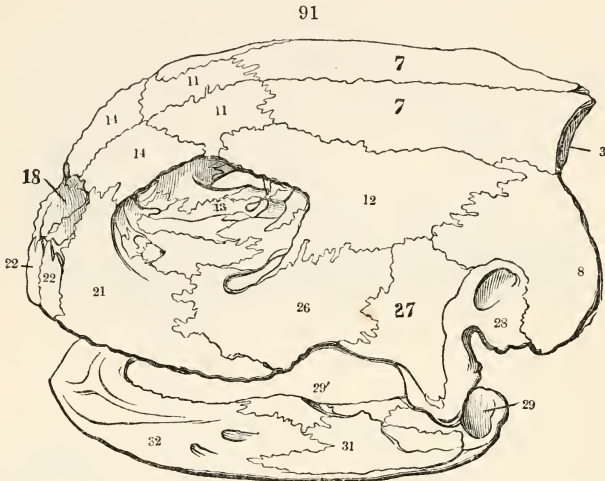
occipital: were ossification to extend into the acoustic capsule, either from an independent centre, like 16, figs. 81, 83, 84, or by continuous growth from any of the otocranial bones, the true homologue of the 'petrosal' or 'petrous portion of the temporal bone' of Anthropotomy would be established. In some Emydians there is a small autogenous bony plate in the acoustic cartilage, close to the foramen caroticum.

The basisphenoid, 5, continues forward the series of cranial centrams, expands beneath the cranial cavity, articulates on each side with the alisphenoid, 6, and sends out from its under and lateral surface a plate to articulate with the pterygoids, fig. 98 B, 24, and, in the *Emys*, with the petrosal. The alisphenoid, 6, fig. 90, protects the side of the mesencephalon (optic lobe), is widely notched anteriorly by the emerging divisions (2nd and 3rd) of the trigeminal nerve, is perforated posteriorly by a filament of the acoustic nerve, where it joins the cartilaginous petrosal; it articulates above with the mastoid, 8, and parietal, 7, and in front with the orbitosphenoid, 11. The anterior semicircular canal is partly lodged in the cavity of the otocrane contributed



by the alisphenoid. Thus in the bone 6, we have all the characters of that so numbered in figs. 81, 83, and 85, and called 'alisphenoid' in the fish. The chief modification is due to the greater developement of 3, fig. 90, in *Chelonia*, which overlaps 6 as well as 2.

The parietals, figs. 90, 91, are united, as in Cyprinoid and Ganoid fishes, by the sagittal suture, and are much expanded both transversely and longitudinally, overlapping, in the Turtle, the



Skull of Turtle (*Chelone mydas*)

superoccipital, fig. 90, 3, and articulated with it and the mastoids, fig. 91, 8, behind; and with the frontals, ib. 11, before. Each parietal, also, sends down a long vertical plate, 7', fig. 90, which unites with the alisphenoid, 6, and orbitosphenoid, 10, this ossification taking the place and function of the latter neurapophyses in fishes.

The bone, figs. 89, 91, 8, which articulates with the paroccipital 4, parietal 7, and postfrontal 12, which affords the surface of attachment to the upper end of the tympanic 28, enters into the formation of the acoustic chamber in some Emydians, and projects outward and backward to give insertion to the latissimus colli and trachelomastoideus, repeats the chief and essential characters of the bone so numbered, and called 'mastoid' in Fishes, figs. 75, 76, 83, 85, 8: and forms the transverse process of the parietal vertebra.

The forward continuation of the vertebral bodies from 5 remains cartilaginous: the lower half of the sides of the prosencephalon

are defended partly by fibro-cartilage, partly by the exogenous descending lamellæ, 7', of the parietals: there are no separate ossifications answering to 9 and 10 in fishes.<sup>1</sup> The frontals, figs. 90, 91, 11, are supported like an arch between the parietals 7 and prefrontals, 14: and each sends down a longitudinal lamella, bounding the sides of the narrow anterior continuation of the brain-chamber, as in *Polypterus*; but continued by an unossified plate to the cartilaginous presphenoid and vomer below. The postfrontal, fig. 91, 12, extends from its connections with the frontal 11, and parietal 7, downward and backward to unite with the mastoid, 8, in the Turtle, and with the malar, 26, and squamosal, 27, in all *Chelonia*. It forms the posterior boundary of the orbit, but does not contribute any share to the proper cranial walls.

The median symmetrical bone, fig. 90, 13, which, like a hypophysis, is developed in the lower part or production of the notochordal capsule, which underlaps the anterior end of the basi-pre-sphenoid, 5, by its narrow hinder part, — expanding as it advances to articulate with the prefrontals, 14, — having the palatine bones, ib. 20, abutting against the broad anterior part, and entering by its under surface into the formation of the roof of the mouth, fig. 98 B, *n*, repeats the essential characters of the bone so numbered and termed 'vomer' in Fishes, figs. 81, 83, 84, 85, 13; and, like it, represents the centrum of the foremost segment of the vertebral series. The vomer is single in *Chelonia*, as in most fishes.

The bones, fig. 90, 14, in neurapophysial relation with the vomer, protecting the sides of the rhinencephalon or olfactory bulbs, entering into the antero-superior boundary of the orbit, forming part of the surface of attachment of the palatines, supporting the fore part of the frontals, and connected, but more commonly connate, with the nasals, ib. 15, fig. 91, 14, repeat the essential characters of the prefrontals of Fishes, figs. 83, 85, 14. Connate, as in *Chelonia* they usually are, with the nasals, their outer expanded plate unites with the maxillary, fig. 91, 21, and completes the upper border of the nostril, 18.

The palatines, figs. 90, 98 B, 20, form the sides of the roof of the mouth, articulating medially with the vomer, 13, *n*, and laterally with the maxillary, 21, and pterygoid, 24. The maxillary, figs. 90, 91, 21, presents a palatal, facial, and orbital plate. The palatal plate, fig. 98 B, 21, developes a masticatory ridge parallel with the sharp alveolar border. The facial plate, fig. 91, 21, shows the connections with the prefronto-nasal, 14, the premaxillary, 22, and the malar, 26; the orbital plate is usually perforated by the lacrymal

<sup>1</sup> xxxviii. ; Tab. xxi. fig. 89, 1, 1'.

canal, the bone so called being ossified continuously, as a process, from the maxillary. The premaxillaries, figs. 90, 91, 22, closing the arch anteriorly, are very small in all *Chelonia*, and the sutures marking them off from the maxillaries are wanting in some Mud-turtles (*Tetronyx longicollis*, Fitz. *Trionyx Bibroni*):<sup>1</sup> the premaxillary part of the facial profile is vertical in many *Chelonia*, as in fig. 91: but in *Tetronyx* it extends from the nostril downward and backward — the reverse of prognathism.

The pterygoid, fig. 90, 24, diverges from the vomer and palatine, or from the palatine and maxillary, fig. 98 B, backward and outward: uniting, in *Chelone*, with its fellow below the basi-sphenoid, fig. 90, 5, and diverging outward and backward to abut, at *a*, against the tympanic, 28. In some Soft-turtles, e.g., *Trionyx* (*Gymnopus*) *indicus*, the vomer is directly continued from the basi-pre-sphenoid, and divides the pterygoids from each other.

A second outer bar of bone, fixing the maxillary arch to the tympanic, is present in all *Chelonia*, and divided into two pieces. The proximal piece, fig. 91, 26, is articulated with the maxillary, 21, enters into the lower and back part of the orbital border, unites superiorly with the postfrontal, 12, and posteriorly with the second piece, 27. To the bone, 26, the term 'malar' is given; to the bone, 27, the name 'squamosal.' The latter, resembling a vertical scale or plate, articulates above with the postfrontal, 12, and mastoid, 8; and behind with the tympanic, 28. It completes the arch called 'zygomatic,' bounding externally the temporal fossa, which is roofed over by bone in the Turtles (figs. 89 and 91), and a few Emyds; but is widely open above in other *Chelonia*.

The tympanic pedicle is a single bone, fig. 91, 28, expanded above, with a more or less circular border for the insertion of the membrana tympani; excavated internally by the tympanic air-cells; notched behind for the reception of the columellar stapes, as in the Turtles, fig. 91; with a narrower cleft in *Tetronyx*, and with the borders uniting in the Tortoises and some other *Chelonia*, reducing the stapedia passage to a foramen or canal, fig. 92, 28. The lower end of the tympanic supports a transversely extended condyle with an undulated or nearly flattened surface. The tympanic articulates above with the paroccipital, fig. 89, 4, in some species with the alisphenoid, in others with the superoccipital, as well as with the mastoid, *ib.* and fig. 91, 8.

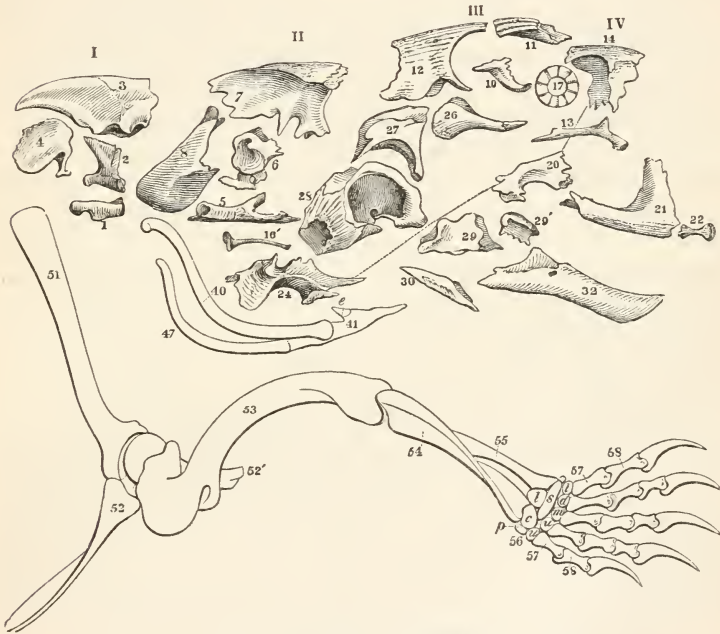
The mandible consists of an 'articular' element, small, but distinct in the Turtle, fig. 91, 30; connate in *Emys* with the 'suran-

<sup>1</sup> XLIV. No. 954, p. 185.

gular,' fig. 92, 29; of an 'angular' continued into a 'splenial,' ib. 30; of a 'coronoid,' ib. 29'; and of a 'dentary,' ib. 32. All *Chelonia* are edentulous: the alveolar borders of both upper and lower jaws are sheathed with horn: but in a few species, especially the soft turtles (*Trionyx*, *Tetronyx*) these borders are notched or produced into tooth-like processes. The dentary elements coalesce at the symphysis; which, in the Snappers, especially *Chelydra* (*Chelonura*) *Temminckii*, is produced into a sharp hook.

The hyoid arch consists of a basihyal, fig. 92, 41, a pair of short

92

Side view of cranial vertebræ, *Emys*

processes, ib. *e*, giving attachment to the genio- and hyo-glossi muscles: of a pair of long ceratohyals, 40, by which the arch is suspended to the mastoids; and of a pair of hyobranchials, 47. To complete the series of skull-bones homologous with those of the fish, represented in fig. 81, it is necessary to bring forward the scapular arch which had receded a short distance from its vertebra in the *Batrachia*, fig. 42, 52, from a more remote position in the *Chelonia*: we then find that 51, fig. 92, answers to the scapula, fig. 81, 51; and that 52, fig. 92, answers to the coracoid, fig. 81, 52: the diverging series of many-jointed rays in the fish, fig. 81, are now developed into the fore-limb, fig. 92, 53 — 58.



In this figure the several bones of the head of the European Box-terrapene (*Emys Europæa*, Wgl.) are represented, disarticulated, in a side view of their vertebral relations. Beneath the Roman figure, I, are the centrum, 1, neurapophysis, 2, neural spine, 3, and parapophysis 4, forming the neural (epencephalic) arch; with the pleurapophysis, 51, and hæmapophysis, 52, forming the hæmal (scapular) arch, with its appendage, of the occipital vertebra. Beneath II are the centrum, 5, the neurapophysis, 6, the neural spine, 7, the parapophysis, 8, forming the neural (mesencephalic) arch: from 8 is suspended by an unossified pleurapophysis the hæmapophysis, 40, the hæmal spine, 41, with the appendage, 47, of the hæmal (hyoidean) arch of the parietal vertebra. Under III are the neurapophysis, 10, neural spine, 11, and parapophysis, 12, forming the neural (prosencephalic) arch; with the pleurapophysis, 28, and composite hæmapophysis, 29—32, forming the hæmal (mandibular) arch of the frontal vertebra, of which the centrum is not an independent ossification. Beneath IV are, the centrum, 13, the connate neurapophyses and neural spines, 14, forming the neural (rhinencephalic) arch; with the pleurapophysis, 20, hæmapophysis, 21, and hæmal spine, 22, forming the hæmal (maxillary) arch of the nasal vertebra. The diverging appendages, for the fixation of this hæmal arch are more developed than in Fishes, where it retains more of its typical mobility. Besides the appendage, 24, of the pleurapophysis, there is now another, extending in two successive segments, 26 and 27, from the hæmapophysis. The splanchnic ossicle, 16', is part of the acoustic organ: the circle of bones, 17, belong to the visual organ. Such are the 'general homologies' of the bones of the chelonian head, in reference to the vertebrate archetype, fig. 21. Compared with bones of the piscine head, fig. 81, previously named and characterised, those of fig. 92 are:—

1. Basioccipital.
2. Exoccipital.
3. Superoccipital.
4. Paroccipital.
5. Basisphenoid.
6. Alisphenoid.
7. Parietal.
8. Mastoid.
9. Presphenoid (unossified).
10. Orbitosphenoid (in great part cartilaginous).
11. Frontal.
12. Postfrontal.

13. Vomer.
14. Prefrontal (with, 15, nasal, distinct in some *Chelonia*).
16. (Petrosal, unossified from an independent centre); 16', a superadded ossicle, 'stapes,' 'columella'; with a gristly representative of 'malleus;' in special relation to an organ of hearing affected by vibrations of air: superadded to all the bones developed in and from the embryonic hæmal arch called 'Meckel's process.'
17. Sclerotals.
19. Turbinal (unossified).
20. Palatine.
21. Maxillary.
22. Premaxillary.
24. Pterygoid, with ossification extending into the seat of 23, ento-pterygoid.
26. Malar (not answering to the bone so numbered in fig. 81).
27. Squamosal (ib. these bones do not exist in Fishes).
28. Tympanic (here a single bone; its subdivisions are 25—28 in fig. 81).
29. Articular with Surangular.
- 29'. Coronal.
30. Angular with Splenial.
32. Dentary.
40. Ceratohyal.
41. Basilhyal.
47. Cerato-branchial, (or 'thyrohyal' in reference to the larynx of air-breathers, a new developement upon the vestige of the branchial apparatus of fishes).
50. Suprascapula (unossified).
51. Scapula.
52. Coracoid.
- 52'. Acromial process of scapula.
53. Humerus (rarely a separate ossification in Fishes).
54. Ulna.
55. Radius.
56. Carpus.
- 57, 58. Digital rays.

The chief differences in regard to the presence and absence of bones between the Tortoise and the Fish are seen in those belonging to the category of 'diverging appendages:' thus the 'branchiostegals,' 43, and 'operculars,' 34—37, fig. 81, are suppressed in the Reptile; while the 'malar,' 26, and squamosal, 27, are not developed in the fish. Some minor, but interesting, modifications of cranial structure present themselves within the

limits of the Chelonian order. Figs. 90 and 91 exemplify that which prevails in the marine species (*Chelone*). In them the head is proportionally larger; and, being incapable of retraction within the carapace, is additionally protected by extension of bone into the fascia covering the temporal muscles, so as to form a complete osseous vaulted roof over the temporal fossæ, due to exogenous growths from the postfrontals, fig. 91, 12, the parietals, 7, and the mastoids, 8.

In the almost sole instance in which such accessory defence is afforded to a non-marine species—the Brazilian Pipitu (*Podocnemis expansa*)—the temporal roof is chiefly formed by the parietals, and is completed laterally by a larger proportion of the squamosal than of the postfrontal, which does not exceed its relative size in other Terrapenes. The present species further differs from the marine Turtles in the non-ossification of the vomer and the consequent absence of a septum in the posterior nostrils; in the greater breadth of the pterygoids, which send out a compressed rounded process into the temporal depressions: the orbits also are much smaller, and are bounded behind by orbital processes of the postfrontal and malar bones: the mastoids and paroccipitals are more produced backward, and the entire skull is more depressed than in the Turtles. In other freshwater Tortoises (*Emys*, &c.), the parietal crista is continued into the occipital one without being extended over the temporal fossæ; the fascia covering the muscular masses in these fossæ undergoing no ossification. The bony hoop for the membrana tympani is incomplete behind, and the columelliform stapes passes through a notch instead of a foramen to attain the tympanic membrane. The mastoid is excavated to form a tympanic air-cell.

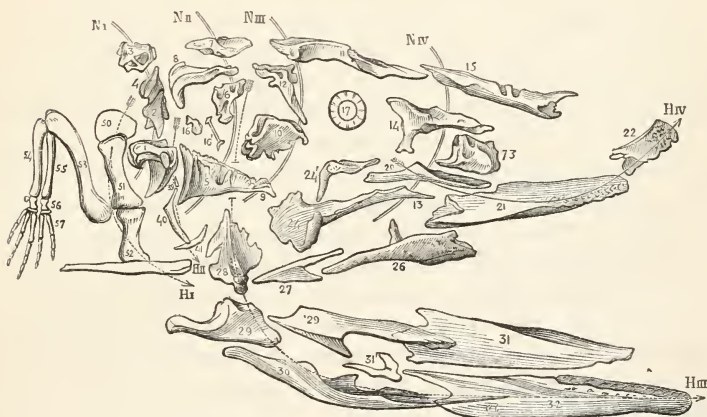
In the true Tortoises the temporal depressions are exposed, as in the Terrapenes: the head is proportionally small and can be withdrawn beneath the protective roof of the carapace. The skull is rounder and less depressed than in the Terrapenes. The tympanic hoop is notched behind, but the columelliform stapes passes through a small foramen. The palatine processes of the maxillaries are on a plane much below that of the continuation of the basis cranii formed by the vomer and palatines.

In the soft-turtles (*Trioncidae*), the skull is long, depressed, triangular, the muzzle forming the obtuse apex, and the base remarkable for its four backward prolongations. The inferior of these is the shortest, and terminates in the occipital condyle; the superior is the longest, and is formed by the superoccipital spine: the two lateral processes are developed from the paroccipitals and

mastoids. The premaxillary is either wanting, or it is very small, and represented by its alveolar border only; the maxillaries meeting above it. The alveolar borders of both upper and lower jaws show a regular series of vascular pits or foramina, indicative of the primitive separate matrices, like those of teeth, which laid the foundation in the young animal of the continuous horny coverings of the jaws.

Temminck's Snapper (*Chelonura Temminckii*) is remarkable for the upper convexity and enormous expanse of the cranium, chiefly due to the temporal fossæ, contrasted with the short and narrow face. In a fossil chelonian from the Portland stone (*Ch. planiceps*) and in another from the Chalk (*Ch. pulchriceps*) the nasals were distinct from the prefrontals, which is a rare exception in existing species.

93



Side view of cranial vertebrae and sense-capsules, Crocodile

§ 32. *Skull of Crocodilia*.—Passing next to the skull of the Crocodile, we find the first difference in the less complex condition of the epencephalic arch, fig. 93, N 1, which consists of four, instead of, as in the Fish and Turtle, six bones. The basioccipital, figs. 93 and 94, 1, presents, like the centrums of the trunk, a convexity at its posterior articular surface; but its anterior one, like the hindmost centrum of the sacrum, unites with the next centrum in advance, *ib.* 5, by a flat rough sutural surface. Like most of the centrums in the neck and beginning of the back, that of the occiput develops a hypapophysis, but this descending process is longer and larger. The exoccipitals, *ib.* 2, articulate suturally, like the neuropophyses of the trunk, with the upper and lateral parts of their



centrum; are concave mesially, fig. 94, 2, towards the brain-segment which they protect, meeting above it to support the neural spine, 3; they develop a petrosal plate, which meets a corresponding one from the alisphenoid; they give exit to the vagal and hypoglossal nerves, and send outward a strong process, fig. 93, 4, which articulates with the mastoid and tympanic. The anterior and inner part of the base of this process is excavated by part of the acoustic cavity: its outer extremity is rough for the attachment of muscles: it thus repeats the essential characters of the 'par-occipital' in the Fish and Turtle; but it is ossified, as an exogenous transverse process, from the neurapophysis (exoccipital, 2). The superoccipital, figs. 93 and 94, 3, is broad and flat, like the similarly detached neural spine of the atlas; it advances a little forward, beyond its sustaining neurapophyses, to protect the upper surface of the cerebellum; it is traversed by tympanic air-cells, and assists with the ex- and par-occipitals, 2, 4, in the formation of the ear-chamber.

Proceeding with the neural arches of the Crocodile's skull, if we dislocate the segment in advance of the occiput, fig. 93, N 2, we bring away, in connection with the long base-bone, 5, the bone, 9. The two connate cranial centrans must be artificially divided, in order to obtain the segments distinct to which they belong. The hinder portion, 5, of the great base-bone, which is the centrum of the parietal vertebra, is the basisphenoid. It supports that part of the 'mesencephalon,' which is formed by the lobe of the third ventricle, and its upper surface is excavated for the pituitary prolongation of that cavity. The basisphenoid develops from its under surface a 'hypapophysis,' which is suturally united with the fore part of that of the basioccipital, but extends further down, and is similarly united in front to the 'pterygoids,' fig. 94, 24. These rough sutural surfaces of the long descending process of the basisphenoid are very characteristic of that centrum, when detached, in a fossil state. The neurapophyses of the parietal vertebra, 6, 6, the alisphenoids, protect the sides of the mesencephalon, and are notched at their anterior margin, for a conjugational foramen transmitting the trigeminal nerve. As accessory functions they contribute, like the corresponding bones in fishes, to the formation of the ear-chamber. They have, however, a little retrograded in position, resting below in part upon the occipital centrum, and supporting more of the spine of that segment, 3, than of their own, 7. The spine of the parietal vertebra (parietal, figs. 93, 94, 95, 7), is a single, depressed bone, like that of the occipital vertebra; it completes the mesencephalic arch, as its crown or key-bone; it is partially

excavated by the tympanic air-cells, and overlaps the superoccipital. The bones, *ib.* 8, 8, wedged between 6 and 7, are developed from independent centres, and preserve their individuality, as in Fishes. They form no part of the inner walls of the cranium, but are partially excavated by the tympanic cavity, and send outward and backward a strong transverse process for muscular attachment. They afford a ligamentous attachment to the hæmal (hyoid, *fig.* 93, *H* 2, 40) arch of their own segment, and articulate largely with the pleurapophyses, (tympanic, *ib.* 28), of the antecedent hæmal arch, whose more backward displacement, in comparison with its position in the fish's skull, is well illustrated in the metamorphosis of the Frog, *figs.* 69 *A* and 71.

On removing the neural arch of the parietal vertebra, after the section of its confluent centrum, the elements of the corresponding arch of the frontal vertebra, *fig.* 93, *N* III, are seen to present the same arrangement. The compressed produced centrum (presphenoid, *ib.* 9) has its form modified like that of the vertebral centrams at the opposite extreme of the body in many birds. The neurapophyses (orbitosphenoids, *ib.* 10) articulate with the upper part of 9; they are expanded, and smoothly excavated on their inner surface to support the sides of the large prosencephalon, showing more plainly their archetypal character than in *Chelonia*; they dismiss the optic nerves by a notch. They show the same tendency to a retrograde change of position as the neighbouring neurapophyses, 6; for though they support a greater proportion of their proper spine, 11, they also support part of the parietal spine, 7, and rest, in part, below upon the parietal centrum, 5. The neural spine, 11, of the frontal vertebra retains its normal character as a single symmetrical bone, like the parietal spine which it partly overlaps; it also completes the neural arch of its own segment, but is remarkably extended forward, where it is much thickened, and assists in forming the cavities for the eyeballs; it is the 'frontal' bone.

In contemplating in the skull itself, or such side view as is given in *fig.* 94, the relative position of the frontal, 11, to the parietal, 7, and of this to the superoccipital, 3, which is overlapped by the parietal, just as itself overlaps the flattened spine of the atlas, we gain a conviction which cannot be shaken by any difference in their mode of ossification, by their median bipartition, or by their extreme expansion in other animals, that the above-named single, median, imbricated bones, each completing its neural arch, and permanently distinct from the piers of such arch, must repeat the same element in those successive arches—in other words, must be 'homotypes,' or serially homologous. In like manner the

serial homology of those piers, called 'neurapophyses,' viz., the laminae of the atlas, the exoccipitals, the alisphenoids, and the orbitosphenoids, is equally unmistakable. Nor can we shut out of view the same serial relationship of the paroccipitals, fig. 95, 4, as coalesced diapophyses of the occipital vertebra, with the mastoids, ib. 8, and the postfrontals, 12, as par- or di-apophyses of their respective vertebræ. All stand out from the sides of the cranium, as transverse processes for muscular attachment; all are alike autogenous in the Turtles; and all of them, in Fishes, offer articular surfaces for the ribs of their respective vertebræ; and these characters are retained in the postfrontals as well as in the mastoids of the Crocodiles.

The frontal diapophysis, figs. 93, 95, 12, is wedged between the back part of the spine, 11, and the neurapophysis, 10; its outwardly projecting process extends backward, and joins that of the succeeding diapophysis, 8; but, notwithstanding the retrogradation of the inferior arch, it still articulates with part of its own pleurapophysial element, 28, which forms the proximal element of that arch.

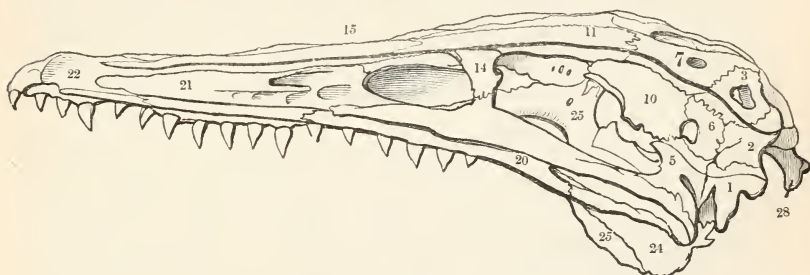
There finally remain in the cranium of the Crocodile, after the successive detachment of the foregoing arches, the bones terminating the fore part of the skull, N 4, fig. 93; but, notwithstanding the extreme degree of modification to which their extreme position subjects them, we can still trace in their arrangement a correspondence with the vertebrate type.

A long and slender symmetrical grooved bone, fig. 93, 13, is continued forward from the coalesced pterygoids, 24, and stands in the relation of a centrum to the vertical plates of bone, 14, which expand as they rise into a broad, thick, triangular plate, with an exposed horizontal superior surface. These bones, the prefrontals 14, stand in the relation of neurapophyses to the rhinencephalic prolongations of the brain commonly called 'olfactory nerves;' and they form the piers or haunches of a neural arch, which is completed above by a pair of symmetrical bones, 15, called 'nasals,' which I regard as a divided or bifid neural spine; the independent basal ossification, answering to the vomer in Fishes, figs. 81, 84, 13, and Chelonians fig. 98 B, *n*, is in advance of its proper segment, and divided in the middle line as in Ganoid Fishes and Batrachia. In some Alligators (*All. niger*) the divided vomer extends far forward, expands anteriorly, and appears upon the bony palate.

Almost all the other bones of the head of the Crocodile are adjusted so as to constitute four inverted arches. These are the hæmal arches of the four segments or vertebræ, of which the neural arches have been just described. But they have been the

seat of much greater modifications, by which they are made subservient to a variety of functions unknown in the hæmal arches of the rest of the body. Thus the two anterior hæmal arches of the head perform the office of seizing and bruising the food; are armed for that purpose with teeth: and, whilst one arch is firmly fixed, the other works upon it like the hammer upon the anvil. The elements of the fixed arch, called 'maxillary arch,' fig. 93, II, iv, have accordingly undergone the greatest amount of change, in order to adapt that arch to its share in mastication, as well as for forming part of the passage for the respiratory medium which traverses it. Almost the whole of the upper surface of the maxillary arch is firmly united to contiguous parts of the skull by rough or sutural surfaces, and its strength is increased by bony

94



Section of cranium, Crocodile

appendages, which diverge from it to abut against other parts of the skull. Comparative Anatomy teaches that, of the numerous places of attachment, the one which connects the maxillary arch by its element, 20, with the centrum, 13, and with the descending plates of the neurapophyses, 14, of the nasal segment, is the normal or the most constant point of its suspension; the bone, 20, being the pleurapophysial element of the maxillary arch: it is called the 'palatine,' because the under surface forms a portion of the bony roof of the mouth, called the 'palate,' as in fig. 98 c, 20. It is articulated at its fore part with the bone, 21, which is the hæmapophysial element of the arch. This bone is called the 'maxillary,' and is greatly developed both in length and breadth, fig. 95, 21: it is connected with 20, figs. 94, 98 c, behind and with 22 in front, which are parts of the same arch, and with the diverging appendages of the arch, viz., fig. 95, 26, the malar bone, and fig. 98 c, 25, the ectopterygoid: the maxillary is also united with the nasals, 15, and the lacrymal, 73, as well as with its fellow of the opposite side. The smooth, expanded



horizontal plate, which effects the latter junction, is called the palatal plate of the maxillary, fig. 98 C, 21; the thickened external border, where this plate meets the external rough surface of the bone, and which is perforated for the lodgment of the teeth, is the 'alveolar border.' The hæmal spine or key-bone of the arch, 22, is bifid, and the arch is completed by the symphyseal junction of the two symmetrical halves; these halves are called 'premaxillary bones:' these bones, like the maxillaries, have a rough facial plate, fig. 95, 22, and a smooth palatal plate, fig. 98 C, 22, with the connecting alveolar border. The median symphysis is perforated vertically through both plates; the outer or upper hole being the external nostril, fig. 95, 22, the under or palatal one being the premaxillary aperture, fig. 98 C, *p*.

Both the palatine and the maxillary bones send outward and backward parts or processes which diverge from the line of the hæmal arch, and give attachment to distinct bones, which form the 'diverging appendages' of the arch, and serve to attach it, as do the diverging appendages of the thoracic hæmal arches in the bird, to the succeeding arch.

The appendage, 24, called 'pterygoid,' effects a more extensive attachment, and is peculiarly developed in the Crocodilia. As it extends backward it expands, unites with its fellow both below and above the nasal canal, encompassing it so as to form the hinder or palatal nostril, fig. 98 C, *n*; the coalesced pterygoids articulate anteriorly with the divided vomer, the palatines, and the basi-sphenoid: posteriorly each broad wing, extending outward, gives attachment to a second bone, *ib.* 25, called 'ectopterygoid,' which is firmly connected with the maxillary, 21, the malar, 26, and the postfrontal, 12. The second diverging ray of the maxillary arch is of great strength; it extends from the maxillary, fig. 95, 21, to the tympanic, 28, and is divided into two pieces, the malar, 26, and the squamosal, 27; both of which begin to assume more lengthened and slender proportions than in the Turtle (compare fig. 95 with 91). Such are the chief Crocodilian modifications of the hæmal arch and appendages of the anterior or nasal vertebra of the skull.

The hæmal arch of the frontal vertebra, fig. 92, H, *iii*, is somewhat less metamorphosed, and has no diverging appendage. It is slightly displaced backward, and is articulated by only a small portion of its pleurapophysis, 28, to the parapophysis, 12, of its own segment; the major part of that short and strong rib articulating with the parapophysis, 8, of the succeeding segment. The bone, fig. 95, 28, called 'tympanic,' because it serves to support

the 'drum of the ear' in air-breathing vertebrates, is short, strong, and immovably wedged, in the Crocodilia, between the paroccipital, 4, mastoid, 8, postfrontal, 12, and squamosal, 27; and the conditions of this fixation of the pleurapophysis are exemplified in the great development of the hæmapophysis (mandible), which is here unusually long, supports numerous teeth, and requires, therefore, a firm point of suspension, in the violent actions to which the jaws are put in retaining and overcoming the struggles of a powerful living prey. The movable articulation between the tympanic, 28, and the rest of the hæmal arch is analogous to that which we find between the thoracic pleurapophysis and hæmapophysis in birds. But the hæmapophysis of the mandibular arch in the Crocodiles is subdivided into several pieces, in order to combine the greatest elasticity and strength with a not excessive weight of bone. The different pieces of this adaptively subdivided element have received definite names. That numbered 29, fig. 93, which offers the articular concavity to the convex condyle of the tympanic, 28, is called the 'articular' piece; that beneath it, 30, which develops the angle of the jaw, when this projects, is the 'angular' piece; the piece above, 29, and *e*, fig. 95, is the 'surangular;' the thin, broad, flat piece, 31, fig. 93, applied, like a splint, to the inner side of the other parts of the mandible, is the 'splenial;' the small accessory ossicle, 31', is the 'coronoid,' because it develops the process, so called, in lizards; the anterior piece, 32, which supports the teeth, is called the 'dentary.' The purport of this subdivision of the lower jaw-bone has been well explained by Conybeare<sup>1</sup> and Buckland,<sup>2</sup> by the analogy of its structure to that adopted in binding together several parallel plates of elastic wood or steel to make a crossbow, and also in setting together thin plates of steel in the springs of carriages. Dr. Buckland adds — 'Those who have witnessed the shock given to the head of a crocodile by the act of snapping together its thin long jaws, must have seen how liable to fracture the lower jaw would be, were it composed of one bone only on each side.' The same reasoning applies to the composite structure of the long tympanic pedicle in fishes. In each case the splicing and bracing together of thin flat bones of unequal length and of varying thickness, affords compensation for the weakness and risk of fracture that would otherwise have attended the elongation of the parts. In the abdomen of the crocodile the analogous subdivision of the hæmapophyses, there called abdominal ribs, allows of a slight change of their length, in the expansion and contraction of the walls of that cavity; and since

<sup>1</sup> 'Geol. Trans.' 1821, p. 565.

<sup>2</sup> 'Bridgewater Treatise,' 1836, vol. i. p. 176.

amphibious reptiles, when on land, rest the whole weight of the abdomen directly upon the ground, the necessity of the modification diminishing liability to fracture further appears. These analogies are important, as demonstrating that the general homology of the elements of a natural segment of the skeleton is not affected or obscured by their subdivision for a special end. The purposive modification of the hæmapophyses of the frontal vertebra is but a repetition of that which affects the same elements in the abdominal vertebræ.

Passing next to the hæmal arch of the parietal vertebra, fig. 93, II, ii, we are first struck by its small relative size. Its restricted functions have not required it to grow in proportion with the other arches, and it consequently retains much of its embryonal dimensions. It consists of a ligamentous 'stylohyal,' retaining the same primitive histological condition which obstructs the ordinary recognition of the pleural element of the lumbar hæmal arches; of a cartilaginous 'epihyal,' 39, intervening between this and the ossified hæmapophysis, or ceratohyal, 40; and of the hæmal spine, 41, which retains its cartilaginous state, like its homotypes, in the abdomen: there they get the special name of 'abdominal sternum,' here of 'basihyal.' The basihyal has, however, coalesced with the thyrohyals to form a broad cartilaginous plate, the anterior border rising like a valve to close the fauces, and the posterior angles extending beyond and sustaining the thyroid and other parts of the larynx. The long bony 'ceratohyal' and the commonly cartilaginous 'epihyal' are suspended by the ligamentous 'stylohyal' to the back part of the tympanic at its junction with the paroccipital process; the whole arch having, like the mandibular one, retrograded from the connection it presents in Fishes.

This retrogradation is still more considerable in the succeeding hæmal arch, fig. 92, II 1; fig. 57, 51. In comparing the occipital segment of the Crocodile's skeleton with that of the Fish, fig. 81, the chief modification that distinguishes that segment in the Crocodile is the apparent absence of its hæmal arch. We recognise, however, the special homologues of the constituents of that arch of the Fish's skeleton, fig. 34, in the bones 51 and 52 of the Crocodile's skeleton, fig. 57; but the upper or suprascapular piece, 50, fig. 92, retains, in connection with the loss of its proximal or cranial articulations, its cartilaginous state: the scapula, 51, is ossified, as is likewise the coracoid, 52, the lower end of which is separated from its fellow by the interposition of a median, symmetrical, partially ossified piece called 'episternum.' The power of recognising the special homologies of 50, 51, and 52 in the Crocodile,

with the similarly numbered constituents of the same arch in Fishes—though masked, not only by modifications of form and proportion, but even of very substance, as in the case of 50—depends upon the circumstance of these bones constituting the same essential element of the archetypal skeleton, viz. the fourth hæmal arch, numbered *pl*, 52, in fig. 17. For although in the present instance there is superadded to the adaptive modifications above cited the rarer one of altered connections, Cuvier does not hesitate to give the same names, ‘suprascapulaire’ to 50, and ‘scapulaire’ to 51, in both Fish and Crocodile; but he did not perceive or admit that the narrower relations of special homology were a result of, and necessarily included in, the wider law of general homology. According to the latter law, we discern in fig. 93, 50 and 51, a compound ‘pleurapophysis,’ in 52 a ‘hæmapophysis,’ and in *hs*, the ‘hæmal spine,’ completing the hæmal arch.<sup>1</sup>

The scapulo-coracoid arch, both elements, 51, 52, of which retain the form of strong and thick vertebral and sternal ribs in the Crocodile, is applied in the skeleton of that animal over the anterior thoracic hæmal arches. Viewed as a more robust hæmal arch, it is obviously out of place in reference to the rest of its vertebral segment. If we seek to determine that segment by the mode in which we restore to their centrums the less displaced neural arches of the antecedent vertebræ of the cranium or in the sacrum of the bird,<sup>2</sup> we proceed to examine the vertebræ before and behind the displaced arch, with the view to discover the one which needs it, in order to be made typically complete. Finding no centrum and neural arch without its pleurapophyses from the

<sup>1</sup> The author of No. CLXXI, in criticising this conclusion, omits consideration of the cartilaginous element, fig. 93, 50: as it exists and required due attention, I was led to regard it as the homologue of the ossified element, figs. 81, 85, 50, in Fishes, and as being part, one might say, half, of the pleurapophysis. No anatomist has impugned such determination of the special homology of the ‘lame cartilagineuse du bord spinal de l’omoplate’ of the Crocodile, with the ‘partie spinal de l’omoplate’ of the Frog, and with the ‘os suprascapulaire’ of the Fish. Now the latter is the homotype of the proximal half of the compound pleurapophysis of the pelvic arch, of which the part called ‘ilium’ answers to the part called ‘scapula.’ There remains, therefore, for Dr. Humphrey’s consideration, the serial and general homologies of the ‘suprascapula;’ in the omission of which lurks the fallacy of his criticism. CLXXI, pp. 27, 28. The alleged difference of development, at most one of direction of growth, is futile.

A ‘hæmal arch’ having been defined as including the ‘pleurapophysis’ as well as ‘hæmapophysis,’ by altering the meaning of the term and restricting the ‘hæmal parts of the vertebra’ to the ‘hæmapophyses and hæmal spine,’ Dr. Humphrey makes ground for pronouncing the part of the hæmal arch, 50 and 51, in figs. 81 and 92, as being the hæm- not the pleur-apophysis.

<sup>2</sup> See ‘On the Archetype and Homologies of the Vertebrate Skeleton,’ pp. 117 and 159.



scapula to the pelvis, we give up our search in that direction; and in the opposite direction we find no vertebra without its ribs, until we reach the occiput; there we have centrum and neural arch, with connate parapophyses, but without the hæmal arch, which arch can only be supplied by a restoration of the bones 50-52 to the place which they naturally occupy in the skeleton of the fish. And since the bones 50-52 in the Crocodile, fig. 57, are specially homologous with those so numbered in the Fish, fig. 34, we must conclude that they are likewise homologous in a higher sense; that in the Fish the scapula-coracoid arch is in its natural or typical position, whereas in the Crocodile it has been displaced for a special purpose. Thus, agreeably with a general principle, we perceive that, as the lower vertebrate animal illustrates the closer adhesion to the archetype<sup>1</sup> by the natural articulation of the scapulo-coracoid arch to the occiput, so the higher vertebrate manifests the superior influence of the antagonizing power of adaptive modification by the removal of that arch from its proper segment.

The anthropotomist, by his mode of counting and defining the dorsal vertebræ and ribs, admits, unconsciously perhaps, the important principle in general homology which is here exemplified; and which, pursued to its legitimate consequences, and further applied, demonstrates that the suprascapula and scapula are the modified rib of that centrum and neural arch, which he calls the 'occipital bone;' and that the change of place which chiefly masks that relation (for a very elementary acquaintance with Comparative Anatomy shows how little mere form and proportion affect the homological characters of bones), differs only in extent, and not in kind, from the modification which makes a minor amount of comparative observation requisite, in order to determine the relation of the shifted dorsal rib to its proper centrum in the human skeleton.

With reference, therefore, to the occipital vertebra of the Crocodile, if the comparatively well-developed and permanently distinct ribs of all the cervical vertebræ prove the scapular arch to belong to none of those segments,<sup>2</sup> and if that hæmal arch be required to complete the occipital segment, which it actually does complete in fishes, then the same conclusion must apply to the same arch in other animals, up to man himself.

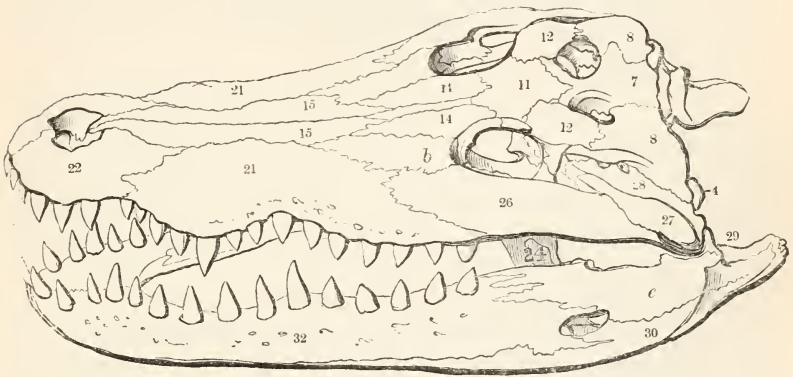
<sup>1</sup> The term 'simple primary form' appears to Dr. Humphrey, CLXXI, p. 34, to be more correct than the word 'archetype.'

<sup>2</sup> Close the eyes to the fact of the suprascapular element in the Crocodile, and you then may, with Dr. Humphrey, see its representative in one of the cervical pleuropophyses. Comp. ib. p. 28, and note, p. 144, of the present work.

The locomotive extremity, fig. 92, 53-57, is the diverging appendage of the arch, under one of its numerous modes and grades of development.

Coadjusted as the above-defined vertebral elements are in the skull of the Crocodile, they compose such a whole as is represented in fig. 95. Each temporal fossa is circumscribed externally by two horizontal bony arches; the upper one formed by the post-frontal, 12, and mastoid, 8; the lower one by the malar, 26, and squamosal, 27: the tympanic, 28, and mastoid, 8, bound the fossa behind: the coarticulated processes from the postfrontal and malar form a partial division between the fossa and the orbit in

95



Skull of Crocodile

front. The orbit is circumscribed by these bones, with the frontal, 11, prefrontal, 14, and lacrymal, *b*. A superorbital or palpebral derm-ossicle strengthens the upper eyelid. The external nostril, single and advanced in *Crocodylia*, is surrounded sometimes, as in Gavials, by the premaxillaries, 22; sometimes, as in fig. 95, admitting also the points of the nasals, 15. The internal nostril opens far back, beneath the occiput, fig. 98 *c, n*, and is exclusively surrounded by the pterygoids, 24: its plane is horizontal in Gavials and some Alligators; but is more or less oblique, looking backward, in Crocodiles. Behind and above it are the median and lateral Eustachian bony outlets, from which the membranous continuations of the tubes converge and unite in the single valvular aperture on the soft palate.<sup>1</sup> The vast extent of the bony roof of the

<sup>1</sup> CLXXII., pl. xii. fig. 5. This paper may be referred to for other cranial foramina, and for the details of the complex bony structure of the median and lateral

mouth is interrupted by the large 'pterygomaxillary' vacuities, *ib. y*, bounded externally by the maxillaries and ectopterygoids: at the fore part is the small 'prepalatine' opening, *ib. p*. In the Gavials each pterygoid expands at its outer and fore border into a large oval bulla. The palatines and maxillaries are excavated by sinuses communicating with the nasal passages. The form of the maxillo-premaxillary palatine suture helps by its variation to the distinction of species.<sup>1</sup> The anterior expanded parts of the divided vomer appear upon the bony palate in some Alligators.<sup>2</sup>

The otic capsule remains in great part cartilaginous: towards the cranial cavity it is defended by the thin otocranial plates of the alisphenoid, superoccipital and paroccipital, with occasionally a small scale, representing a rudimental petrosal. The eye-capsule is not defended by bony plates, as in *Chelonia*. The turbinals remain cartilaginous.

The cranial cavity is miserably small in these huge cold-blooded Carnivora; its main part, shown in section, *fig. 94, 2, 6, 10*, may be filled by a man's thumb in a skull of three feet in length. The proper brain-chamber is, however, continued along the groove beneath the interorbital platform to the second slight expansion between the prefrontals, 14, where the rhinencephalic (olfactory) lobes send forward the true olfactory nerves.

If the foregoing statement of the grounds for determining the homologies, general and special, of the skull-bones of the *Crocodylia* may have seemed tedious or unnecessary, I excuse myself by the importance attached to the subject by Cuvier, who, in the last lecture which he delivered, stated: 'If we were agreed as to the Crocodile's head, we should be so as to that of other animals; because the Crocodile is intermediate between mammals, birds, and fishes.' Admitting, with some latitude, the reason, a sense of the importance of a determination of the bones answerable to those previously defined in *Chelonia* and Fishes, has influenced me in the foregoing description of the skull of the *Crocodylia*.

§ 33. *Skull of Ophidia*.—The skull in Lacertians and Ophidians departs from the vertebral pattern by a greater degree of confluence and a minor extent of neurapophysial ossification, than in *Crocodylia*: and that of Serpents manifests more strongly the principle of adaptive development.

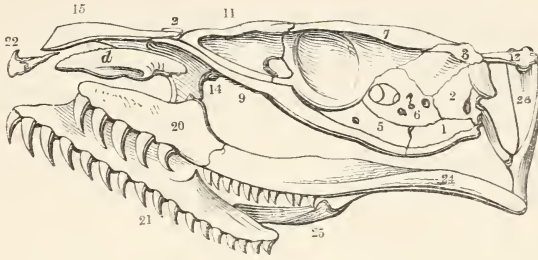
Eustachian canals in *Crocodylia*. See also the preparations, *XLIV.*, Nos. 706, 727, 728, 750, pp. 154—164.

<sup>1</sup> *Ib.* *XLIV.*, p. 163, where that characteristic of *Crocodylus rhombifer* is specified.

<sup>2</sup> *Ib.* No. 764, p. 166.

In the Python, figs. 96 and 97, the basioccipital, 1, is subhexagonal, broadest anteriorly, smooth and concave above, suturally rough on each side, with a recurved pointed hypapophysis: the hinder facet forms the lower half of the occipital condyle, on each

96



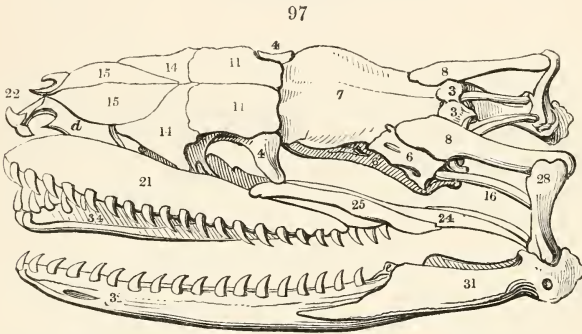
Section of the Skull of a Python

side of which is a small sharp process. The basioccipital unites above with the exoccipital, 2, and alisphenoid, 6; and in front with the basisphenoid, 5. The exoccipitals (2, 2) are each produced backward into a peduncular process supporting a moiety of the upper half of the occipital condyle: at the outer side of the base of the peduncle is an obtuse process, forming the upper part of the ridge continued upon the basioccipital. The outer and fore part of the exoccipital expands, and is perforated by a slit for the eighth pair of nerves, articulates below with the basioccipital, is excavated in front to lodge the petrosal cartilage where it articulates with the alisphenoid, and unites above with the superoccipital, 3. This is of a subrhomboidal form, sends a spine from its upper and hinder surface, expands laterally into oblong processes, is notched anteriorly and sends down two thin plates from its under surface, bounding on the mesial side the surface for the cerebellum, and by the outer side forming the inner and upper parts of the acoustic cavities. The superoccipital articulates below with the exoccipitals and alisphenoids, and in front with the parietal, by which it is overlapped in its whole extent. The occipital vertebra is as if it were sheathed in the expanded posterior outlet of the parietal one, the centrum resting on the oblique surface of that in front, and the anterior base of the neural spine entering a cavity in and being overlapped by that of the preceding neural spine: the analogy of this kind of 'emboitement' of the occipital in the parietal vertebra with the firm interlocking of the ordinary vertebræ of the trunk is



very interesting: the end gained seems to be, in grovelling reptiles liable to have the head bruised, an extra protection of the epencephalon—the most important segment to life of all the primary divisions of the cerebrospinal axis. The thickness of its immediately protecting walls (formed by the basi-, ex-, and super-occipitals) is equal to that of the same vertebral elements in the human skull; but they are moreover composed of very firm and dense tissue throughout, having no diploë: the epencephalon also derives a further and equally thick bony covering from the basisphenoid and the parietals, the latter being partly overlapped by the mastoids, fig. 97, 8, which form here a third layer of the cranial wall.

The basisphenoid, fig. 96, 5, and presphenoid, 9, form a single



Skull of a Python

bone, and the chief keel of the cranial superstructure. The posterior articular surface looks obliquely upward and backward, and supports that of the vertebral centrum behind, as the posterior ball of the ordinary vertebræ supports the oblique cup of the succeeding one: here, however, all motion is abrogated between the two vertebræ, and the co-adapted surfaces are rough and sutural. The basisphenoid presents a smooth cerebral channel above for the mesencephalon, in front of which a deep depression (sella) sinks abruptly into the expanded part of the bone, and there bifurcates, each fork forming a short cul-de-sac in the substance of the bone. The transverse processes from the under and lateral surfaces are well marked, strong, but short, much thicker in the Python than in the Boa. The alisphenoids, 6, form the anterior half of the fenestra ovalis, which is completed by the exoccipitals; and in their two large perforations for the posterior divisions of the fifth pair of nerves, as well as in their

relative size and position, the alisphenoids agree with those of the Frog. Each alisphenoid is a thick suboval piece, with a tubercular process on its under and lateral part: it rests upon the basisphenoid and basioccipital, supports the posterior part of the parietal and a portion of the mastoid, 8, and unites anteriorly with the descending lateral plate of the parietal bone.

The parietal, 7, is a large and long, symmetrical roof-shaped bone, with a median longitudinal crest along its upper surface, where the two originally distinct moieties have coalesced. It is narrowest posteriorly, where it overlaps the superoccipital, and is itself overlapped by the mastoid: it is convex at its middle part on each side the sagittal spine, and is continued downward and inward to rest immediately upon the basisphenoid, 5. This part of the parietal seems to be formed by an extension of ossification along a membranous space, like that which permanently remains so in the Frog, between the alisphenoid and orbitosphenoid: the mesencephalon and the chief part of the cerebral lobes are protected by this unusually developed spine of the mesencephalic vertebra. The optic foramina are conjugational ones, between the anterior border of the lateral plate of the parietal and the posterior border of the corresponding plate of the frontal.

The frontals, 11, rest by descending lateral plates, representing connate orbitosphenoids, upon the presphenoidal prolongation of the basisphenoid: the upper surface of each frontal is flat, subquadrate, broader than long in the Boa, and the reverse in the Python, where the roof of the orbit is continued outward by a detached superorbital bone: there is a distinct, oval, articular surface near the anterior median angle of each frontal to which the prefrontal, 14, is attached: the angle itself is slightly produced to form the articular process for the nasal bones. The smooth orbitosphenoidal plate of the frontal joins the outer margin of the upper surface of the frontal at an acute angle; the inner side of each frontal is deeply excavated for the prolongation of the cerebral lobes, and the cavity is converted into a canal by a median vertical plate of bone at the inner and anterior end of the frontal. The frontals join the parietals and postfrontals behind, and, by the connate orbitosphenoid plates, the presphenoid below, the prefrontals and nasals before, and the superorbitals at their lateral margins. The orbitosphenoidal plates have their bases extended inward, and meet below the prosencephalon and above the presphenoid, as the neurapophyses of the atlas meet each other above the centrum. The anterior third part of such inwardly produced base is met by a downward production of the mesial margin of the frontal, forming a septum

between the olfactory prolongations of the brain, but is not confluent with the frontal septum: the outer portion of the orbitosphenoïdal plate is smooth externally, and deeply notched posteriorly for the optic foramen.

The post-frontal, fig. 97, 4, is a moderately long trihedral bone, articulated by its expanded cranial end to the frontal and parietal, and bent down to rest upon the outer and fore angle of the ectopterygoid, 25. It does not reach that bone in the Boa, nor in poisonous Serpents. In both the Boa and Python it receives the anterior sharp angle of the parietal in a notch.

The natural segment which terminates the cranium anteriorly, and is formed by the vomerine, prefrontal and nasal bones, is very distinct in the Ophidians.

The vomer is divided, as in some ganoid Fishes and Batrachians, but is edentulous: each half is a long, narrow plate, smooth and convex below, concave above, with the inner margin slightly raised: pointed anteriorly, and with two processes and an intervening notch above the base of the pointed end. The prefrontals, 14, are connate with the lacrymals. The two bones which intervene between the vomerine and nasal bones are the turbinals, fig. 96, *d*, they are bent longitudinally outwards in the form of a semicylinder about the termination of the olfactory nerves.

The spine of the nasal vertebra is divided symmetrically as in the Frog, forming the nasal bones, fig. 97, 15; they are elongated, bent plates, with the shorter upper part arching outward and downward, completing the olfactory canal above; and with a longer median plate forming a vertical wall, applied closely to its fellow, except in front, where the nasal process of the premaxillary is received in the interspace of the nasals.

The acoustic capsule remains in great part cartilaginous: there is no detached centre of ossification in it: to whatever extent this capsule is ossified, it is by a continuous extension from the alisphenoid. The long stapes, fig. 97, 16, extends from the 'fenestra vestibuli' to the subcutaneous ear-drum attached to the tympanic bone, 28. The sclerotic capsule of the eye is chiefly fibrous, with a thin inner layer of cartilage; the olfactory capsule is in a great measure ossified, as above described.

*Maxillary arch.*—The palatine, fig. 96, 20, or first piece of this arch is a strong, oblong bone, having the inner side of its obtuse anterior end applied to the sides of the prefrontals and turbinals, and, near its posterior end, sending a short, thick process upward and inward for ligamentous attachment to the lacrymal, and a second similar process outward as the point of suspension of the

maxillary bone: between these processes the palatine is perforated, and behind them it terminates in a point. The chief part of the maxillary bone, 21, is continued forward from its point of suspension, increasing in depth, and terminating obtusely: a shorter process is also, as usual, continued backward. The point of suspension of the maxillary forms a short, narrow, palatine process: the dental branch of the supramaxillary nerve penetrates the upper and fore part of this process, and its chief division escapes by a foramen on the outer and fore part of the maxillary. A space occupied by elastic ligament intervenes between the maxillary and the premaxillary, 22, which is single and symmetrical, and firmly wedged into the nasal interspace: the anterior expanded part of this small triangular bone supports two teeth. Thus the bony maxillary arch is interrupted by two ligamentous intervals at the sides of the premaxillary key-bone, in functional relation to the peculiar independent movements of the maxillary and palatine bones required by Serpents during the act of engulfing their usually large prey.

Two bones extend backward as appendages to the maxillary arch; one is the 'pterygoid,' 24, from the palatine, the other the ectopterygoid, 25, from the maxillary. The pterygoid is continued from the posterior extremity of the palatine to abut against the end of the tympanic pedicle: the under part of its anterior half is beset with teeth, fig. 96, 24. The ectopterygoid, 25, overlaps the posterior end of the maxillary, and is articulated by its posterior obliquely cut end to the outer surface of the middle expanded part of the pterygoid.

*Mandibular arch.*—The tympanic bone, 28, is a strong, trihedral pedicle, articulated by an oblique upper surface to the end of the mastoid, 8, and expanded transversely below to form the antero-posteriorly convex, transversely concave, condyle for the lower jaw. This consists chiefly of an articular 31, and a dentary 32, with a small coronoid and splenial piece. The articular piece, 31, including the angular and surangular elements of the Crocodile, ends obtusely, immediately behind the condyle: it is a little contracted in front of it, and gradually expands to its middle part, sends up two short processes, then suddenly contracts and terminates in a point wedged into the posterior and outer notch of the dentary piece. The articular is deeply grooved above, and produced into a ridge below. The coronoid is a short compressed plate: the splenial is a longer plate applied to the inner side of the articular and dentary. The outer side of the dentary has a single perforation near its anterior end: this is united to that of the opposite ramus by elastic ligament.



The skull of the Boa Constrictor differs from that of the Python, not only in the greater breadth of the frontals, but in that of the nasals; in the absence of the superorbital, in the more slender and cylindrical form of the ectopterygoid, and in the larger and higher internal border of the coronoid. But the mechanism of the jaws is the same. By the elastic matter joining together the extremities of the maxillary and mandibular bones, those on the right side can be drawn apart from those on the left, and the mouth can be opened not only vertically, as in other vertebrate animals, but also transversely, as in insects. Viewing the bones of the mouth that support teeth in the great constricting serpents, they offer the appearance of six jaws—four above and two below; the inner pair of jaws above are formed by the palatine and pterygoid bones, fig. 96, 20–24, the outer pair by the maxillaries, ib. 21, the under pair by the mandibles, or ‘rami,’ as they are termed, of the lower jaw, fig. 97, 31–32.

Each of these six jaws, moreover, besides the movements vertically and laterally, can be protruded and retracted, independently of the other: by these movements the Boa is enabled to retain and slowly engulf its prey, which may be much larger than its own body. At the first seizure the head of the prey is held firmly by the long and sharp recurved teeth of all the jaws, whilst the body is crushed by the overlapping coils of the serpent; the death-struggles having ceased, the Constrictor slowly uncoils, and the head of the prey is bedewed with an abundant slimy mucus: one jaw is then unfixed, and its teeth withdrawn by being pushed forward, when they are again infixed, further back upon the prey; the next jaw is then unfixed, protruded, and reattached; and so with the rest in succession—this movement of protraction being almost the only one of which they are susceptible whilst stretched apart to the utmost by the bulk of the animal encompassed by them: thus, by their successive movements, the prey is slowly and spirally introduced into the wide gullet.

In comparing the skull of a poisonous with that of a constricting Serpent, the differential characters consist, in the Rattlesnake (*Crotalus*) e. g., chiefly in the modification of form and attachments of the maxillary, which is movably articulated to the palatine, ectopterygoid, and lacrymal bones; but chiefly supported by the latter, which presents the form of a short, strong, three-sided pedicle, extending from the anterior external angle of the frontal to the anterior and upper part of the maxillary. The articular surface of the maxillary is slightly concave, of an oval shape: the surface articulating with the ectopterygoid on the poste-

rior and upper part of the maxillary is smaller and convex. The maxillary bone is pushed forward and rotated upon the lacrymal joint by the advance of the ectopterygoid, which is associated with the movements of the tympanic pedicle of the lower jaw by means of the true pterygoid bone. The premaxillary is edentulous. A long, perforated poison-fang is ankylosed to the maxillary. The palatine bone has four or five, and the pterygoid from eight to ten, small, imperforate, pointed, and recurved teeth. The frontal bones are broader than they are long: there are no superorbitals. A strong ridge is developed from the under surface of the basisphenoid, and a long and strong recurved spine from that of the basioccipital; these give insertion to the powerful 'longi colli' muscles, by which the downward stroke of the head is performed in the infliction of the wound by the poison-fangs.

The skull of the typical Ophidian reptiles most resembles that of Lizards, but lacks the outer diverging appendage, formed by the malar and squamosal, of the maxillary arch. It differs from that of Batrachians in the distinct basi- and superoccipitals; in the superoccipital forming part of the ear-chamber; in the basioccipital combining with the exoccipital to form a single articular condyle for the atlas; in the ossification of the membranous space between the elongated parietals and the sphenoid; in the constant coalescence of the parietals with one another; in the connation of the orbitosphenoids with the frontals, and in the meeting of the orbitosphenoids below the prosencephalon upon the upper surface of the presphenoid; in the presence of distinct postfrontals, and the attachment thereto of the ectopterygoids, whereby they form an anterior point of suspension of the lower jaw, through the medium of the pterygoid and tympanic bones; in the connation of the prefrontals and lacrymals.

In the *Amphisbæna fuliginosa* coalescence still further simplifies the cranial structure: the parts of the epencephalic arch constitute a single occipital bone; the superoccipital crest extends forward into a sagittal one; a small foramen marks the boundary: the premaxillary is single, and, with the rest of the upper jaw, is fixed; the tympanic is short, compared with that of true Serpents, and extends almost horizontally forward, in a line with the lower jaw which it supports; the coronoid is more developed. The nostrils, divided by the premaxillary, are terminal; or even, as in *Lepidosternon*, may open behind the fore end of the skull: in this Amphisbænian the maxillaries overlap the nasals to join the premaxillary.<sup>1</sup>

<sup>1</sup> CLXXIII., pl. 15, figs. 8, 11.

§ 34. *Skull of Lacertilia*.—Lizards, like Serpents, have the cranial bones, especially those of the hæmal arches and appendages, more elongated, slender, and liberated than in Crocodiles and Chelonians; the temporal vacuities and orbits are large, and the external nostrils are apart. Lizards retain the malo-squamosal bar connecting the maxillary with the tympanic; and some of them develop, as in the Crocodile, the upper zygomatic arch formed by the post-frontal and mastoid. The neurapophysial walls of the parietal and frontal segments retain much of their fibro-cartilaginous tissue; and the cranial roof is there sustained by a bony pillar on each side ('columella' of Cuvier), which has its base implanted in a fossa of the pterygoid, and underprops the parietal near its outer border. The homologies of the cranial bones of the Python, figs. 96 and 97, with those of the Crocodile, figs. 93, 94, and 95, being recognised, those of any Lizard will be readily understood.

In a New Zealand Gecko (*Rhynchocephalus*<sup>1</sup>) the occipital condyle is unusually elongated transversely, and presents the form of a crescentic, convex bar, bent upward. The basisphenoid sends down two short processes to abut against the pterygoids. The parietal bone is perforated by a small median fontanelle close to the sagittal suture: its upper surface presents two strong curved and approximated temporal crests, divided by a median, angular, longitudinal furrow: the crests are continued outward upon the posterior bifurcated part of the parietal to be continuous with that forming the upper border of the mastoid: the frontal is divided by a median suture, as is the parietal in the common Gecko. The posterior frontal supports a strong, obtuse ridge forming the back part of the frame of the orbit, and unites below with the malar and behind with the mastoid. The premaxillary bones are divided by a median suture, and their dentigerous border projects below the level of that of the maxillary bones. The vomer is likewise divided by a median suture. The palatal apertures of the nostrils are bounded behind by the vomer and palatal plate of the maxillary: this plate is of unusual breadth, as compared with the Lizards generally, and presents the unusual peculiarity of a dentigerous ridge parallel with the posterior half of the alveolar border. It is situated close to the inner side of this border, leaving only space sufficient for the reception of the teeth of the under jaw. The teeth are confluent with the summits of the proper and accessory alveolar ridges. The palatine bones are united together along the anterior halves. The rami of the lower jaw are not anchylosed at the symphysis. The alveolar border is

<sup>1</sup> CLVIII.

serrated by a single row of anchylosed teeth. The coronoid piece is triangular, rises into a point, and presents a smooth articular surface on its inner side, adapted to the anterior lateral projection of the pterygoid.

In the skull of the black Scink (*Cyclodus niger*), the frontal and parietal bones are thick and expanded; the parietal is bifurcated behind, and articulated with the mastoids and paroccipitals. The postfrontals are separated from the malars by the squamosals, which extend between the malars and the mastoids to form the strong lateral bony arch resting anteriorly upon the malar and the maxillary, and posteriorly on the parietal and tympanic. Concomitantly with the strong osseous roof of the cranium, there is an arrest of osseous developement in the fibro-membranous neurapophysial walls of the cranium: two lateral processes extend downward into these walls from the parietal and forward from the exoccipitals; but the protective office of the alisphenoids is solely performed by the columnar 'columellæ,' which extend from the interspaces of the processes above mentioned, to rest upon the upper groove of the pterygoids. The orbitosphenoids are represented by still more slender bony styles, which circumscribe the outlets for the optic nerves, and form the anterior boundary of the prosencephalic division of the cranium. The lacrymal bones are large and divided on each side, as in most Lizards. The premaxillaries are confluent, and their nasal process separates the external nostrils from each other. Each pterygoid presents a rough surface towards the palate, but does not support teeth. There is a small ossicle between the pterygoid processes of the sphenoid and the true pterygoid bones. The columelliform stapes is extremely long and slender.

In the Iguana the parietal supports a single median crest: the posterior margin of the frontal is notched by the fronto-parietal fontanelle: both lacrymal and postfrontal are subdivided into two pieces; the lacrymal foramen is a 'conjugalional' one between the two pieces. The upper portion of the lacrymal represents the facial part of the prefrontal; it does not send down a neurapophysial plate to join the vomer or palatines, nor forms any part of the lateral walls of the rhinencephalic cavity, or of the foramen for the transmission of the olfactory nerves. The palatine nostrils, fig. 98, *D, n*, are very long, and notch the large palatines, 20; the pterygoids, 24, each support a row of small teeth.

In the skull of the Monitor Lizard (*Varanus niloticus*) the basioccipital sends down a pair of short, obtuse hypapophyses: those of the basisphenoid are larger and abut against the ptery-



goids: these bones are applied to the back part of the tympanic, and the slender 'columella' rests upon the middle of their upper surface. The parietal is perforated near its anterior border. The postfrontal has a descending postorbital process. The prefrontal develops a partial post-lateral wall for the rhinencephalic chamber; externally it supports an antorbital dermal bone: the small perforated lacrymal is a distinct bone. The nasal and premaxillary are both single bones, as in most Lacertians. The malar, wedged anteriorly between the maxillary, palatine, lacrymal and ectopterygoid, curves backward as a slender style terminating in a point, leaving the orbit uncircled by bone behind: the squamosal, wedged behind between the mastoid and tympanic, curves forward to a point beneath the postfrontal.

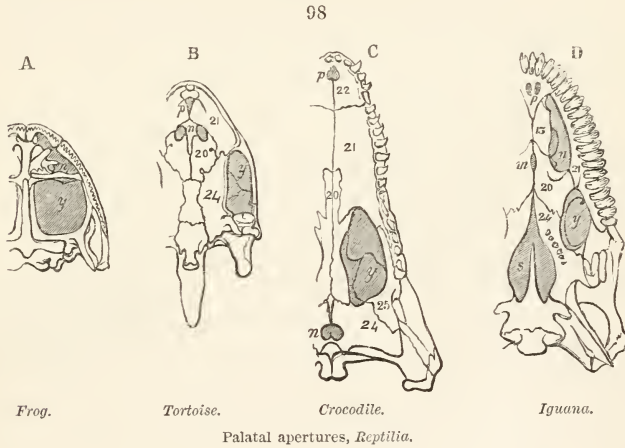
In the American Monitor (*Tejus nigropunctatus*) the nasals are divided: the malar articulates behind with the postorbital—a dismemberment of the postfrontal, which continues the zygomatic arch with the squamosal: there is no 'foramen parietale.'

In the Chameleon the teeth are short, and so confluent with the jaws that these appear to have simply a serrated margin. The external nostrils perforate the maxillary bone; a long, compressed, serrated crest arches upward and backward from the superoccipital and parietal bones, and joins the processes of bone continued from the mastoids. In the *Chameleo bifurcus* the anterior fork-like productions are formed by the maxillary and prefrontal bones. The premaxillary at the bottom of the cleft is very small.

In *Draco volans* there is merely the rudiment of a spine or ridge from the superoccipital; an arched transverse ridge separates the occipital from the parietal region of the skull. The postfrontal, mastoid, and paroccipital project successively from their respective cranial segments, and well manifest their character as the transverse processes of these.

The vacuities in the bony palate are many, and show much variety in the cold-blooded, especially the reptilian, series, in regard to their number, kind, and relative size. The most constant are those which are more or less circumscribed by the maxillary and pterygoid, and constitute a pair. They are present in *Polypterus* and most Ganoids, bounded outwardly by the maxillary, medially by the palatine, and behind by the pterygoid. In the Menopome the vomer, fig. 73, *l*, forms the median and the pterygoid, *f*, the posterior boundary. In the Frog, fig. 98, *A*, the pterygo-maxillary vacuities, *y*, are divided from each other by the basisphenoid; whilst the palatine forms the front boundary and separates them from the nasal apertures, *n*. In

Lizards, *ib. D*, the palatine 20, and pterygoid 24, form the median boundary, the maxillary, 21, and ectopterygoid the outer one of *y*. In the Crocodiles, *ib. c*, the palatine 20 forms the median, the ectopterygoid 25 the outer, the maxillary 21 the fore, and the pterygoid 24 with the ectopterygoid the hind, boundary. In the Chelonia there is no ectopterygoid to divide the pterygo-maxillary vacuity from the lower opening of the temporal fossa. The next openings in point of constancy are the palatal, or posterior, or internal nostrils — ‘palatonares;’ but they are variously formed and situated. In the Menopome, *fig. 73*, there is no palatine bone to divide them from the pterygo-maxillary vacuity; in *fig. 98 A*, the Frog, the transverse palatine forms the posterior boundary of the palatonares, *n*, the vomer the inner, and the maxillary the outer, boundary; they are similarly encompassed in the Lizards,



*ib. D, n*. In the Crocodiles, the palatonares, *ib. c, n*, form a single aperture surrounded by the pterygoids, and situated far back. There is also a single premaxillary foramen, *ib. c, p*, at the fore part of the bony palate. This is sometimes divided into two by the premaxillary, like the external nostrils, as in the Iguana, *ib. D, p*. In most Lizards there is a more or less elongate ‘interpterygoid’ vacuity, *ib. D, s*, bounded behind by the hypapophyses of the basisphenoid, laterally by the pterygoids, and usually extending some way between the palatines. In the *Mosasaurus* the interpterygoid fissure does not extend far back between the pterygoids, but is bounded in a greater proportion by the palatines. Sometimes there is a distinct small ‘interpalatine’ vacuity, *ib. m*, in

advance of the interpterygoid; and more rarely there occurs an 'intervomerine' vacuity still more in advance.

Thus there are definable and nameable, in the bony palate of reptiles, the 'pterygo-maxillary,' 'palatonarial,' 'premaxillary,' 'interpterygoid,' 'interpalatal,' and 'intervomerine' vacuities or foramina—more or less valuable as characters of recent and extinct species.

§ 35. *Skull of Ichthyopterygia*.—Amongst the illustrations of extreme varieties in the reptilian skull which Palæontology has brought to light, may be cited the *Ichthyosaurus*, the *Dicynodon*, and the *Pterodactylus*.

That of the first combines in a peculiar manner some piscine with reptilian characters. It differs from all existing *Reptilia* in the great size of the premaxillary, fig. 105, 22, and small size of the maxillary, 21; in the lateral aspects and antorbital position of the nostrils; in the immense size of the orbits, and in the large and numerous sclerotic plates, which latter structures give to the skull of the *Ichthyosaurus* its most striking features.

The two supplemental bones of the skull, which have no homologues in existing Crocodilians, are the postorbital and supersquamosal; both, however, are developed in *Archegosaurus* and the Labyrinthodonts. The postorbital is the homologue of the inferior division of the postfrontal in those Lacertians—e. g., *Iguana*, *Tejus*, *Ophisaurus*, *Anguis*, in which that bone is said to be divided; but in *Ichthyosaurus* it more resembles a dismemberment of the malar, 26. Its thin obtuse scale-like lower end overlaps and joins by a squamous suture the hind end of the malar: the postorbital expands as it ascends to the middle of the back of the orbit, then gradually contracts to a point as it curves upward and forward, articulating with the supersquamosal and postfrontal, 12. The supersquamosal may be in like manner regarded as a dismemberment of the squamosal, 27; were it confluent therewith, the resemblance which the bone would present to the zygomatic and squamosal parts of the mammalian temporal bone would be very close; save that the squamous part would be removed from the inner to the outer wall of the temporal fossa. The nostril is bounded by the lacrymal, 73, nasal, 15, maxillary, 21, and premaxillary, 22, bones. It is distant from the orbit about half its own long diameter. Like the orbit, the plane of its outlet is vertical.

The pterygo-maxillary vacuities are very long and narrow, broadest behind, where they are bounded, as in Lizards, by the anterior concavities of the basisphenoid, and gradually narrowing to a point close to the palatine nostrils. These are smaller than

in most Lizards, and are circumscribed by the palatines, ectopterygoid, maxillary, and premaxillary. The pterygomalar fissures are the lower outlets of the temporal fossæ; their sudden posterior breadth, due to the emargination of the pterygoid, relates to the passage of the muscles for attachment to the lower jaw. The parietal foramen is bounded by both parietals and frontals, 11; its presence is a mark of labyrinthodont and lacertian affinities; its formation is like that in *Iguana* and *Rhynchocephalus*. The occipitoparietal vacuities are larger than in *Crocodylia*, smaller than in *Lacertilia*; they are bounded internally by the basi-, ex-, and super-occipitals, externally by the parietal and mastoid. The auditory apertures are bounded by the tympanic and squamosal: the tympanic, 28, takes a greater share in the formation of the 'meatus auditorius' in Lizards; in Crocodiles the bone 28 is restricted to that which it takes in *Ichthyosaurus*.<sup>1</sup>

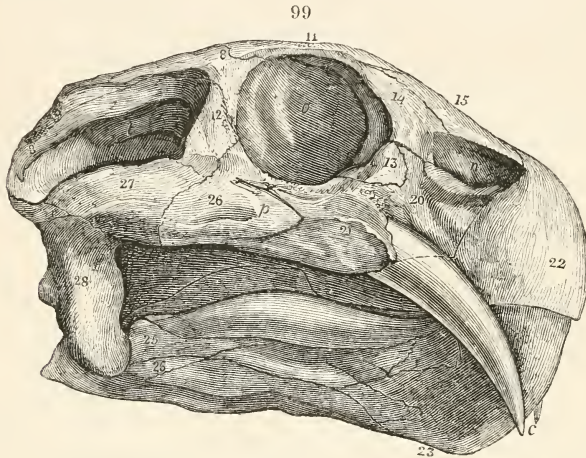
In comparing the jaws of the *Ichthyosaurus tenuirostris* with those of the gangetic Gharrial, an equal degree of strength and of alveolar border for teeth result from two very different proportions in which the maxillary and premaxillary bones are combined together to form the upper jaw. The prolongation of the snout is the same: the difference of structure relates to the collective tendency of the affinities of the *Ichthyosaurus* to an antecedent hæmatocryal type of structure still partly shown by Lizards. The backward or antorbital position of the nostrils, like that in whales, is related to the marine existence of the Ichthyosaurs. But in the Labyrinthodonts, in which the nostrils are nearer the fore part of the head, their anterior boundaries are formed by the premaxillaries, as in modern Lizards: it appears, therefore, to be in conformity with these affinities that the premaxillaries of the Ichthyosaur should enter into the same relation with the nostrils, although this involves an extent of anterior development proportionate to the length of the jaws, the forward production of which sharp-toothed instruments fitted the Ichthyosaur, like the modern Dolphin for the prehension of agile fishes.

§ 36. *Skull of Dicynodontia*.—The skull of the *Dicynodon*, fig. 99, is articulated with the atlas by a single condyle, formed by the basi- and ex-occipitals in equal proportions: the latter have coalesced, as in the Crocodiles, with the paroccipitals. The parietals form one bone, perforated by a small 'foramen parietale' close to the coronal suture. The frontals, 11, contribute a share to the superorbital border; their median suture is distinct, as is that

<sup>1</sup> CXLVII. p. 388.



between the nasals, 15. The prefrontal, 14, extends to the nostril, *n*. The lacrymal, 13, forms the rest of the fore part of the orbit, extending forward upon the face. The sides of the premaxillary, 22, bend abruptly down in front of the nostrils, to join the maxillary, 20, 21; this forms the lower boundary of the nostril, *n*, and joins above and behind with the prefrontal, lacrymal, and nasal bones: the maxillary projects below the orbit, like a forward continuation of the zygoma, becomes more prominent as it advances, and soon forms the outer angle of the three-sided socket of the canine tusk, *c*. There is a single but strong zygomatic arch formed by the malar, 26, and squamosal, 27, abutting against the upper end of the tym-



Skull of *Dicynodon*

panic pedicle, 28. The rami of the lower jaw augment in depth from the angle to the symphysis, where they are confluent. The angle projects a very little way beyond the articulation. The articular surface is moderately concave, and looks obliquely upward and backward. The elements of the posterior half of the ramus answer to the articular, angular, 26, and surangular, 25. A thin vertical splenial plate, on the inner side of the ramus, begins about an inch in advance of the angle, and extends forward to the symphysis, at the back part of which it appears to become confluent with its fellow. The part answering to the angular diverges from the surangular, and forms the hind boundary of an oblong vacuity at the middle of the side of the ramus, the fore part of which vacuity is formed by a bifurcation of the dentary element, 23. This is thickened and strengthened by a ridge, subsiding at the vertical channel upon the side of the symphysis, receiving the

tusk, *s*, when the mouth is closed. The symphysis of the mandible is peculiarly massive—broad, high, and thick. Anteriorly it is convex in every direction; it is bent or produced upward, terminating in a broad trenchant margin, like the fore part of the lower mandible of a macaw. The modification of the back part of the cranium, especially the great expansion due exclusively to the development of ridges for augmenting the surface of attachment of muscles (for the brain of the cold-blooded reptile would need but a small spot of the centre of the occipital plates for its protection), indicates the power that was brought to bear upon the head as the framework in which were strongly fixed the two large tusks. The strength or resistance of the cavities receiving the deeply implanted bases of the tusks was increased by the ridges developed from the outer part of their bony wall.

Only the Crocodiles now show a like extent of ossification of the occiput, and only the Chelonians the trenchant toothless mandible; but in both the outer nostril is single and median: the Lizards repeat the divided apertures for respiring air: in Mammals alone do we find a development of canine tusks like that in the Dicynodonts.

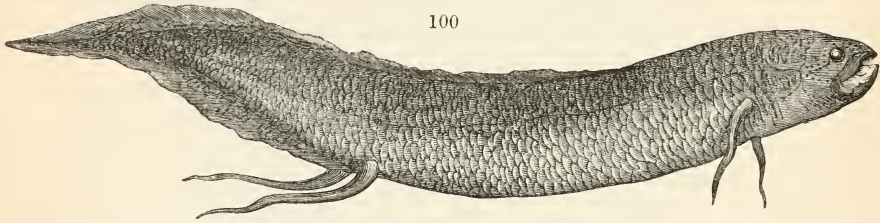
§ 37. *Skull of Pterosauria.*—The skull of the Pterodactyle, fig. 111, was as remarkable for its light and delicate structure as that of the Dicynodont for its compact massiveness. It had a single occipital condyle: a post-fronto-mastoid arch and a malosquamosal arch on each side; the latter abutting against the end of the tympanic pedicle. The orbit was large, and the eyeball defended by sclerotic plates. The external nostrils were divided, and placed about midway between the orbits and the muzzle. There was a large vacuity between the orbits, *o*, and nostrils, *n*. The jaws varied much in length in different species.

§ 38. *Scapular arch and appendage.*—Parts which project from the body to act on the surrounding medium commence as a bud or fold of skin, within which is formed the framework, in texture and structure according to the work to be done. The reaction of the medium, whether air, water, or earth, calls for the due resistance usually afforded by junction of the projecting part with a segment of the endoskeleton. Thus, in Fishes, the frame of the opercular flap articulates with the tympano-mandibular arch: that of the branchiostegal (gill-covering) flap with the hæmal arch of the parietal vertebra: that of the pectoral flap or limb with the same arch of the occipital vertebra. The frame of the caudal flap or fin is attached to the terminal vertebræ of the body: those of the dorsal and anal fins are less firmly inter-

locked with the neural and hæmal spines of more advanced vertebræ.

All these various supports of flaps, fins, or limbs belong to the same natural genetic group of skeletal parts: their peripheral rays are not 'dermal bones;' they are developed between folds, not in the substance, of the integument; although in some instances they press away the skin and become coated by a ganoid conversion or calcification of its outer layer.

The most simple condition of the parial (pectoral and pelvic) limbs is manifested by the *Lepidosiren*, fig. 100. A filamentary appendage is sustained by a single many-jointed cartilaginous ray, fig. 101 A, a. In one species there are attached at right angles to the pectoral ray fine filaments sustaining the narrow fold of membrane continued from its posterior side. A similar series of finer rays supports the membrane continued from the dorsal detached dermoneurals of *Polypterus*.



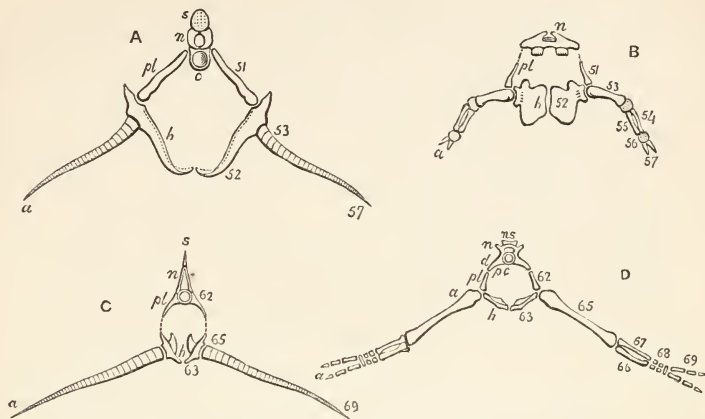
*Protopterus (Lepidosiren) annectens.* XXXIII.

The arch sustaining the pectoral limbs of *Lepidosiren* is also simple, departing least from its archetypal condition. A long straight cylindrical bone, fig. 101, A, 51, *pl*, is attached by a short ligamentous mass to the epencephalic arch, *ib. n*, of which it is the rib, or 'pleurapophysis,' assuming in ulterior developements the special name of 'scapula.' With each scapula is articulated a larger and more flattened bone, *ib. 52*: the two converge and meet at their lower ends, completing, as hæmapophyses, a widely expanded hæmal arch. The entire segment, A, conforms to the thoracic modification of the archetype vertebra, fig. 19; and, similarly, is expanded in order to encompass and protect the heart: but it is simplified by the absence of the hæmal spine in *Protopterus*, as the neural spine is sometimes wanting in a neural arch. The hæmapophysis, *h*, in ascending the vertebrate scale, assumes special forms, signified by the term 'coracoid,' with the number 52. In

*Protopteri*, as in more piscine *Hæmatocrya*, the coracoid exclusively supports the appendage or limb.

From the condition exemplified in fig. 101, A, the development

101



Elementary limbs, A, C, *Lepidosiren*; B, D, *Amphiuma*, cxl.

of the pectoral member diverges in two directions: one by multiplication of many-jointed rays, the other by simplification as to number of rays and joints, with special modification and differentiation of the latter.

§ 39. *Pectoral limb of Fishes.*—The first series of modifications is now confined to Fishes: but, before describing the appendage, a brief notice of the arch is requisite.

In most Osseous Fishes the pleurapophysis of the occipital, like that of the two antecedent cranial vertebræ, is in more than one piece; but the divisions do not exceed two. The upper piece (*suprascapula*) is commonly bifurcate, as in the Cod, figs. 34, 75, 81, 50, the lower prong answering to the 'head,' the upper one to the 'tubercle' of the thoracic rib in the Crocodile: the latter articulates with the transverse process (*paroccipital*). The lower piece (*scapula*), ib. 51, is a slender straight bone, pointed below, and mortised into a groove of the coracoid, ib. 52. The two parts of the scapula are confluent in the Siluroid Fishes. In the Murenoids the suprascapula is ligamentous, and loosely appends the scapular arch to the skull. In the *Plagiostomi* the arch is detached from its vertebra, and has receded in position, to allow, as it seems, for the great expanse of the appended fin.

The hæmapophysis, or 'coracoid,' figs. 34, 38, 39, 75, 85, 52, is longer and usually broader than the scapula. In the Cod-tribe,



its pointed upper extremity projects behind that bone and almost touches the suprascapula; a broad angular plate of the coracoid projects backward and gives attachment to the radiated appendage, below which it bends inward and forward, gradually decreasing to a point, which is connected by ligament to its fellow, and to the urohyal bone, fig. 43. The inner side of the coracoid is excavated, and its anterior margin folded inward and backward, lodging the origin of the great lateral muscle of the trunk.

In most fishes the lower end of the arch is completed, as in the Cod, by the ligamentous symphysis of the coracoids; but in the Siluri and Platycephali the coracoids expand below, and are firmly joined together by a dentated suture. In all Fishes they support and defend the heart, and form the frame, or sill, against which the opercular and branchiostegal doors shut in closing the great branchial cavity; they also give attachment to the aponeurotic diaphragm, dividing the pericardial from the abdominal cavity.

To the inner side of the upper end of the coracoid there is attached, in the Cod and Carp, a bony appendage in the form of a single styloform rib; but in other Fishes this is more frequently composed of two pieces, as in the Perch. This single or double bone, figs. 34, 38, 85, 58, is slightly expanded at its upper end in the Cod-tribe, where it is attached by ligament to the inner side of the angular process of the coracoid: its slender pointed portion extends downward and backward, and terminates freely in the lateral mass of muscles. In the *Batrachus* its upper extremity rises above the coracoid, and is directly attached to the spinous process of the atlas. In some Fishes, as the Snipe-fish (*Centriscus Scolopax*), the Cock-fish (*Argyreiosus Vomer*), the Lancet-fish (*Siganus*), it is joined by the lower end to the corresponding bone of the opposite side, thus completing an independent inverted arch, behind the scapular one. There is some reason, therefore, for viewing the bone 58 as representing the hæmal arch of the atlas, or its hæmapophysial portion.

The usually free lower extremities of these hæmapophyses, together with their taking no share in the direct support of the pectoral fins, and their inconstant existence, oppose the view of their special homology with the coracoids of higher Vertebrates. To that with the 'clavicles' of higher classes it has been objected that these bones are always situated in those classes in advance of the coracoids; but this inverted position may be a consequence of the backward displacement of the scapula and coracoid in the air-breathing Vertebrates.

The appendage of the scapular arch, in most Osseous Fishes,

is composed of three segments: the first, of two, rarely of three, bones immediately articulated with the coracoid; the next, of a series of from two to six smaller bones; which, lastly, support a series of spines or jointed rays. These rays serially repeat the branchiostegal rays in the hyoidean appendage, and the opercular rays in the tympanic appendage. The vegetative repetition of digits and joints, and the vegetative sameness of form in those multiplied peripheral parts of the fins of Fishes, accord with the characters of all other organs on their first introduction into the animal series. The single row of fewer ossicles, figs. 34 and 81, 56, supporting the rays, 57, obviously represents the double carpal series in Mammals; and the bones of the brachium and antibrachium seem in like manner to be reduced to a single series, 54, 55. In the ventral fin, fig. 34, *v*, no segment is developed between the arch, 63, and the digital rays, 70: it is in this respect like the branchiostegal fin, 40, 44.

The pectoral fin is directed backward, and being applied, prone, to the lateral surface of the trunk, the ray or digit answering to the thumb is toward the ventral surface. The lowest of the bones supporting the carpus should, therefore, be regarded as the *radius* (figs. 34 and 81, 54), holding the position which that bone unquestionably does in the similarly disposed pectoral fin of the Plesiosaur, fig. 45, 54, and Cetacea. The upper bone, which commonly affords support to a smaller proportion of the carpal row, may be compared to the ulna (ib. 55). As a third small bone is articulated to the coracoid, in some Osseous Fishes, at least in their immature state, the name of humerus may be confined to that bone: but in these it is generally above and on the inner side of the ulna, and seems to be rather a dismemberment of it. In the *Salmonidæ*, it is more distinctly developed; it is articulated in the Bull-trout (*S. eriox*)<sup>1</sup> to the middle of the back part of the coracoid by a transversely elongated extremity; and is expanded at its distal end, where it articulates by cartilage with the radius and ulna. In the Cod, Haddock, and most other Fishes there is no separate representative of the humerus: in these the ulna is a short and broad plate of bone, deeply emarginate anteriorly, attached by suture to the coracoid, and by the opposite expanded end to the radius, and to one or two of the carpal ossicles, and directly to the upper or ulnar ray of the fin.

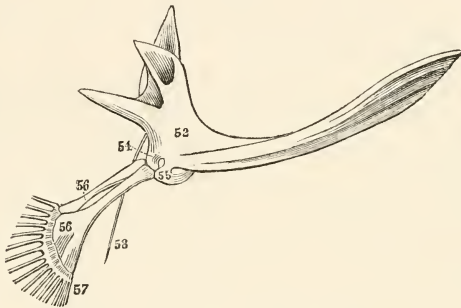
In the Bull-head and Sea-scorpion (*Cottus*), the radius and ulna are widely separated, and two of the large square carpal

<sup>1</sup> XLIV. p. 18, No. 46.

plates in their interspace articulate directly with the coracoid. A similar arrangement obtains in the Gurnards and the Wolf-fish; but the carpals in the interspace of the radius and ulna are separated from the coracoids by a space occupied by clear cartilage; and in the Wolf-fish the intermediate carpals are almost divided by two opposite notches. The ulna is perforated in all these fishes. The radius is of enormous size in the Opah (*Lampris*), the Cock-fish, fig. 38, and the Flying-fish; it is ankylosed with the coracoid in the *Silurus*, to give firmer support to the strong serrated pectoral spine. Both radius and ulna are connate with the coracoid in the Angler (*Lophius*, fig. 102, 54, 55).

The ossicles called *carpals* are usually four or five in number,

102



— Coracoid and bones of pectoral fin, Angler (*Lophius*)

as in the Cod tribe, fig. 81, 56; they progressively increase in length from the ulnar to the radial side of the carpus, especially in the Parrot-fish (*Scarus*) and the Mulletts (*Mugil*). They are three in number and elongated in the Polypterus, fig. 103, 56, but are reduced to two in number, and more elongated in the *Lophius*, fig. 102, 56; thus they retain in this species and in the Sharks, fig. 104, their primitive form of 'rays;' but change to broad flat bones in the Wolf-fish, just as the rays of the opercular fin exchange that form in the Plagiostomes for broad and flat plates in ordinary Osseous Fishes.

The rays representing the *metacarpal* and *phalangeal* bones are, in the Cod, twenty in number, and all soft, jointed, and sometimes bifurcate at the distal end. Their proximal ends are slightly expanded and overlap each other, but are so articulated as to permit an oblique divarication of the rays to the extent permitted by the uniting fin-membrane, the combined effect being a movement of the fin, like that called the 'feathering of an oar.' Each

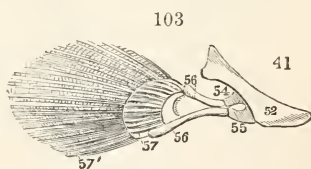
soft and jointed ray splits easily into two halves as far as its base, and appears to be essentially a conjoined pair.

In the series of Osseous Fishes the rays of the pectoral and ventral fins offer the same modifications as those of the median fins, on which have been founded the division into 'Malacopterygians' and 'Acanthopterygians': in the former, the last or ulnar fin-ray, is usually thicker than the rest; in the latter it is always a hard, unjointed spine: in some Fishes it forms a strong pointed or serrated weapon (*Silurus*). In the Gurnards, fig. 82, the three lowest rays are detached and free, like true fingers; and are soft, multi-articulated, and larger than the rest; they are supplied by special nerves, which come from the peculiar ganglionic enlargements of the spinal chord, and are organs of exploration and of subaqueous reptation.<sup>1</sup> In all the Gurnards the natatory part of the pectoral member is of large size; but in one species (*Dactylopterus*) it presents an unusual expanse, and is able by its stroke to raise and sustain for a brief period the body of the fish in the air. The pectoral fins present a still greater development in the true Flying-fish (*Exocetus*).

In some Malacopteri and Ganoidei a segment analogous to a metacarpus may be distinguished by modification of structure from the phalangeal portion of the fin rays: in the *Polypterus* there are seventeen simple cylindrical metacarpal bones, fig. 103, 57, the middle ones being the longest: they sustain thirty-five digital rays, and are supported by carpal bones, ib. 103, 56, of which two are almost as remarkable for their length as in the *Lophius*; the third, shorter and broader, is wedged into the interspace of the two longer ones, but does not directly join the metacarpus.

The carpus is supported by a small radius, 55, and ulna, 54, which articulate directly with the coracoid. A further approach to the higher conditions of the pectoral member is made by the same Fish in the carpal portion projecting freely from the side of the body, as in the *Lophioid* Fishes. In the *Salmon*, where eleven such metacarpals support thirteen or fourteen fin-rays, the carpus is short and consists of four bones.

In the *Plagiostomes* the scapular arch is detached from the occiput, the conditions of its displacement being the more varied and vigorous use, or the enormous expanse, of the pectoral fin; per-



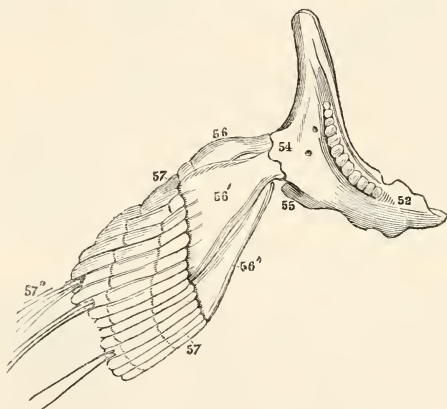
Bones of pectoral fin of *Polypterus*

<sup>1</sup> CLIX. p. 46.



haps, also, the more posterior position of the heart in these Fishes. In the Sharks and Chimæra the arch is loosely suspended by ligaments from the vertebral column: in the Rays the point of resistance of their enormous pectoral fins has a firmer, but somewhat anomalous attachment, by the medium of the coalesced upper ends of the suprascapular pieces to the summits of the spines of the confluent anterior portion of the thoracic abdominal vertebræ. In the Sharks the scapular arch consists chiefly of the coracoid portions, fig. 104, 52, which are confluent together beneath the pericardium which they support and defend; the scapular ends of the arch, connected to the coracoids by ligament, project freely upward, backward, and outward. To a posterior prominence of the coracoid cartilage corresponding with the anchylosed radius and ulna, ib. 54, 55, in the Lophius, there are attached, in the Dog-fish and most other Sharks, three sub-compressed, sub-elongated carpal

104



Cartilages of the pectoral fin and arch of the Dog-fish (*Spinax acanthias*)

cartilages, the uppermost, ib. 56, the smallest, and styliiform; it supports the upper or outer phalangeal ray. The next bone, ib. 56', is the largest and triangular, attached by its apex to the arch, and supporting by its base the majority of the phalanges. The third carpal, ib. 56'', is a smaller but triangular cartilage, and supports six of the lower or radial phalanges. Three joints (metacarpal and digital) complete each cartilaginous ray or representative of the finger, ib. 57; and into the outer surface of the last are inserted the fine horny rays or filaments, ib. 57'', the homologues of the claws and nails of higher Vertebrata, but which on their first appearance, in the present highly organised class of Fishes, mani-

fest, like other newly introduced organs, the principle of vegetative repetition, there being three or four horny filaments to each cartilaginous unguial phalanx.

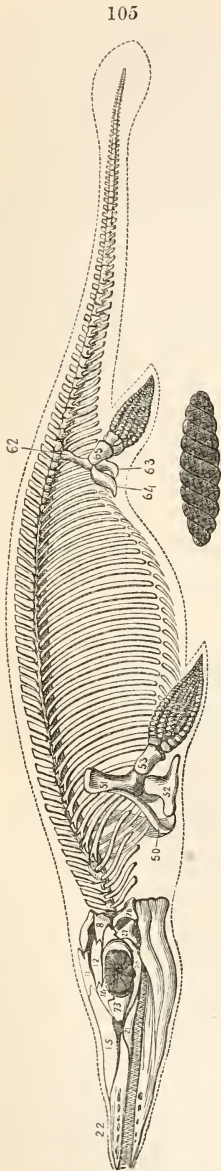
On the fore part of the coracoid arch, near to the prominence supporting the fin, there are developed a vertical series of small bony cylindrical nuclei in the substance of the cartilage in most Sharks. In the Rays the coraco-scapular arch forms an entire circle or girdle attached to the dorsal spines: it consists of one continuous cartilage in the *Rhinobates*, but in other Rays is divided into coracoid, scapular, and suprascapular portions, the latter united together by ligament. The scapula and coracoid expand at their outer ends, where they join each other by three points, to each of which a cartilage is articulated homologous to the three above described in the Shark, and which immediately sustain the fin-rays. The posterior cartilage answering to the upper one in the Shark curves backward and reaches the ventral fin: the anterior cartilage curves forward, and its extremity is joined by the antorbital process as it proceeds to be attached to the end of the rostral cartilage; the middle proximal cartilage is comparatively short and crescentic, and sustains about a sixth part of the fin-rays, which are the longest, the rest being supported by the anterior and posterior carpals, and gradually diminishing in length as they approach the ends of those cartilages.

Development by irrelative repetition of parts reaches a maximum in the present plagiostomous group. In the common Ray, fig. 64, there are upwards of a hundred many-jointed fingers in each pectoral limb: but all are bound up in a common function of the simplest kind.

§ 40. *Pectoral limb of Reptiles.* — The other route of development from the prototypal condition exemplified in fig. 101, A and C, leads to a differentiation of the several divisions and parts of the limb, and their adaptation to particular functions or parts of combined and varied mechanical actions.

The first step, as manifested in the Amphiume, ib. B, C, is the formation of a long inflexible segment, as a lever of greater resistance, 53 and 65; this is followed by a pair of similar, but shorter cylindrical bones, each sustaining a ray of few joints. The proximal bone assumes through ulterior developements the special name 'humerus,' or arm-bone, with the symbol 53, in the fore limb; and of 'femur,' or thigh-bone, with the symbol 65, in the hind limb. The two bones of the next segment become, in the fore limb, 'radius,' 54, and 'ulna,' 55 — collectively, antibrachium or 'fore-arm;' in the hind limb, tibia, 66, fibula, 67 — collectively,

the cnemion or leg. The mass of fibro-cartilage, in which more or fewer ossicles are subsequently developed, interposed between the antibrachium and terminal rays, is the 'carpus,' 56: the corresponding mass in the hind limb is the tarsus, 68. The terminal rays are the digits, called 'hand,' and 'fingers,' 69, in the fore limb; 'foot' and 'toes' in the hind limb. The proximal joints of these rays, being bound together in a sheath of integument, are differentiated as 'metacarpals' in the hand, and 'metatarsals' in the foot. The other joints are the 'phalanges,' ultimately distinguished as 'proximal,' 'middle,' 'distal' or 'ungual,' as usually supporting a claw or nail.



Skeleton of *Ichthyosaurus*, with cast of spiral intestine. CLXIII.

In the extinct *Ganocephala*, and in the few surviving ichthyomorphous or pennibranchiate Batrachia, the simple type of limb, as in fig. 101, B, is retained; only that the digital rays increase in number from the 'two' in *Amphiuma*, to 'three' in *Proteus*, and to 'four' in *Menopoma*, fig. 43, 57, and *Axolotes*.

In the extinct *Ichthyopterygia* the digits may be seven, eight, or nine in number, and consist of numerous short joints — a significant mark of piscine affinity: they are bound together, but converge towards a point: the joints are of a flattened angular form, and interlock with those of the contiguous digit, the whole forming a continuous, broad, slightly flexible basis of support to the fin. The essential distinction from the fin of the fish is shown by the well developed 'humerus,' 53, and by the complex scapular arch. The two antibrachial bones retain the piscine shortness and breadth; and the metacarpal series is less distinctly defined than in some fishes.

The scapula, 51, is short and straight, displaced backward from the occiput, and contributing to form the shoulder-joint, as in the *Batrachia* and higher air-breathers: but it shows a certain breadth and flatness. The coracoid, 52, is still broader, not cartilaginous as in most perennibranchs, but well ossified, and united below with its fellow, and with a small 'episternum' of a triradiate form, one ray of which is wedged into the fore part of the intercoracoid fissure. There is also a pair of bones, 50, long and slender, articulated with the fore border of the scapula and the transverse rays of the episternum: they are the clavicles. A supplementary flattened bone, the 'epicoracoid,' is wedged between the scapula, clavicle, and coracoid. The above complex and powerful scapular arch would enable the fore-paddles to act upon the land with sufficient power to effect a shuffling forward movement of the body, as in the Turtle (*Chelone*) and Seal tribe: but the main office of the fore-limb in the Ichthyosaurus was that of a pectoral fin.

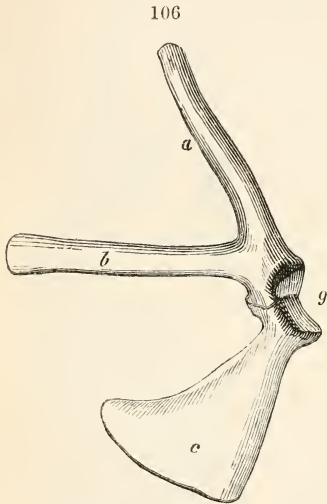
In the *Plesiosaurus*, fig. 45, the limbs acquired a development more closely accordant with that in *Chelone*. The scapula, 51, develops an acromial process representing the clavicle. The coracoid, 52, is unusually extended in the trunk's axis, and is united with its fellow by a long symphysis interposed between the anterior abdominal rib and the episternum; it articulates at its fore part with the episternum and clavicular process, and, further back, with the lower end of the scapula to form the humeral joint.

The humerus is proportionally longer than in *Ichthyosaurus*; the radius is better developed, and slightly expanded at both ends; the ulna retains a flattened reniform shape. The carpal series is distinct, in a double row of ossicles, the largest at the radial side of the wrist, the opposite side retaining more unossified material. The digits are five in number, with the proximal and more elongated joints representing a metacarpus. The phalanges are shorter, and decrease in size to the tips of the digits, which converge. The first or radial digit has generally 3 phalanges, the second from 5 to 7, the third 8 or 9, the fourth 8, the fifth 5 or 6: all are flattened and included in a common sheath of integument like those of the Turtle; but the paddle had no claws.

The scapular arch retains the same essential simplicity in the Chelonian as in the Sauropterygian order, only the acromial or clavicular process is relatively longer, more like a collar bone; it extends from near the articular part of the scapula toward the median line, in advance of the coracoid, fig. 51, o, with the medial end ligamentously attached to the episternal. In the



Tortoise (*Testudo*) it is shorter, in *Chelys*, fig. 106, *b*, it is longer than the scapula, *a*. This bone in all Chelonians is a strong, straight columnar one, with the upper end connected by ligament with the inner surface of the first costal plate, fig. 51, *n*; it descends almost vertically to the shoulder-joint, of which it forms, in common with the coracoid, the 'glenoid' cavity, fig. 106, *g*. The coracoid, suturally united at that end with the scapula, passes inward and backward, fig. 51, *o*, expanding and becoming flattened at its median end, which does not meet its fellow nor articulate with the sternum. The coracoid is broad and short in the Tortoise;



Scapular arch, *Chelys*. CLI.

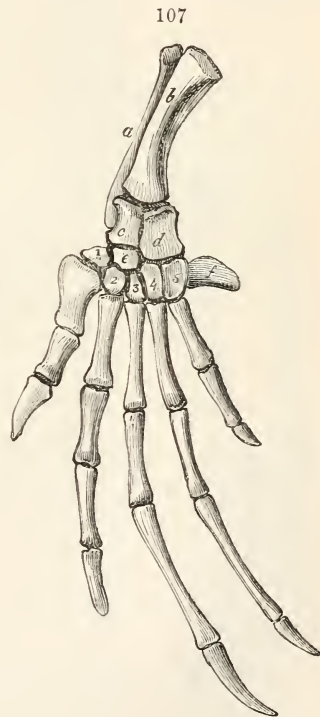
long and slender in *Chelone* and *Emys*, fig. 51, *o*, of intermediate proportions in *Trionyx* and *Chelys*, fig. 106, *c*. The scapular arch and proximal part of the limb being included in the thoracic abdominal box, the humerus is peculiarly bent and twisted in the terrestrial species in order to emerge from the front fissure, and plant the foot on the ground, fig. 51, *p*. In the Tortoise the ordinary position of the fore-limb is that of extreme pronation, with the olecranon forward and outward, and the radial side of the hand downward. The capsule of the shoulder-joint includes a considerable part of the neck of the

humerus. The hemispheroid head projects unusually from the back part of the bone, which looks upward: the tuberosities are large and bent toward the palmar aspect: that which is internal in most animals is here 'postero-superior;' that called 'external' is 'postero-internal' in position; from the former is continued the 'deltoid crest.' The distal end is expanded and rather flattened from before backward. In the Turtle the humeral shaft and its lower end is compressed laterally: and the bone is almost straight in those marine species; in all Chelonia it is solid throughout. The ulna is shorter, and in the Turtle, fig. 107, *b*, the olecranon is less developed than in the Tortoise, fig. 108, *b*, 55. The contrast between the marchers and the swimmers is most striking in the proportions of the toes. In the Turtle, fig. 107, the pollex, *i*, is short and has two phalanges after the

metacarpal: the last phalanx supporting a claw. The three middle digits, *ii*, *iii*, *iv*, have each three long phalanges, the last being flattened and without a claw; the fifth has two phalanges. All these are connected together by a web. In the Tortoise, fig. 108, all the toes are very short and subequal; and each has one metacarpal and two phalanges, the last supporting a claw; the few species in which the fifth has but one phalanx and no claw form the genus *Homopus*, Dum. and Bib. In *Emys europæa*, fig. 51, T, U, the first and fifth digits have each a metacarpal and two phalanges; the others have three phalanges; the last bears a claw in each digit. In the Soft or Mud-turtles, the pollex has two phalanges, the second with a claw; the three middle digits have each three phalanges, but only the index and medius have the claw; the fifth digit has two phalanges and no claw, whence the generic name *Trionyx*, proposed for these frequenters of the muddy estuary.

In the Crocodilia the scapular arch consists of a simple scapula, fig. 57, 51, and coracoid, ib. 52, and fig. 54, 8: these compressed, narrow, moderately long plates of bone, are thickest where they are united together to form the glenoid cavity for the humerus. In each, the bone contracts beyond the articular expansion, becomes sub-cylindrical, but soon again flattens and expands to its opposite end; that of the scapula is free, that of the coracoid joins the lateral border of the sternum. There is no trace of clavicle, no acromial projection from the scapula.

The humerus, fig. 51, 53, presents two curves: the articular head is a transversely elongated, sub-oval convexity; it is continued upon the short, obtuse, angular prominence, answering to the inner or ulnar tuberosity. The radial crest begins to project from the shaft at some distance from the head of the bone. There is a longitudinal ridge on the anconal surface close to the radial border.



Bones of fore-arm and paddle, *Chelone*. CLI.

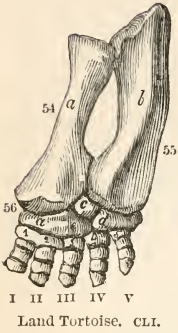
The distal end is transversely extended and divided anteriorly into two condyles. The shaft has a medullary cavity smaller than in land lizards. The radius, fig. 57, *t*, fig. 109, *b*, 54, has an oval head, an almost cylindrical and straight shaft, with an oblong and subcompressed distal end. The ulna, fig. 57, *s*, fig. 109, *a*, 55, articulates with the outer condyle of the humerus by an oval facet, the thick convex border of which swells out behind like the beginning of an 'olecranon;' the shaft of the ulna is compressed transversely and curves slightly outward; the distal end is less than the proximal one, and articulates with the second and third bones of the carpus. The first metacarpal supports two phalanges, I, the second three, II, the third and fourth, each four, the fifth, V, three phalanges which are very slender; but the proportions are shown in the cut; only the toes, I, II, and III, have the claw. All are basally united by a short web, but the fore-foot is chiefly used in movements upon land.

In the Monitor (*Varanus niloticus*) the supra-scapula is a broad semio ossified plate: the scapula is short and broad, and appears to have coalesced with the coracoid. This bone is much expanded, and has two deep notches anteriorly, and a perforation near the humeral articulation. In some Lizards it sends forward an acromial process. The coracoid is shorter and broader than in the Crocodile, abuts against the upper margin of the rhomboidal sternum, and sends off two processes from its anterior border, the one next the scapula abutting against the transverse branch of the episternum; the other against the sub-ossified epicoracoid: this element overlaps that of the opposite side. In the Monitor, as in most Lizards, there are distinct clavicles: usually long and slender bones, with more or less expanded extremities, extending from the body of the episternum and accompanying the transverse branch to abut against the scapula; and sometimes also reaching the outer process of the coracoid. In *Lacerta*, Cuv.

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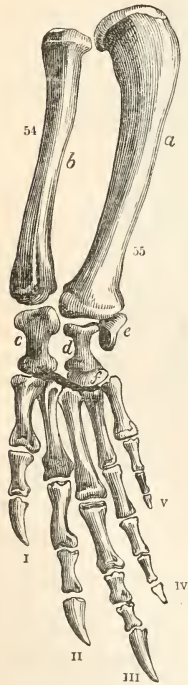
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108



I II III IV V  
Land Tortoise. CLI.

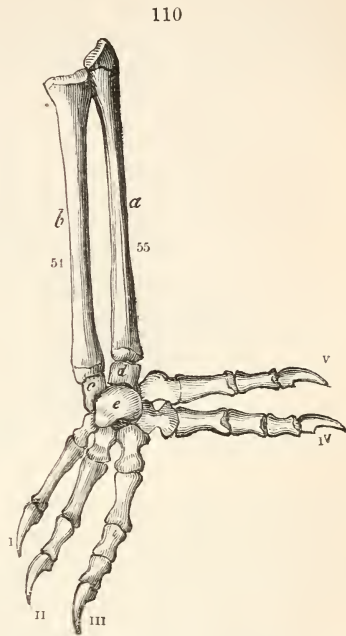
109



Bones of fore-arm and  
foot, Crocodile. CLI.

and *Scincus*, the clavicle expands at its medial half, which has a large vacuity or perforation occupied by membrane. In the Chameleon the scapular arch is as simple as in the Crocodile, but the coracoid is shorter and broader.

The humerus in Lacertians is usually larger and straighter, fig. 50, *Draco volans*, than in the Crocodiles, with a more compact wall and wider medullary cavity. The radius, ib. and fig. 110, *b*, 54, is almost straight, and slender, with an oval proximal articular concavity, and a distal surface partly convex, partly concave. The ulna, fig. 110, *a*, 55, shows the olecranon better developed than in the Crocodile: its distal articular surface is convex. The digits are five in number, the phalanges are 2, 3, 4, 5 and 3, counting from the metacarpal of the first to that of the fifth digit: each has a claw supported on a moderately long, compressed, curved, and pointed phalanx. The Chameleon offers an exception



Bones of fore-arm and foot, Chameleon. CLI.

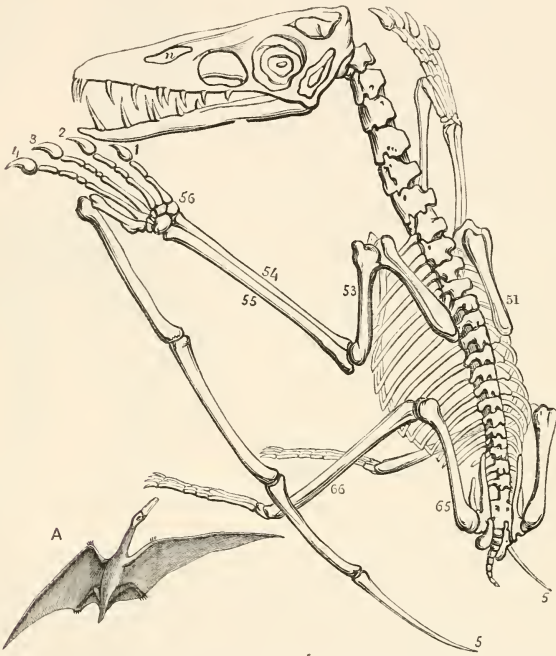
to the numerical rule, the phalanges being 2, 3, 4, 4, 3; and the direction of the digits modified for the scansorial function in these arboreal Lacertians: I, II, and III, enveloped by the skin as far as the claws, are directed forward; IV, and V, similarly sheathed, are directed backward: and the joints are shorter and broader than in Land-lizards.

The fore limbs in *Draco volans* accord with the usual lacertian type, and take no share in the support of the parachute. But in the extinct order of truly volant Reptiles (*Pterosauria*) they were modified for the exclusive support and service of the wings. The scapula, fig. 111, 51, long, narrow, flattened, and slightly expanded, lay more parallel with the spine than in land and sea Reptiles. The coracoid, strong and straight, and combining, as usual, with the scapula to form the glenoid cavity, articulated at the opposite end with a groove at the fore-part of a discoid sternum, which part is produced and keeled. The humerus, ib.



53, is more expanded at its proximal end than in the Crocodile or Lizard; the inner (ulnar) tuberosity is more prominent, the radial crest much more developed: with a base coextensive with one fifth of the shaft of the bone, it extends in a greater proportion from the shaft, affording a powerful lever to the muscles inserted into it. The articular head is reniform. The shaft is cylindrical:

111



Skeleton of *Pterodactylus crassirostris*. A. Restoration of Pterodactyle. CLXXX.

the walls thin and compact, the cavity large, and was filled with air as in birds of flight.<sup>1</sup>

The 'pneumatic foramen,' or that by which the air passed from a contiguous air-cell into the bone, is situated on the fore (palmar) side, a little below the radial end of the head of the bone. The radius, ib. 54, and ulna, ib. 55, are very long, straight, and closely connected together. The digits show the lacertian number of

<sup>1</sup> CXLIX. p. 16. CLXVI. p. 451. This discovery breaks down the following distinction: 'Au reste, on distingue toujours l'humérus d'un lézard de celui d'un oiseau, parceque le premier n'est pas creux ni percé de trous pour l'entrée de l'air dans son intérieur.' CLI. v. pt. 2, p. 296.

phalanges from the first to the fourth, and slightly increase in length: each terminated by a deep compressed, curved and pointed unguis phalanx. The modification converting the limb into a wing is confined to and concentrated upon the fifth digit, *ib. 5*: its metacarpal presents almost the thickness of an antibrachial bone: the proximal phalanx, of equal thickness, has more than twice the length, and at the proximal joint shows a process like an olecranon. This is usually followed, as in *Pterodactylus crassirostris*, by three similarly elongated phalanges, of which the last gradually tapers to a point. The fore limb thus exceeds in length the whole body, and is presumed to have supported a membranous wing, as in the sketch A, fig. 111.

Such are the chief modifications by which the fore-limb, in the Reptilian series of cold-blooded air-breathers is or has been adapted for aquatic, amphibious, terrestrial, arboreal, and aerial life. Before, however, quitting this subject, it may facilitate the comprehension of the homologies of the carpal series of ossicles, by concluding with a separate and serial review of them in the Reptilian group.

In the Toad (*Bufo*) the carpus includes eight bones: the two principal are the 'lunare,' fig. 44, C, *l*, and 'cuneiforme,' *ib. c*, respectively articulating with the radial and ulnar divisions of the antibrachial bone, *ib. 54, 55*; the scaphoid, C, *s*, presents its 'inter-medial' position between the lunare and the four ossicles on the radial side of the distal series: these consist of the trapezium *t*, trapezoides *tr*, magnum *m*, and the divisions of the unciform *u* for the fourth and fifth digits; that for the fifth being the largest of the five bones. The thumb, I, is represented by its metacarpal only; the index, fig. 44, A, II, and medius, III, have each a metacarpal with two phalanges; the digits IV and V have each three phalanges.

In the Tortoise (*Testudo*, fig. 108), the antibrachium articulates with three carpals forming the proximal row; the first or radial bone, *ib. a*, answers to the 'scaphoid' with the 'intermedium' *e*; the second *ib. c*, to the lunare; the third, *ib. d*, to the cuneiforme; the lunare being interposed between the ends of the radius and ulna. In the *Emys*, fig. 51, *s*, the carpus has a similar structure; but in some species there is a distinct pisiforme. In the Turtle (*Chelone*), the scaphoid is reduced in size, and represents only the intermedium, fig. 107, *e*; it is separated by the lunare *c*, from the radius *a*, and is pushed into a position analogous to that which its homotype the 'naviculare' holds in the mammalian tarsus. Without the light from the testudinate modification,

fig. 108, the bone *c*, fig. 107, might be taken for a connate 'scapholunar.' In both tortoise, terrapene, and turtle, the distal row of carpals consists, as in the Toad, of five bones, one to each of the five metacarpals. About their homology there is no difficulty; the bone, fig. 107, 1, which supports the pollex, 1, is the trapezium; the next 2, the trapezoïdes; the third 3, the magnum; and the fourth and fifth are the two parts showing the type-state of the connate bones, called 'unciform' in mammals. A bone analogous to a 'pisiform, *f*, fig. 107, is attached to the ulnar division, 5, of the unciform, and, usually, also articulates with the cuneiform in the Turtle. In *Chelys* and *Trionyx*, the bone answering to *a*, *e*, fig. 108, is divided; the part, *e*, answering to the 'intermedium;' *Trionyx* has also a 'pisiform.' The carpus in most Lacertians, e. g. in *Varanus niloticus*<sup>1</sup>, has the scaphoid reduced, as in *Chelone*, to the intermedial portion; but the trapezium unites directly with the lunare, and this articulates exclusively with the radius, simulating the scaphoid in position; it has, however, on its ulnar side, the 'cuneiform' articulating with the ulna, and a 'pisiform' terminates the proximal row. The distal row consists of five distinct bones; the unciform being divided, as in Chelonians. In the Chameleon, fig. 110, the proximal carpal series consists of the bones *c* and *d*, answering to the two respectively articulating with the radius and ulna in *Varanus*, and with those marked *c* and *d* in figs. 107 and 108. The second carpal row has received two interpretations. In one they are represented by the five subelongate bones having the distal joints of metacarpals; in the other they have coalesced into the single bone *c*, which otherwise would be merely an enlarged 'intermedium.' We shall afterwards see how the principle of 'serial homology' helps in the solution of such problems. The five bones radiating from the bone *c* are metacarpals; the first supports two, the second three, the third four phalanges, as in other Lacertians; and the equality of length in the opposing pair of digits, IV and V, is preserved by the deduction of a phalanx from the lacertian number.

The correspondence of the Chameleon's scapular arch with that of the Crocodile has been adverted to; and, similarly, the distal row of carpals is reduced to a single bone, fig. 109, *f*, in the Crocodile, supporting the medius, III, annularis, IV, and minimus, V, digits; and answering to the magnum and unciforme connate. The proximal row includes three bones answering to the lunare, *c*, and cuneiforme, *d*, in *Chelone*, fig. 107, and *Chameleo*, fig. 110;

<sup>1</sup> CLI. pl. XVII, fig. 45.

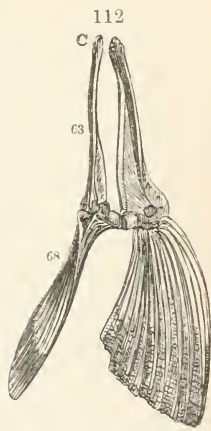
to which is added a pisiforme, fig. 109, *e*, in the usual position. The peculiarity of the bones *c* and *d* in *Crocodilia*, is their unusual length, showing a constricted shaft between the expanded ends, thus simulating metacarpals in shape, for which, when found as detached fossils, they have been mistaken.

The digits in the class *Reptilia* are generally characterised by a progressive increase in the number of their joints, from the first or innermost to the third or fourth; the *Chelonia* being the chief exceptions. In *Testudo*, fig. 108, each digit has one metacarpal and two phalanges; in *Test. tabulata* the fifth digit has but one phalanx.<sup>1</sup>

§ 41. *Pelvic arch and limb of Fishes.*—Some cold-blooded vertebrates, e.g. Murænoids and Ophidians, have neither fore nor hind limbs. In a few, e.g. *Anguillidæ*, *Gymnoti*, *Xiphias*, *Siren*, the scapular arch and limbs are present, but not the pelvic arch and limbs. In most fishes the latter exist, but less developed than the pectoral ones, and less fixed in position.

Only the hæmapophysial portion of the pelvic arch is developed in connection with the diverging appendages, termed in Fishes the 'ventral fins.' Their rays in osseous fishes, fig. 112, 68, are directly supported by the bones, 68, which, uniting together, near the point of attachment of the fins without an intervening bone, resemble their homotypes, the coracoids; by virtue of which 'serial homology,' we infer their special one with the ischia of higher animals. Each bone is a subtriangular plate, supporting the fin by its expanded end; and, either suspended in the flesh, as in the Salmon and Sturgeon, fig. 29, v, or attached by the narrower end to the coracoid, 52, as in the Cod, fig. 36, 63. The representatives of tarsal, tibial, and femoral bones, are wanting in all Fishes. In Acanthopterans one or more of the anterior rays of the ventral fin may be hard unjointed spines, as in the other fins; in Malacopterans all the ventral rays are soft, multiarticulate, and bifurcate.

In no fish is this incomplete pelvic arch directly attached to the vertebral column. If we may judge from the position in which the ventral fin appears in the development of the embryo fish, as



Pelvic arch and limbs,  
Trout (*Salmo*)

<sup>1</sup> XLIV. p. 205, No. 1079: see also pp. 206, 207, Nos. 1079, 1083, 1087, 1091, 1093, for further details of the bony structure of the fore foot in *Chelonia*.



a little bud attached to the skin of the belly, and from the fact that all the fishes in the geological formations anterior to the chalk are abdominal, that is, have the ventral fins near the posterior end of the abdomen, as in the Sturgeon, fig. 29, v, we may conclude that the supporting bones are, essentially, the hæmapophyses of the last rib-bearing (or pelvic) abdominal vertebra. Being suspended more or less freely from the under or ventral part of the body, these fins are subject to great diversity of position in relation to the two extremes of the abdomen. On these differences Linnæus based his primary classification of Fishes; he united together, for example, those fishes which have the pelvic or ventral fins near the anus, fig. 29, to form the order called '*Pisces Abdominales*;' those with the ventral fins beneath the pectorals, fig. 38, into an order called '*Pisces Thoracici*;' and those with the ventrals in advance of the pectorals, fig. 34, v, into an order called '*Pisces Jugulares*;' lastly, those fishes in which the ventral fins were absent formed the order called '*Pisces Apodes*,' indicating his recognition of the homology of such fins with the hinder or lower limbs of higher animals.

In the *Salmonidæ* (*S. Eriox*, fig. 112, c) the ischia, 63, are united by a cartilaginous symphysis at the medial line, and underlie the last six abdominal vertebræ. Each supports a ventral fin of nine rays, 68. In the Angler (*Lophius piscatorius*) the ischium is attached by one end to the coracoid, and expands at the opposite end to join its fellow, and support the six rays of the ventral. It also sends up a vertical process, simulating an ilium. The 'thoracic' character depends on the greater length of the ischia, as compared with that in the 'jugular' fishes. In the Lepidosiren, fig. 41, as in the Sturgeon, fig. 29, and other 'ventral fishes,' the ischia, 64, are suspended beneath their proper vertebra. They support in Lepidosiren a single-jointed ray, 66. In *Lepidopus*, in the Blennies, the Forked Hake (*Phycis*), the Forked Beard (*Raniceps*), and some other fishes, the ventral fins are likewise mere filamentary feelers. In the Lump-suckers (*Cyclopterus*), the ventrals unite together, and combine with part of the pectorals to form a sucking disc or organ of adhesion, below the head, just as the opercular and branchiostegal fins are united together to form the gill-cover. The ventral fin is better developed in the Plagiostomes than in other fishes. The supporting arch consists indeed of the same simple elements, hæmapophysial, cartilaginous, confluent at the middle line, and loosely suspended in the abdominal walls; but they do not immediately support the fin-rays. Two intermediate cartilages are articulated to the expanded outer ends of the inverted arch; the anterior is

the shortest in the Dog-fish, and supports three or four rays; the posterior one is much longer, and supports the remainder of the rays, fifteen or sixteen in number. To the end of this cartilage likewise is attached, in the male Plagiostomes, the peculiar accessory generative organ or clasper. In the *Torpedo* the arch sends forward two processes, and these are of greater length in the extinct *Cyclobates oligodactylus*, XL. p. 225, pl. 5. In the Chimeroids the short narrow processes which extend above the place of articulation of the ventral fins simulate iliac bones: the expanded portions which meet below represent the ischia; they are each of them perforated by a large round aperture, filled by membrane. The cartilage, answering to the tibia, supports the rays of the ventral fin and the clasper.

§ 42. *Pelvic arch and limb of Reptiles.* — Passing from the *Protopterus*, fig. 101, c, to the *Proteus*, ib. D, we find the pair of cartilages answering to the piscine 'ischia' aided by a second pair, 62, called 'ilia,' in supporting the diverging appendage; and this pair is attached to the ribs of the last abdominal or 'sacral' vertebra. The appendage or 'limb' now consists of definable segments, which are specialised through subsequent developments: the first, as the 'femur;' the second — a pair of shorter and smaller joints — respectively as 'tibia' and 'fibula;' these being followed, with the intervention of a cartilaginous 'tarsal' mass, by a pair of many-jointed rays or 'digits.'

A closer correspondence, however, with the piscine type was, in some respects, retained by the extinct *Ichthyosauri*, fig. 105.

Although the iliac element, 62, was joined with the ischial, 63, in supporting the fin, such sustaining arch remained freely suspended, as in the 'ventral fishes' of Linnæus. A second hæmapophysial arch, 64, was likewise present, in advance of the ischial one, answering to the 'pubis;' this afforded the extent of origin required by the muscles of the better developed fin. The next step in progress is exemplified by the single long and inferiorly flattened and expanded bone, 65, answering to the 'femur,' and through which, as on a pedicle, the fin could be more freely rotated, and moved to and fro. To the end of the femur were ligamentously articulated the two short flattened bones representing the tibia and fibula; followed by the series of multiarticulate digits, joined together to form the common basis of the fin, which, like the pectoral one, tapered to a point.<sup>1</sup>

With the increased length, and progressive differentiation of the several segments of the fin, as in *Plesiosaurus*, fig. 45, the pubic

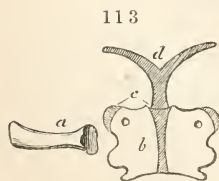
<sup>1</sup> No twist, real or imaginary, of humerus or femur obscures or is needed to explain the homotypes in the pectoral and pelvic members. CLX.

basis, 64, for muscular attachments, became co-expanded; the ischia also, 63, assumed the form of flattened triangular plates; and the ilia, though still 'long bones,' were stronger, and attached by ligament to the riblets of one or two vertebræ; and these, in *Nothosaurus*, became expanded for more effective fixation of the pelvic arch. A 'tarsus,' 68, and 'metatarsus,' are now definable; and the 'digits,' with fewer joints, do not exceed five in number. All the bones are solid in both *Ichthyo-* and *Sauro-pterygia*.

From the Sauropterygian type of pelvic arch and limb, the transition is easiest to that in the marine *Chelonia* of the present day. But the course of development from the *Proteus* will be here resumed and traced to the saltatory grade which the hind-limb acquires in the Batrachian order.

*Amphiuma tridactylum*, with proportionally shorter hind-limbs than in *Proteus* (fig. 101, D), has them terminated by three toes. *Menobranthus* shows four toes: and *Menopoma* five, which is the number usual in the hind-limbs of Newts and Salamanders. In *Menopoma*, fig. 43, the sacral vertebra, *s*, has a longer and stronger transverse process, *t*, and riblet, *pl*, than the vertebræ before and behind; and *pl* is united to the cartilaginous elements, 63 and 64, closing the inverted arch by the rib-like continuation, 62. To the lower end of this simple 'ilium' and conjoined part of the 'ischio-pubic' cartilage is ligamentously attached the short and simple femur. To this succeeds a shorter tibia and fibula — the latter reminding us of the plesiosaurian fibula, by its outward curve. The tarsus is cartilaginous in *Menopoma*; the metatarsals support 1, 2, 3, 3, 2 phalanges, respectively, from the innermost, 1, to the fifth, v. The toes are webbed to near the last joint. Every joint in the limb is syndesmotic, and the ossification of the bones is limited to an outer crust, covering persistent solid cartilage. In the decomposing body this dissolves away; and if the ossified parts become petrified, the fossil bone appears to have had a large medullary cavity.

In the Land-salamander the broad ischio-pubic plate, fig. 113,



Pelvis, Salamander.

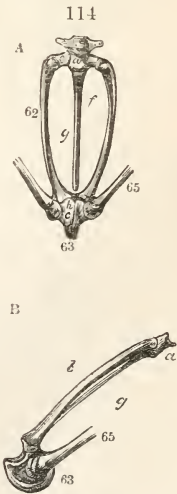
becomes ossified at *b*, but remains cartilaginous at the angles *c*, and the symphysis; whence it extends forward, and bifurcates, as at *d*, representing the last pair of abdominal ribs in higher reptiles. There is a vascular perforation in each pubic part of the plate. The ilium, *a*, retains its simple rib-like character.

The Tadpole, fig. 42, affords a significant example of the trans-

mutation of a natatory to a saltatory type of hind-limb, irrespective of efforts and exercises through successive generations producing and accumulating small changes, and independently of any selection by nature of such generations as were enabled, through the accidental variety of a slightly lengthened hind-limb, to conquer in the battle of life, and to transmit the tendency towards such disproportion to their posterity.

If the law by which so much of the change of structure adapted to terrestrial life takes place in the active independent aquatic animal be a mystery, and seeming exception, it does not the less impress the believer in the derivative origin of species with the idea of unseen and undiscovered powers, that may operate in producing such result, 'according to a natural Law or Secondary Cause.'<sup>1</sup>

The hind-limb of the Frog (*Rana*) closely accords at first with that of the Menopome; a rib-like continuation, fig. 42, 62, of the pleurapophysis, *pl*, of the last abdominal vertebra, gives attachment to a short femur, 65; ossification of the shorter tibia, 56, and fibula, 57, speedily unites them proximally; five subequal digits bud out of the primitive fin-like projection from the integument; and a simple cartilaginous tarsus, 68, at first intervenes between the toes and the leg. The due length and power of the hind-limb is produced by elongation of all its elements, including the iliac parts of the sustaining arch. In the Toad (*Bufo*) the sacral process, or anchylosed riblets, transmitting thereby the weight of the trunk upon the legs, are depressed and expanded at their extremities; in *Pipa*, fig. 44, B, *s*, remarkably so, and resting upon the anterior halves of the ilia. In the Toad the femur is shorter than the ilium, and the tibia is shorter than the femur. In the Frog, fig. 44, contrary proportions prevail. The impulse of the hind-limbs is applied, in all tailless Batrachia, to the hindmost part of the body, beyond the lengthened coccygeal style, fig. 114, A, *g*, by the remarkable backward production of the ilia, *ib*. A, 62, which expand and unite, forming a symphysis, above the acetabula; thence they transmit the impulse of the limbs to the short and strong transverse processes of the sacrum, *a*. A pair of commonly anchylosed semicircular bony plates, 'ischia,' 63, unite with the iliac symphysis to form the lower half of the joints for the femora, 65.



Front and side views of the pelvis, Frog

<sup>1</sup> CXLI. p. 86.



The femur in the Frog, fig. 44, 65, is a long slender bone, with a slight double bend; the head is expanded, convex, and terminal; the back part of the upper fourth of the shaft shows a longitudinal ridge; the distal end is expanded and truncate. Both ends of the femur are usually in the state of epiphyses. The tibia and fibula are confluent longitudinally, but preserve their respective medullary canals, and indicate their transcendental distinction by an anterior and posterior longitudinal furrow at the expanded ends of the seeming single bone; usually, also, by a perforation from before backward. A single epiphysis constitutes each articular end. The astragalus *a*, and calcaneum *cl*, are much elongated. The former is slightly bent. They commonly coalesce at their proximal and distal extremities; at the former, by means of an epiphysis; at the latter, with the connate representatives of the naviculare, *s*, and cuboides, *b*. Two cuneiform bones remain distinct and support the three inner toes, *i*, *ii*, *iii*: a third expanded bone projects, like a supplemental digit, *ci*, from the inner (tibial) side of the tarsus; it may represent the 'entocuneiform.' One (*Rana*) or two (*Pipa*) sesamoid bones are developed in the extensor tendons behind the tibio-tarsal joint: their function is that of the lever part of the calcaneum. The first metatarsal supports two phalanges, 1; the second, two; the third, three; the fourth, four; and the fifth, three.

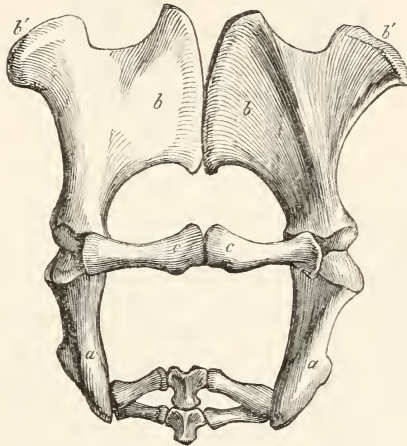
In *Bufo agua* I found a semiossified tubercle upon the proximal end of each ilium. In *Pipa*, the confluent calcaneum and cuboid form a long three-sided bone with the angles sharp: the long astragalus presents a similar form.

To the student of Comparative Anatomy entering upon the vast domain of that science with ideas of the bones derived from those of the human skeleton, and associating the special shapes and proportions they there present with the names that have been learnt from Anthropotomy, few parts are more perplexing or deceptive than the pelvis in the Chelonian reptiles. Viewing, for example, that of the *Trionyx*, as it is represented in fig. 116, he would conclude *h* to be the iliac bones, and *i* the pubic bones, separated at the symphysis; or as answering to the parts so called in the single 'os innominatum' of man. The rectification of the error affords a valuable lesson of the unimportance of size and shape in determining special homology, and of the necessity of knowing the foetal as well as the adult conditions of the human pelvis. He would learn, first, that the threefold nature of the 'innominate' bone, which is transitory in man, is permanent in the reptile; next, that the bone which is largest and

broadest in the human fœtal pelvis is the least and slenderest in that of the Turtle. To comprehend the nature of the Chelonian pelvis, the connections and relative positions of its bones must be studied in the entire skeleton.

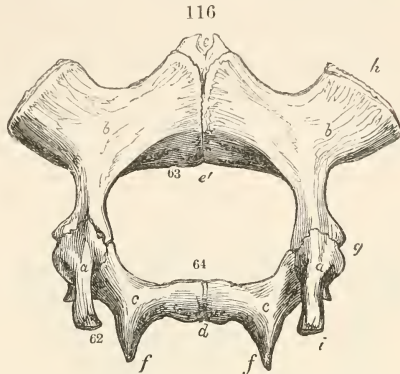
The two bones that articulate with the transverse processes of vertebræ and, extending 'hæmad' (downward or forward), combine at the opposite end with the other bones forming the acetabulum, are those alone which show the essential characters of the ilia in air-breathing vertebrates. In the figure of the pelvis of the Turtle viewed from below or from the hæmal aspect, fig. 115, that surface of the sacrum is figured to illustrate the

115

Pelvis of *Chelone* (from below). CLX.

above character of connection. Two stunted pleurapophyses converge from the two centrums, and afford a close ligamentous attachment to the proximal or upper ends of the ilia, *a, a*. These bones are also attached to the contiguous costal plates of the carapace, which they support as stout strong pillars. They slightly expand at their acetabular ends, where each unites with two other bones. The bone *c* descends and meets its fellow at the mid line, as does likewise the bone *b*: *c c* being posterior in position answer to the ischia of the human fœtus; *b b* to the pubics. These are remarkably expanded, and, besides forming an extensive symphysis between *b, b*, each developes a broad angular process or tuberosity which is ligamentously attached to the plastron, forming the foundation for the support of the pillar, *a*, that underprops the carapace.

A slight modification is presented by *Trionyx*, in which a view of the pelvis is given from the dorsal aspect, the sacrum being removed, in fig. 116: here *i* shows the end of the ilium, 62, which was attached to that part of the vertebral column: *a* is the expanded acetabular end of these short, straight, columnar bones.



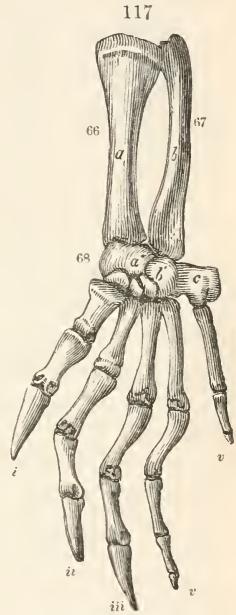
Pelvis of *Trionyx*, (from above, without the sacrum). CLI.

The ischia, *c, c*, develop tuberosities *f, f*, and unite at the ischial symphysis, 64, *d*. The pubics *b, b*, articulate by a broader tuberosity, *h*, with the plastron, and have a greater transverse extent. The 'outlet' of the pelvis is not, as might be supposed, between *e'* and 64, but between *i* and *f*. The wider space answers to the obturatorial one in Man; and, were ossification to be extended from the ischial, 64, to the pubic, *e'*, symphysis, it would be divided into the two vacuities called 'foramina ovalia seu obturatoria' in the human pelvis. Such division does actually take place in the Tortoises (*Testudo*) and Terrapenes, as shown at *v*, fig. 51, in *Emys Europæa*.

In the Tortoise (*Testudo*) the iliac bones are vertical and columnar, like the scapula, but are shorter and more compressed. The pubis expands to join its fellow at the median symphysis and the ischium posteriorly: it sends outward and downward a long thick obtuse process from its anterior margin. The ischia, in like manner, expand where they unite together to prolong the symphysis backward. The 'foramen ovale seu thyroideum' is nearly circular on each side. In *Hydraspis* the ilia articulate directly by part of their under surface to the xiphisternals, and the pubis becomes confluent with the same parts of the plastron by the tuberos process.

The femur is shorter than the humerus in the Turtles: the head is round, surmounted by a broad, thick, short trochanter: the

shaft is almost straight, slightly expanded at the distal end, at the back part of which the condyles are feebly indicated. In *Terrapenes*, fig. 51, w, and *Tortoises*, the femur equals or exceeds the humerus in length: its shaft is more bent: the trochanter is divided into two processes, most distinct in *Trionyx*. In no Chelonian is there a medullary cavity: ossification extends throughout the bone: the two bones of the leg, *ib. x, y*, are nearly straight; the tibia is the largest, with the proximal end almost semi-circular, and the distal one less expanded and subconcave, with a slightly-developed malleolus in *Testudo* and *Emys*. The fibula, fig. 117, 67, is a little bent, enlarging the interosseous space in *Trionyx*: it presents a convexity to the tarsus. There is no bony patella in any Chelonian. In *Testudo tabulata* I found a synovial joint between its fibrous representative and the femur, distinct from the proper capsule of the knee-joint. The proximal row of the tarsus consists of two bones, astragalus, *a*, and calcaneum, which in most *Tortoises* become confluent. The distal row consists of five bones, four of which support the four normal toes, and the fifth a rudiment of the metatarsal of the fifth toe, *v*; the fourth and fifth of the second row of tarsals answer to the os cuboides of higher animals; the other three bones to the three ossa cuneiformia. The astragalular part of the single proximal bone includes also the naviculare.



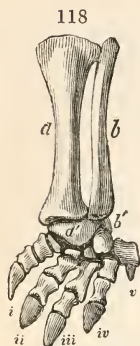
Bones of leg and foot,  
*Trionyx*. CL1.

In the *Trionyx*, fig. 117, the proximal row consists of a single bone, *a*, answering to the astragalus and naviculare: the distal row consists of five bones, of which the three cuneiformia are very small: the two divisions of the cuboides, *b, c*, are very large; the first may include the articular part of the calcaneum; the outermost is dilated and angular. In *Chelone* and *Chelys* the calcaneum is distinct from both the cuboid and the astragalus-navicular bones. The digits are moderately long, rather flattened and divaricated, supporting the hind webbed foot; the metatarsal supports two phalanges in the first toe; in the other toes it supports three, the last having a claw.

In *Trionyx* the fifth digit, fig. 117, *v*, has two small phalanges and no claw. In *Emys* and *Cistudo* the digits decrease in strength



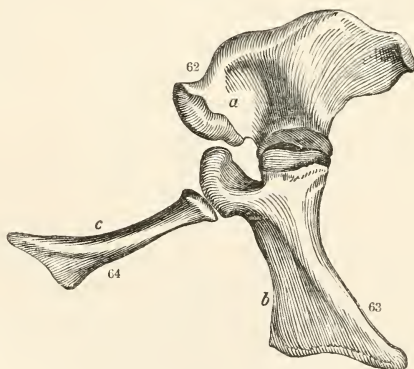
from the first to the fifth, and in length from the second to the fifth. In the Land tortoises, the fifth toe is reduced to a metatarsal rudiment: the others are short and thick, fig. 118, each with two phalanges, the second supporting a claw, and adapted, like those of the fore foot, for burrowing. The two extremes of modification of the hind foot in the chelonian series are presented by the Turtle and Tortoise: the great comparative weight and bulk of the body to be supported on dry land involve a form of limb and foot resembling that in the Elephant; whence the largest kind of Land-tortoise has been termed '*Testudo elephantopus*.'



Bones of leg and foot, *Testudo*

The general homology of the pelvic bones of the Crocodile has been previously discussed, pp. 67-69, and illustrated, figs. 55, 56, 57. The serial homology of the two hæmapophysial elements derives satisfactory elucidation from their crocodilian condition. Of those of the scapular arch, called 'clavicle' and 'coracoid,' in the vertebrates possessing both, the anterior very rarely enters into the formation of the joint for the appendage; whilst the posterior invariably does so.

119



Left pelvic bones Crocodile. CLI.

In the fœtal mammal, before the coalescence of the stunted coracoid, this relation may be seen. So in the Crocodile, the posterior hæmapophysial, fig. 119, 63, combines with the ilium, 62, to the exclusion of the pubis, 64, in the formation of the acetabulum, repeating the articular characters of the coracoid; whilst the more slender pubis placed anterior to the joint, and abutting by its mesial end against the abdominal sternum, figs. 5, 6, 10, repeats

those characters of the clavicle of lizards. Accordingly in the progressive reduction of the pelvic arch to a single hæmapophysial element sustaining the appendage, as in Osseous Fishes, we may discern the characters of the 'ischium' in that element, rather than of the pubis.

The ilium of the Crocodile is twice as broad as long, produced beyond the two vertebræ to which it is articulated: it descends vertically to the acetabulum, of which it forms the upper half. The anterior production or tuberosity, *a*, is the thickest, the posterior is the longest. The ischium develops a strong bent process from the fore part of the acetabular end, to which the pubis is articulated: as it descends and inclines inward, it becomes flattened and expanded, *b*, and joins its fellow by a moderately extended ischial symphysis. The pubis is directed more forward, and though smaller and more slender, resembles the ischium by the expanse of the medial end. As ossification is not extended along the mid-line from the ischial symphysis to the pubis, no 'obturator foramina' are defined, but a wide vacuity intervenes, as in *Chelone* and *Trionyx*.

The femur, fig. 57, *v*, is bent in curves opposite to those of the humerus: the head is convex, subcompressed laterally, flattened externally: the chief process is from the inner side, at the upper third of the shaft: there is a ridge external and above this process: the distal end expands transversely, and develops backward two condyles; the outermost receives part of the head of the fibula. It is longer than the humerus, but in a less degree in modern than in mesozoic crocodiles. The tibia, figs. 57 and 120, 66, presents a large triangular head to the femur, the division of the back part of which into two condyles is feebly indicated: it offers a smaller convex crescentic surface to the tarsus. The fibula, ib. 67, is slender and subcylindrical; much compressed above, more expanded and triangular below. Each of the foregoing long bones has a medullary cavity. There is no patella; but there is a fibrocartilaginous 'fabella,' with granular bone, in old crocodiles, behind the outer condyle.

The principal tarsal bone, fig. 120, *c*, represents the astragalus, naviculare, and entocuneiform, connate, of the human series; articulating with the distal end of the tibia and a small part of the fibula above, with the calcaneum and cuboid externally, and with the first and second metatarsals and the ectocuneiform below. The calcaneum, *d*, intervenes between the fibula and cuboid, and has a short but thick posterior tuberosity, *y*, fig. 57. The cuboid, fig. 120, *e*, supports the fifth, *v*, fourth, *iv*, and part of the third,

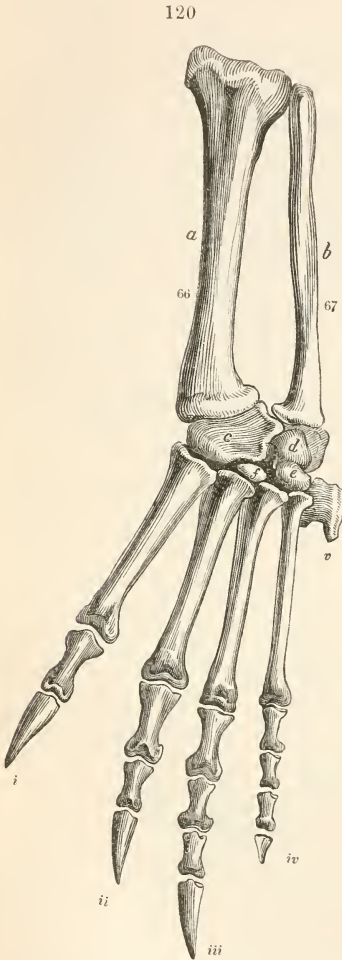
*iii*, metatarsals. The ectocuneiform, *f*, is wedged between the bases of the second and third metatarsals. These, by the oblique overlapping arrangement of their expanded bases, resemble the

articulations of the ventral fin-rays in most fishes. The fifth is flattened and expanded to support the broad scale from the outer side of the foot, but is curtailed in length and supports no toe.

The four normal metatarsals are much larger than the corresponding metacarpals. That of the first toe, *i*, is the shortest and strongest; it supports two phalanges: the other three are of nearly equal length, but lose thickness from the second, *ii*, to the fourth, *iii*: the second supports three phalanges; the third, four; the fourth, also four, the claw and its phalanx being absent in this toe: *ii*, *iii*, and *iv*, are webbed in true Crocodiles, but semipalmate in Alligators.

In most Lacertians two vertebræ are modified for articulation with the iliac bones, as in the Monitor (*Varanus*, fig. 121, *a*): but in the Chameleon there are three sacrals. In the great Monitor the ilium, *b*, extends backward beyond the junction, terminating obtusely, and bends down as it passes forward with a short process above the acetabulum.

Both ischium and pubis combine with the ilium in forming this cavity. The ischium, *c*, is usually most expanded at its symphyseal border, which is produced backward. The pubis, *f*, appears as a more direct continuation of the ilium, and is perforated near its acetabular end, anterior to which it develops a process. The symphyseal cartilage is continued from the ischium to the pubis, dividing the

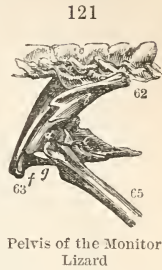


Bones of leg and foot, Crocodile

interspace into the 'obturator foramina,' and becoming ossified in old Monitors. The femur resembles that of the Crocodile, but with the inner trochanter better developed, with a larger medullary cavity, and with a more marked depression on the outer condyle for the fibular articulation. The division of the back part of the head of the tibia is usually more marked. The head of the fibula, fig. 122, 67, *b*, rises higher than in the Crocodile.

In *Varanus niloticus*,<sup>1</sup> the elongated iliac bone abuts against the transverse processes of the two sacral vertebræ, the first on the right side and the second on the left side being applied on a plane higher than the opposite processes: that of the first caudal vertebra also abuts against the ilium on the left side. The ilium sends off a tuberosity in front of the sacro-iliac syndesmosis, and it joins the pubis and ischium by a broad suture. The trochanter arises from the inner and back part of the proximal end of the shaft of the femur. There are two ossified patellæ in the tendon of the great extensor of the leg. The tarsus differs from that of the Crocodile chiefly in there being a 'mesocuneiform' supporting the second metatarsal, fig. 122, *ii*: but this is wanting in many lacertians. The bone *a'* is as composite as in the crocodile. The fifth metatarsal is flattened, and articulated farther back than the rest, extending along the outer side of the cuboid, *c*, to the calcaneum, *b'*: it supports an unguiculate toe of four phalanges, fig. 122, *v*: the number of phalanges in the other toes progressively increases from two in the first, *i*, to five in the fourth, *iv*, with proportionate increase of length.

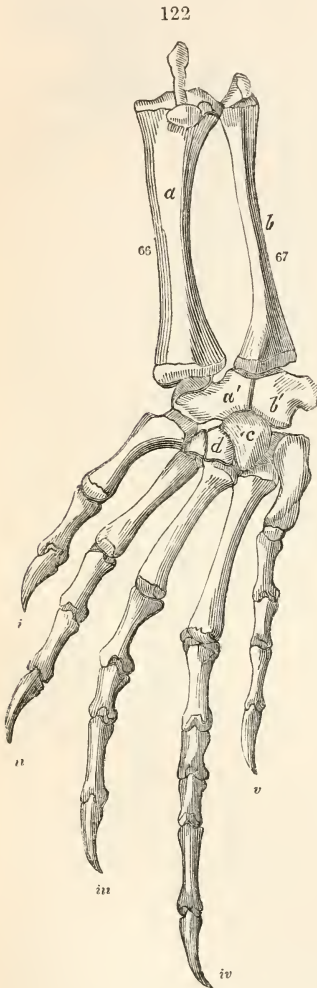
The chief modification of the hind limb of Lacertians is found in the Chameleon, fig. 123. The ilium is a simple elongate, subcompressed bone descending vertically from the converging ends of the sacral processes to the acetabulum. The fibula, fig. 123, *b*, 67, is bent outward. In the tarsus may be seen a stunted homologue of the astragalo-navicular bone, *a'*, receiving the end of the tibia; and a larger calcaneum, *b'*, in like relation with the fibula: these form a cavity for the spheroid 'cuneiform,' *d*, by which the prehensile foot rotates on the leg; and there is a cuboid, *c*, exclusively supporting the fifth metatarsal, *v*. This determination of the homologies of the tarsal bones with those of the ambulatory lizards, shows the nature of the five short but metatarsially shaped bones supporting the toes, and settles the



<sup>1</sup> XLIV. p. 149, No. 678.



homology of their homotypes in the fore-foot, fig. 110. The first metatarsal supports two phalanges, fig. 123, *i*; the second, three; the third and fourth, each four phalanges; and the fifth, three. The first and second toes are opposed to the other three in the hind foot, contrariwise to the arrangement in the fore foot.



Bones of leg and foot, Monitor

In the Pterodactyle, fig. 111, the hind limb adhered closely to the lacertian type; the metatarsals were distinct; the phalanges increased in number from the first to the fourth toe, but retained more equality of length than in lizards: all the five toes were unguiculate, the claw phalanx compressed and deep. Although in some species there were four or five sacral vertebræ, the hindlimbs were too feeble to sustain the body, as in Birds: they more probably served to suspend it, as in Bats, with a concomitant strengthening of the claws.

The reptilian hind-limbs, with their arch, acquired the most complex structure in the great extinct *Dicynodont*<sup>1</sup> and *Dinosaurian*<sup>2</sup> orders. In *Dicynodon tigriceps* ossification extended over the whole of the interspace between the ischium and pubis, obliterating altogether the obturatorial foramina: and both iliac and ischial bones articulated, as in edentate mammals with a long sacrum. In the *Iguanodon* six vertebræ were modified with interlocking centrums and neural arches, the latter resting on, and suturally joined to, the contiguous halves of two centrums. The femur exhibited an upper and external 'great trochanter,' besides the inner tro-

<sup>1</sup> CLV.

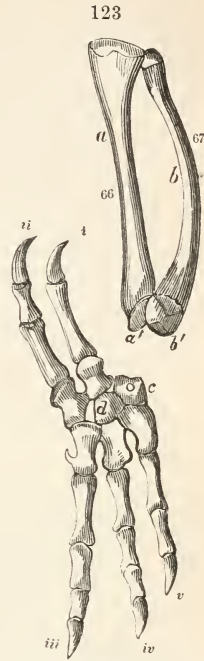
<sup>2</sup> CXLVI. (1841), pp. 114, 130.

chanter better developed than in modern lizards: examples of this bone four feet in length have been discovered. In the almost equally colossal *Scelidosaur* the toes of the hind foot were reduced to four in number by suppression, as in the *Crocodile*, of the fifth. In the *Iguanodon* they were reduced to three by the suppression also of the first toe; the retained toes were short and broad, with phalanges in number respectively three, four, and five; but the latter so much shorter as to reduce the outer to the same length as the inner toe, and with the middle one both longer and larger; showing in the great herbivorous Saurian an interesting analogy to the hind limb of the *Rhinoceros*.<sup>1</sup>

§ 43. *Dermoskeleton of Fishes*.—The scales of fishes may be regarded, from their seat and mode of development, as parts of the dermoskeleton: and in the palæo- and meso-zoic species they were ossified, in the form of granules, tubercles, plates, or imbricated scales. Bony fishes, with scales so soft and soluble as to leave no trace in fossilization, seem not to have existed before the cretaceous period: for even the exoskeleton of the *Leptolepidæ* of the lower and middle oolites has been preserved to us through the thin coating of petrifiable ganoine with which their minute and delicate scales were covered. Tubercular integument, like the ‘shagreen’ of sharks and dog-fishes, has come down to us from a period as remote as the Silurian. In skates and rays the skin is studded by bone in larger masses; sometimes, as in the ‘Thornback,’ developing a small bent spine.

The hard-rays in the fin of the *Perch* and other *Acanthopteri*, the larger and fewer spear-like weapons of the *Sticklebacks* (*Gasterosteï*), *Sheat-fishes* (*Siluridæ*), *Trigger-fishes* (*Balistes*), and some *Snipe-fishes* (*Centriscus*), are all parts of the dermoskeleton.

In *Balistes capriscus* — a rare British fish — the anterior dorsal is preceded by a strong erectile spine: its base is expanded and perforated, and a bony bolt from the supporting plate passes freely through it: when the spine is raised, a hollow at the back part of



Bones of the leg and foot, Chamæleon. CLI.

<sup>1</sup> CLIV.

the base receives a prominence from the next bony ray, which fixes the spine in the erect position, as the hammer of a gun-lock acts at full cock; and the spine cannot be forced down till the small spine or 'hammer' has been depressed, as by pulling the trigger. This mechanism may also be compared to the fixing and unfixing of a bayonet. When the spine is unfixing and bent down it is received into a groove on the supporting plate, and offers no impediment to the progress of the fish through the water. The generic name (*Balistes*) and the common Italian name of the fish (*Pesce balestra*), refer to this structure: the spine is roughened by ganoid grains, whence our English name of 'File-fish.' The hind border of the analogous weapon of the *Centriscus humerosus* and of most Sheat-fish is denticulated, so that they inflict a ragged wound. In all such weaponed osseous fishes, the base of the spine is modified for articulation with another bone. In gristly fishes so armed the base of the spine is simple, smooth, hollow, implanted deeply in the flesh and attached to ligament and muscle.

The great majority of such weapons found in a fossil state, called 'ichthyodorulites,' show by their basal structure that they come from Plagiostomous fishes, and exemplify in a remarkable manner the efficiency, beauty, and variety, of the ancient armoury of that order. In some, the marginal serrations were themselves denticulate (*Edestes*).<sup>1</sup> Certain Rays (*Trygon*) have spines with both margins serrate.<sup>2</sup>

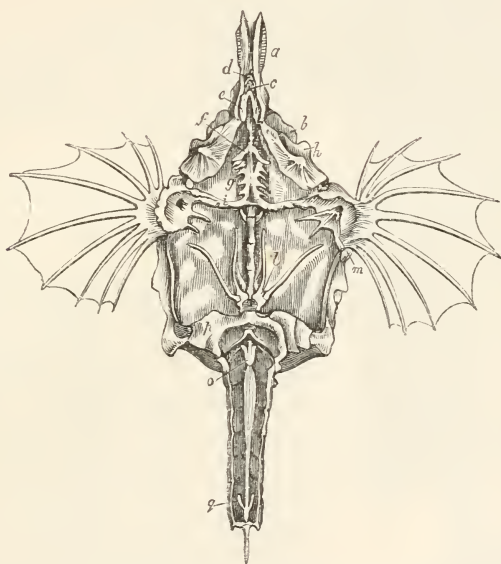
The series of side-scales perforated by the mucous duct in the modern soft-scaled fishes are usually more or less ossified. In the Eel tribe the lateral mucous ossicles are tubular and concealed by the epiderm. In the Sole and Plaice the mucous scale bones of the lateral line are quite superficial. There are many circular radiated ossicles scattered over the dark or upper side of the skin of the Turbot. A row of small chevron-shaped dermal bones extends along the median line of the belly of the Herring, and the extremity of each lateral process, fig. 37, *dh*, is connected with that of the long and slender vertebral rib, completing the inferior arch, like a sternum and sternal ribs. The Dory has two rows of thick osseous plates along the under part of the abdomen; but their superficial position indicates their essentially dermal character. Parts analogous to a sternum are thus supplied from the exoskeleton as they are from the splanchnoskeleton in the Lamprey, fig. 11; but the true homologues of the sternum are first

<sup>1</sup> CLXXX. p. 124, fig. 38.

<sup>2</sup> Ib. 123.

seen in the endoskeleton of the Batrachia. In the Trunk-fishes (*Ostracion*), and Pipe-fishes (*Syngnathus*), the dermal scale bones form a continuous coat of mail, like a tessellated quincuncial pavement, over the entire body, as shown in the transverse section, fig. 16, *d n*, *d p*, *d h*, and the endoskeleton is but little ossified. The like is seen in the Hippocamps. Thus, in *Pegasus draco*, fig. 124, with the exception of the small premaxillaries *d*, and mandible *e*, all the visible hard parts of the head are due to the dermoskeleton: such, e. g., as the rostrum, *a*; the plates in which the eyes are placed, *b*; the gill-covers, *h*; the median plate, *g*,

124

Dermoskeleton of the Flying Hippocamp (*Pegasus*)

supporting the hyobranchial arches; the zone, *i*, sustaining the large pectoral fins; and the hard case of the incubating pouch, *o*, *q*.

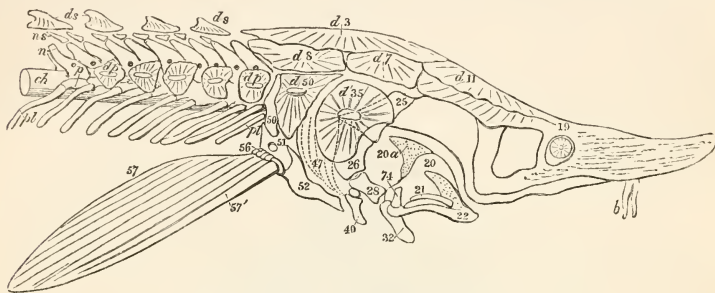
In the *Ganoidei*, parts of the exoskeleton coalesce with endoskeletal bones of the skull, especially the sclerogenous ones, while others overlie the true cranial bones. Thus, in the Sturgeon, the ganoid plate, marked *d 3*, fig. 125, simulates a superoccipital;<sup>1</sup> but its homologue in *Polypterus* and *Lepidosteus* is subdivided: and as the cartilaginous homologue of the epencephalic arch

<sup>1</sup> cxlv. (1846) p. 134.



underlies the plate *d* 3, in *Acipenser Sturio*, so also do the ossified ex- and super-occipitals underlie in *Polypterus* the three dermal plates corresponding in position with *d* 3 in *Ac. Sturio*. The true par-occipital is equally distinct from the plate marked *d* 8, in *Ac. Sturio* and its representative subdivisions in *Polypterus*. The dermal plates in advance of these coalesce with the true parietals, frontals, postfrontals, and part of the mastoids. But the varieties in the dermal plates within the limits of a genus, as exemplified by the

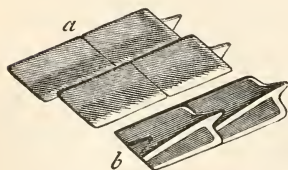
125



Fore part of endo- and exo-skeleton of Sturgeon

single interfrontal in *Acipenser Sturio*, by the three interfrontals in *Ac. Scypha*, by the divided superoccipital plate in *Ac. brevirostris*, &c., sufficiently warn against the confusion arising from applying to dermal plates the names of the true cranial bones in recent and extinct ganoid and placogonoid fishes. The median cranial ganoid plates in the Sturgeons are plainly a continuation forward of the dermal plates, (ib. *d* 8, fig. 125), of the mid-line of

126

Scales of *Amblypterus striatus*

the back; and examples of a like repetition occur amongst the Osseous Fishes in the dermal epicranial spines, for example, of the Angler (*Lophius*), which support the long fishing-filaments upon the head, or in those modified ones forming the sucking disk on the head of the *Remora*.

In certain fishes of the Devonian or Old Red Sandstone period the head and part of the trunk were encased by coarticulated ganoid bony plates. Fig. 127 shows the proportions in which the exo- and endo-skeleton entered into the conservable framework of one of these ancient fishes, termed *Coccosteus* (*kokkos* berry, *osteon* bone), in reference to the tubercular enamelling of the exterior of the combined helmet and

cuirass. In the composition of this armour, as defined by sutures, not mucous grooves, may be discerned the following plates: 5, median; 6, lateral; 7, premedian; 8, prelateral; 9, rostral; 12, dorsomedian; 14, postdorsomedian; 18, sublateral; 20, postventrolateral; 22, preventrolateral; 24, suborbital.

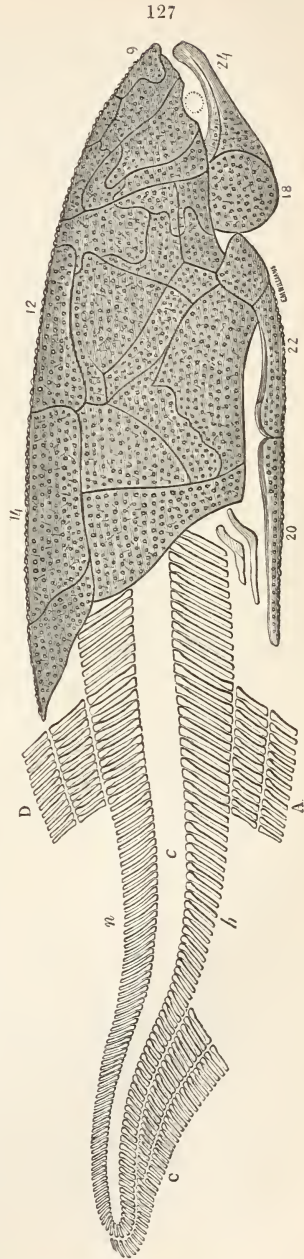
The blank space between the neural, *n*, and hæmal, *h*, spines of the fossil endoskeleton indicates the position of the soft 'notochord,' *c*, which has been dissolved away.

In the *Pterichthys* of the same geological formation, the helmet was moveably articulated with the trunk-buckler.

In *Cephalaspis* the armour of the head was shield-shaped, with the posterior angles produced backward in a pointed form.

The fishes with enamelled dermal bones in the form of plates, whether coarticulated, fig. 127, or detached as in the Sheat-fishes and Sturgeons, fig. 125, *d p*, *d s*, are called 'placoganoid:' those in which they have the size, form, and overlapping arrangement of scales, fig. 126, are called 'lepidoganoid.' The genera *Polypterus* and *Lepidosteus* exceptionally exemplify the latter condition of the dermoskeleton at the present day: it was the rule with the fishes of the mesozoic period, and with those of the palæozoic which were not 'placoid' or 'placoganoid.'

In fig. 126, *a* indicates the outer surface of parts of two series of the rhomboidal ganoid scales of the extinct *Amblypterus*: and *b* the inner surface of two scales, showing the ridge produced at one end into a projecting peg, which fits into a notch of the next



Endo- and exo-skeleton, *Coccoosteus*. CLVI.

scale, in the way that tiles are pegged together in the roof of a house.

In the Porcupine-fishes (*Diodon*) the spines are supported by triradiate interlocking dermal bones.

§ 44. *Dermoskeleton of Reptiles*.—In the Scincoid family of the Lacertians, the scales are more or less ossified; least so in the smooth-scaled genera (*Scincus*, *Tiliqua*); but in *Cyclodus* resembling scutes, and giving a knobby character to the surface. In *Cyclura*, *Lophura*, and *Xiphosurus velifer*, dermal bones in the form of spines project or raise the skin above the dorsal or caudal vertebræ. The horizontal plates connate with the neural spines, and with the ribs, are dermal ossifications, as are the neural plates and marginal plates which remain distinct from the endoskeleton, in the composition of the carapace of the Chelonia. The plastron is also formed by dermal plates, connate with the sternum and sternal ribs.

In existing Crocodilia the upper surface of the trunk is defended by bony scutes, usually quadrate in form, smooth on the inner surface, sculptured and longitudinally ridged on the outer; arranged in transverse series, more or less apart, of twos or fours, upon the neck; but six or eight in a transverse line and close set, so as to have a longitudinal as well as transverse arrangement along the back. The numbers and patterns of these scutes are noted in zoological comparisons and characters of genera and species.<sup>1</sup> The Alligators are defended by a ventral as well as dorsal cuirass, separated, as Natterer observed in *Champsia palpebrosa*, *Ch. trigonata*, *Ch. gibbiceps*, only by a narrow and soft longitudinal groove along the sides of the neck and trunk.<sup>2</sup> But the most remarkable anatomical modifications are presented by the extinct and especially the mesozoic Crocodilia.

The presence of a ventral as well as a dorsal series of scutes and their distinctive characters were first noted in the *Teleosauri*. The dorsal scutes are in close-set sub-imbricate transverse rows, the posterior margin overlapping the anterior one of the next row. I counted twenty such rows in a specimen of the Whitby Teleosaur, of which sixteen covered the vertebræ between the last cervical and first caudal. In the ventral shield or plastron, only the two scutes in each row are on the same transverse parallel which border the mid-line of the abdomen; the others have an alternate interlocking arrangement. These ventral scutes are

<sup>1</sup> CLI. tom. v. pp. 79, 80, pl. II.

<sup>2</sup> CLVII. tom. II. (1840) p. 320.

not carinate; and such is the case likewise with the dorsal scutes of certain species<sup>1</sup> of Teleosaur. In a Wealden Crocodile (*Goniopholis*), the angles of the oblong quadrilateral dorsal scutes are well marked, and from one of them was continued a peg-like process, which fitted a depression on the under surface of the contiguous angle of the next scute, thus serving to bind together the scutes in the way in which the enamelled scales were united in many extinct ganoid fishes, fig. 125. The outer surface was impressed by numerous deep, round, or oblong pits; but a larger proportion of the fore part of this surface was overlapped by the antecedent scute than in *Teleosaurus*, and this part is smooth and thinner than the rest of the scute. Associated with the quadrate toothed scutes, ascribed to the back of *Goniopholis*, and irregularly scattered in the matrix, I have observed others of a hexagonal form, with a similarly pitted outer surface, but without the peg, and with thick sutural margins. They indicate a similar alternate arrangement and interlocking of the ventral scutes, as in *Teleosaurus*.

The dermal armour of *Hylæosaurus* and *Scelidosaurus* appears to have consisted of series of detached scutes of an elliptical or circular form, without sutural or smoothly overlapping margins: of great thickness, with the outer surface, in most, pyramidal, or rising to a longitudinal ridged summit. In *Hylæosaurus* certain scutes situated above the dorsal spines were of a very long and narrow triangular form with the base oblique; and seem to have formed a defensive fringe of strong spines along the back, as in *Xiphosurus*. In *Scelidosaurus* the surface was defended by several longitudinal series of massive unconnected bones: those in the middle of the dorsal surface being in pairs upon the nape, and single along the tail, where three are coextensive with from five to seven subjacent vertebræ: a corresponding medial series of rather smaller and less vertically developed scutes defended the under surface of the tail; and there were one or more lateral series of a more depressed and fuller ovate form, in that region.<sup>2</sup>

<sup>1</sup> CXLVI. p. 79. The volume of the Serial containing Natterer's memoir, though bearing the date 1840, had not reached this country when I communicated the second part of my 'Report on Fossil Reptiles' to the British Association.

<sup>2</sup> CXIII.

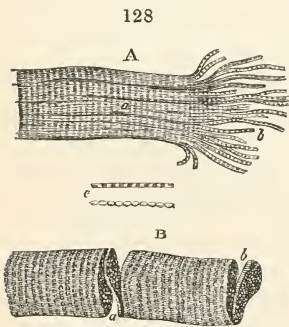


## CHAPTER III.

## MUSCULAR SYSTEM OF HÆMATOCRYA.

§ 45. *Structure of Muscle*.—Muscular tissue is fibrous, and resolvable into fine threads inclosed in a delicate sheath, called ‘elementary fibres.’ These, in Vertebrates, are of two kinds; in one the fibre is crossed by close parallel lines; in the other it is smooth. The transversely striped character is too fine to be seen without the aid of the microscope; but may be indicated to the naked eye by the iridescence of the surface in certain lights.<sup>1</sup> All the muscles subject to the influence of the will, or cerebral action, have striped fibres. Most of the involuntary muscles have unstriped fibres; those of the heart and gullet are among the exceptions; and, on the other hand, the muscles performing the rhythmical movements of the gill-covers in fishes, like those of the thoracic walls in

higher air-breathers, have the striped fibre. But besides the close cross parallel lines, longitudinal ones, darker, wider apart, and of varying extent, often present themselves on the elementary fibre of voluntary muscle, as in fig. 128, A *a*.<sup>2</sup>



Portions of striped elementary fibres, showing a cleavage in opposite directions, magnified 300 diam. CLXXXV.

termed ‘fibrils,’ fig. 128, A, *b* and *c*, and these have a show of segments equalling in length the breadth of the transverse striæ. Sometimes such segments appear by alternate dark and light parts of a continuous rectilinear fibril, as in the upper portion at *c*, fig. 128. Sometimes the segments are marked off by

<sup>1</sup> XX. vol. i. p. 10.

<sup>2</sup> CLXXXV. p. 508.

<sup>3</sup> *Ib.*

constrictions, giving a scalloped border and beaded character to the fibril, as in the lower portion, at *c*. Sometimes the striped fibre cleaves into transverse portions or discs, fig. 128, B, *a*, *b*, corresponding in breadth to the cross-stripes, and to the seeming segments of the fibrils.

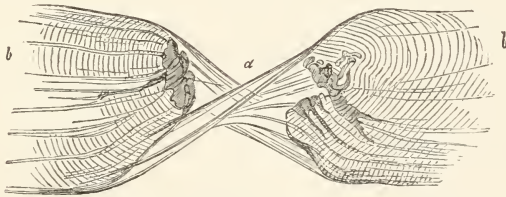
The following is the average diameter of the striped fibre, of different classes, in fractions of an inch:—

Fishes . . . .	from	$\frac{1}{755}$	to	$\frac{1}{65}$
Reptiles . . . .	”	$\frac{1}{1000}$	”	$\frac{1}{100}$
Birds . . . .	”	$\frac{1}{1500}$	”	$\frac{1}{350}$
Mammals . . . .	”	$\frac{1}{1100}$	”	$\frac{1}{192}$ . <sup>1</sup>

Thus, among vertebrates, fishes, and in fishes the Skates (*Raia*), have the thickest elementary striped muscular fibre; and its elastic tunic, the ‘sarcolemma,’ can be best demonstrated in them. When the fibre is broken across, as in fig. 129, the sarcolemma *a* may remain, connecting the severed portions, *b*, *b*.

The characteristic vital property of muscular fibre is to alter,

129



Portions of a broken elementary striped muscular fibre *b*, held together by the untorn twisted sarcolemma *a*. *Raia batis*. CLXXXV.

under stimulus, its relative dimensions of length and breadth. When it becomes shorter and thicker it is said ‘to contract;’ and by these contractions the movements of the body, and of its parts, are produced.

In the contraction of a smooth elementary muscular fibre it has been seen to grow thicker at a part, and shorter, without falling out of the straight line.<sup>2</sup> In the contraction of a striped elementary fibre it has been seen to grow thicker at successive parts, by approximation of the cross stripes, as in fig. 130, at *a*, *a*, *a*, along one side; or engaging the whole thickness of the fibre, as at *b*, *b*, *b*; and these successive partial thickenings, with concomitant shortening of the fibre, have been termed ‘waves of contraction.’<sup>3</sup>

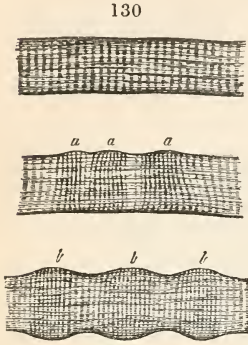
On the cessation of the act, the fibre may fall into zig-zag folds

<sup>1</sup> CLXXXV. p. 510.

<sup>2</sup> XCIV. Editor’s note, p. 261. (1837).

<sup>3</sup> CLXXXV. p. 525.

on resuming its length; but it is commonly drawn out straight, as before the contraction, by ‘antagonistic’ muscles, in the living animal. The uncontracted state of muscular fibre is sometimes termed ‘relaxation,’ but is more properly a state of quiescence or equipollency.

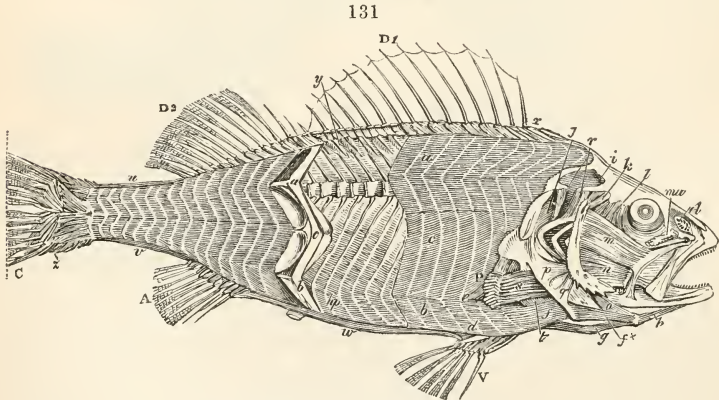


130  
Stages of contraction seen in an elementary fibre of the Skate. The uppermost state is that previous to the commencement of contraction. CLXXXV.

Muscles consist of series or bundles of the elementary fibres, with their vessels and nerves, connected together by areolar tissue: either in lengthened or flattened masses, fixed at the two extremities, called ‘solid muscles;’ or disposed around cavities or canals, and called ‘hollow muscles.’

The non-contractile fibrous parts by which the ‘solid muscles’ are attached to the endo- sclero- and exo-skeletons, are called ‘tendons’ when long and slender, and ‘aponeuroses’ when broad and flat.

§ 46. *Myology of Fishes.*—The modification of the active organs of motion, and their deviation from the fundamental vertebrate type, proceed concomitantly with the metamorphosis of the passive organs, as Vertebrates rise in the scale and gain higher and more varied endowments: therefore, as the segments of the skeleton



131  
Muscular system, *Perca fluviatilis*

preserve the greatest amount of uniformity in the lowest class, so does the principle of vegetative repetition most prevail in the corresponding segments of the muscular system.

The chief masses of this system in ordinary Osseous Fishes are disposed on each side of the trunk, in a series of vertical flakes or

segments, corresponding in number with the vertebræ. Each lateral flake (*myocomma*, fig. 131, *a*, *b*, *c*)<sup>1</sup> is attached by its inner border to the osseous and fibrous parts of the corresponding vertically extended segment of the endoskeleton, by its outer border to the skin, and by its fore and hind surfaces to an aponeurotic septum common to it and the contiguous myocommas. The gelatinous tissue of these septa is dissolved by boiling, and the muscular segments or flakes are then easily separated, as we find in carving a fish at table. The vegetative similarity of the myocommas of the trunk has led to their being described as parts of one 'great side-muscle,' extending from the occiput and scapular arch to the bases of the caudal fin-rays. The modifications of the cranial vertebræ impress corresponding changes on their muscular segments, and special names have been conveniently applied to their constituent, and in fact often separated and independently acting, fasciculi.

The fibres of each myocomma of the trunk run straight and nearly horizontally from one septum to the next; but they are peculiarly grouped, so as usually to form semi-conical masses, of which the upper, *a*, and lower, *b*, have their apices turned backward; whilst a middle cone, *c*, formed by the contiguous parts of the preceding, has its apex directed forward; this fits into the interspace between the antecedent upper and lower cones, the apices of which reciprocally enter the depressions in the succeeding segment, whereby all the segments are firmly locked together, their general direction being from without obliquely inward and backward, and their peripheral borders describing the zig-zag course represented in fig. 131, in which one myocomma is represented partly detached, and others quite removed from the side of the abdomen. Thus, guided by the fundamental segmental type of the vertebrate structure, we come to recognise the 'grand muscle latérale,' of Cuvier, as a group of essentially distinct vertical masses or segments. A superficial view of these segments, or an artificial analysis, has led to their being regarded as forming a series of horizontal muscles, extending lengthwise from the head to the tail: the upper portions, *a*, of the myocommas being grouped together, and described as a dorsal longitudinal

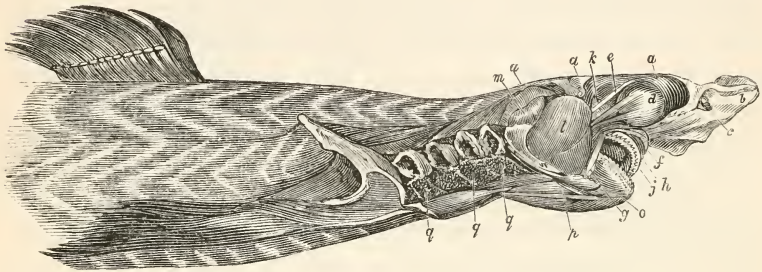
<sup>1</sup> Professor Goodsir proposes (CLXXVIII.) to alter this term to 'myotome,' and to substitute for 'vertebra' or 'osteocomma' (CXLI, 1849, p. 88) the term 'sclerotome,' &c.: but this form of compound has been pre-engaged, for their special cutting instruments, by the sclerotomists, neurotomists, lithotomists, and other classes of operating surgeons and their instrument-makers. If the itch of change be uncontrollable, I would suggest 'osteomere,' 'scleromere,' 'neuromere,' &c. (Gr. μέρος, *part* instead of κόμμα, *segment*).



muscle, with tendinous intersections directed downward and backward — the lower portions, *b*, as a ventral longitudinal muscle, with tendinous intersections directed downward and forward, whilst the margins of the middle portions of the myocommas, *c*, being curved, and usually bisected by the lateral mucous line, have been taken as indications of two intermediate longitudinal muscles.

In the Sharks, instead of a curve the margins of the middle portions of the myocommas form an angle with the apex turned forward, fig. 132; and in the Rays the dorsal portions have

132



Muscles of fore part of Shark (*Squalus glaucus*). XLIII.

actually become insulated from the middle ones, and metamorphosed into a continuous longitudinal muscle, fig. 139, *a*, the change being essentially the same with that which the bony segments themselves undergo, when by ankylosis the sacral or cranial vertebrae are blended into a continuous longitudinal piece. In many bony fishes the middle fibres of the caudal myocommas are disposed in two cones; a transverse section of the tail as in fig. 133, shows the two concentric series of cut segments of the sheathed cones, on each side of the spine. The portions of the myocommas above the lateral line become grouped, in fish-like Batrachia and in Ophidia, into three longitudinal muscles, comparable respectively to the 'spinalis dorsi,' 'longissimus dorsi,' and 'sacrolumbalis,' the portions below the line responding to certain intercostals and the 'rectus abdominis,' of higher vertebrates.

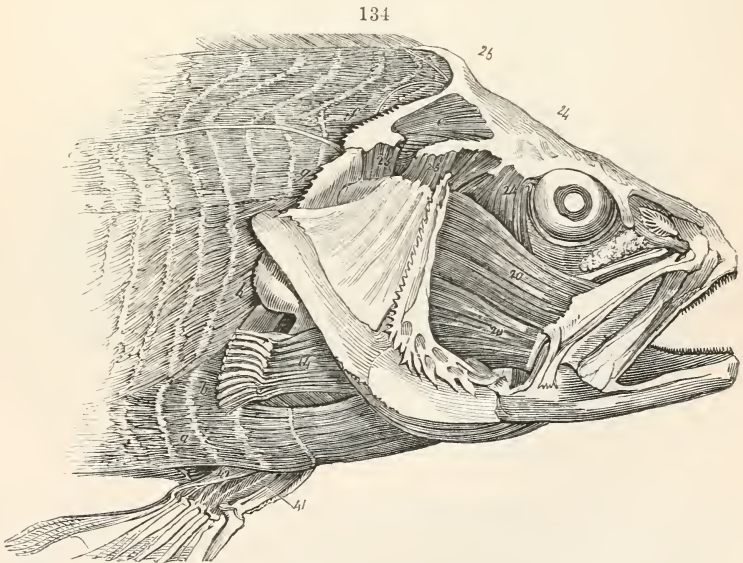


Caudal section of  
Mackarel.

The myocommas of one side are separated from those of the opposite side of the body by the vertebrae, by the interneural and interhaemal aponeuroses, and by the abdominal cavity and its proper walls, fig. 131, *h, p*. The ventral portions recede from each other to give passage to the ventral fins, *v*, as in fig. 135, *a*: and

the ventral and lateral tracts separate to give passage to the pectoral fins, as at *a*, *h*, fig. 134.

From this part forward, portions of the myocommas undergo that change, analogous to anchylosis, which justifies their being regarded as distinct longitudinal muscles: here the separated ventral tract, fig. 135, *a*, derives a firmer origin from the clavicle, and, in consequence of the forward curve of the coracoid, it is not only expanded but lengthened out, in order to be inserted there. But the serial homology of this fasciculus with the more normal ventral portions of the succeeding myocommas, the hæmaphysial attachments of which have not risen above the aponeurotic state, is unmistakeable. The lateral portion of the anterior myocomma, fig. 134, *h, g*, is attached to the upper end of the coracoid and to the scapula; the dorsal portion, *f*, to the suprascapula, paroccipital and superoccipital. We recognise the dorsal portion of the posterior cranial myocomma in the fasciculus called 'protractor scapulæ,' fig. 134, *e*, the middle portion in that which is exposed by the removal of the operculum, and which extends from the scapula to the mastoid, fig. 137, 26; the ventral portions in the fasciculi continued from the coracoid forward to the hyoid, *c, c*,



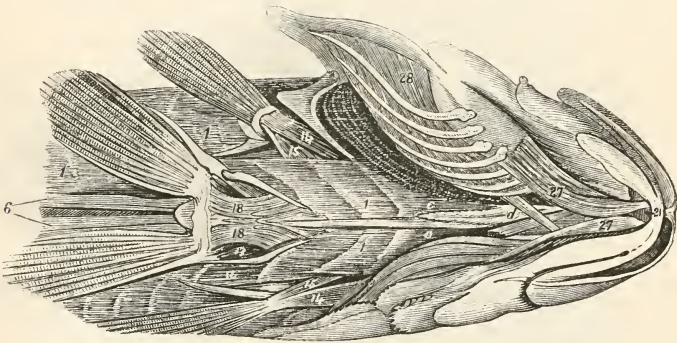
Side muscles of head, Perch. XXXIII.

fig. 135: the corresponding portions of the more anterior cephalic muscular segments may be recognised in *d* and 27, fig. 135.

Other dismemberments of the cranial myocommas are specialised to act upon the branchiostegal appendages, the branchiæ, the upper and lower jaws, &c. ; and the chief of these, under their special denominations will next be noticed.

The upper and lower jaws are so connected together in Osseous Fishes that one cannot be moved without affecting the other, and both are alike moveable. Protrusion and retraction affect them equally, and usually to a greater extent than divarication and approximation, or the opening and shutting of the mouth: in a minor degree, also, the two halves of both maxillary and mandibular arches have transverse movements, varying the angle at which they severally meet at the premaxillary or premandibular symphysis. The most important retractor, which tends in that action also to close the mouth, is the large subquadrate muscle, *retractor oris*, fig. 134, 20, 20, which arises from the tympanic pedicle and anterior border of the preoperculum, and is inserted by the upper fasciculus into the maxillary; by a lower fasciculus into the mandible behind the coronoid process; and by an aponeurosis into the membrane uniting the two jaws near the angle of the mouth. The muscle which tends to open the mouth by depressing the mandible, on which it

135



Lower muscles of head and fins, Perch. XXXIII.

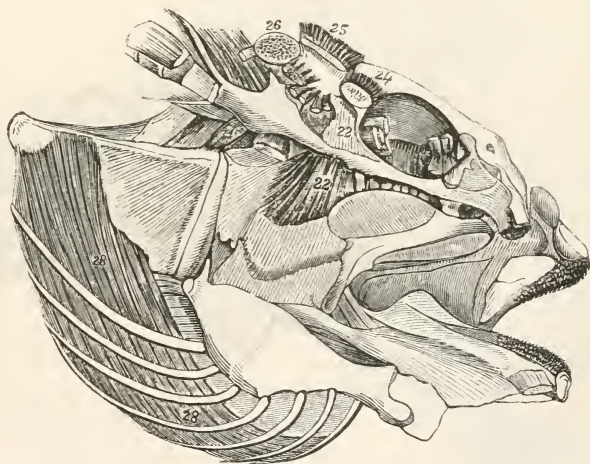
exclusively acts, is that marked 27 in fig. 135; it arises from the ceratohyal, and is inserted into the back part of the dentary, near the symphysis. Cuvier deems it the homologue of the *geniohyoideus*. Above the insertions of the geniohyoid pair is a muscle, the *intermandibularis*, fig. 135, 21, which passes transversely from one dentary to the other, approximating the halves of the man-



dible after they may have been divaricated. The latter movement depends upon the drawing upward and outward of the tympanic pedicle. This action is performed chiefly by the muscle, *levator tympani*, figs. 134 and 137, 24, which arises from the postfrontal and expands to be inserted into the epi- and pre-tympanics and into the ectopterygoid. In raising or drawing outward the tympanic pedicle and attached part of the pterygoid, this muscle tends to dilate the branchial cavity and the back part of the mouth. It is antagonised by the muscle, *depressor tympani*, fig. 136, 22, 22, which arises from the basi- and ali-sphenoids, and expands with diverging fibres to be inserted into the epi- and pre-tympanics and into the entopterygoid. It depresses the tympanic, or approximates it to the opposite pedicle, and contracts the branchial cavity.

The movements of the opercular appendage are like those of its supporting arch, and are performed by muscles placed behind those of that arch. The *levator operculi*, figs. 134 and 136, 25, arises from the mastoid crest, and is inserted into the upper and outer part of the opercular bone. The *depressor operculi*, fig. 136,

136



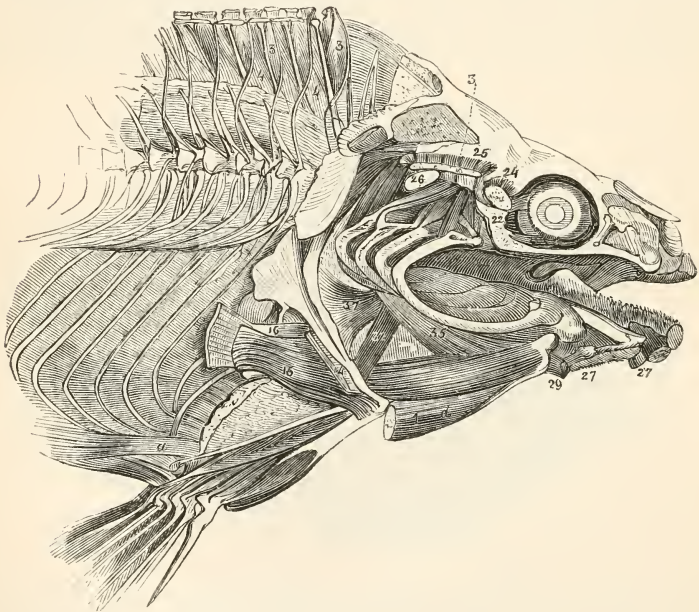
Muscles of hyoid and operculum, Perch. XXXIII.

26, arises from the alisphenoid and petrosal, and is inserted into the inner ridge of the opercular bone. The *retractor hyoidei*, fig. 137, 1 d, fig. 135, c, c, extends from the coracoid to the uro- and basi-hyals, but is chiefly implanted into the sides of the



former, and becomes through the medium of 27, a retractor of the mandible. When the retractor hyoidei relaxes and the mandible is the fixed point, the genio-hyoidei, fig. 135, 27, become protractors of the hyoid arch. In some fishes a transverse muscle, repeating the characters of 21, fig. 135, passes from one ceratohyal to the other. The branchiostegal appendage has muscles for raising and depressing, divaricating and approximating the rays. The *levator branchiostegorum*, figs. 135 and 136, 28, arises from the inner surface of the hinder half of the opercular bone and from a contiguous part of the subopercular, and is continued from ray to ray to the lowest, being loosely attached to their inner surface. It forms a kind of muscular capsule of the branchial chamber. The *depressor branchiostegorum*, fig. 135, *d*, arises from the lower end of the ceratohyal and passes obliquely backward, crossing its fellow, to be inserted into the inferior branchiostegal ray. These muscles regulate the capacity of the branchial chamber,

137



Muscles of fins and gills, Perch. XXXIII.

and mainly act upon the water it contains: they show accordingly much diversity, especially 28, in relation to the respiratory characteristics and connected peculiarities in different fishes. In

the Angler (*Lophius*) the levator is enormous, forming the wall of the capacious reservoir on each side and behind the gills, and uniting extensively with its fellow at and beyond the urohyal: each long branchiostegal ray has, likewise, its peculiar muscles, originating from the supporting arch. In the *Anguillidæ* the isthmal union or raphé of the levatores reaches from the basi- and uro-hyals to the coracoid.

The branchial arches are supplied with muscles attaching them to surrounding parts, or passing from one part to another of the arch itself.

The *branchi-levatores*, fig. 137, 3, arise from the alisphenoid and divide into four fasciculi, respectively inserted into the epibranchial of its own arch. The *masto-branchialis*, ib. 26, arises from the extremity of the mastoid, and divides into two fasciculi, one inserted into the fourth epibranchial, the other into the third pharyngobranchial and the contiguous part of the pharynx.

The *branchi-retractores* consist of two fasciculi, one superior, fig. 137, 37, which arises from the upper half of the coracoid, passing horizontally to its insertion: the other inferior, ib. 32, passing from the lower part of the coracoid obliquely upward: they retract and partly depress the branchial arches.

The *branchi-depressor*, fig. 137, 35, arises from the basilial and ascends obliquely backward to its insertion into the ceratobranchials: it is the more direct antagonist of the levatores.

The *protractor scapulæ*, fig. 134, *e*, arises from the back part of the masto-parietal ridge, and is inserted into the coarticulated parts of the suprascapula and scapula. The middle portion of the great lateral muscle, ib. *g, h*, serves, by its insertion, as a *retractor scapulæ*. The corresponding insertion of the lower portion of the great muscle into the coracoid retracts that part of the scapulo-coracoid arch, and is so modified as to have received the name *subcoracoideus*, ib. *a*, fig. 131, *f*.

The muscles of the pectoral fin form a pair, in two layers, on both the outer and inner sides of its antibrachio-carpal base: and the fibres of one layer run obliquely in a different direction from those of the other layer in both pairs of muscles. The outer pair abducts or protracts the fin, the inner pair adducts or retracts it, sweeping it back into contact with the flank: the first movement might be called 'extension,' the second, 'flexion.' The superficial abductor, fig. 134, 14, arises from the upper and outer part of the coracoid; it tends to elevate as well as extend the pectoral: the deep abductor, fig. 137, 15, comes from the outer border of the lower part of the coracoid; it depresses as well as extends the fin.

The lower portions of both muscles are shown in fig. 135, 14, 15. Of the inner pair of muscles, a portion of the deeper layer, disposed so as to raise as well as adduct the pectoral fin, is shown at 16, fig. 137. Each muscle is inserted into the bases of the fin-rays, resolving itself into fasciculi and short tendons corresponding in number with those rays: by different combinations of action these fasciculi divaricate or approximate the rays.

The ischial basis of the ventral fins in abdominal fishes may be moved a little forward or backward by the action of the 'infra-carinales' according as they lie in front or behind the pelvis. The latter, '*retractor ischiï*,' fig. 131, *w*, pass backward to the vent, inclose it, and are continued to the base of the anal fin. The '*protractor ischiï*,' fig. 135, 18, passes forward to be attached to the lower end of the coracoid. The protractors are short in thoracic fishes, e. g., the Perch, and less distinct from the lower parts of the myocommas than in ventral fishes, e. g., the Salmon. In fishes, e. g., the Lophius, where the ischia are wide apart, there is a transverse muscle to draw them together, and antagonise the portions of the side muscles that tend to draw them further apart. The muscles which act upon the ventral rays, like those of the pectoral ones, form a pair, or two layers of slightly decussating fibres, on both the outer and inner sides of the base of the fin. The outer or inferior muscles, fig. 135, 16, 17, depress or extend the ventral fins; the opposite muscles raise or flex them. The portion of the deeper depressor shown at 17, fig. 135, serves to expand or dilate the ventrals.

The movements of the rays of the median fins are effected by three or four pairs of small muscles attached to each ray. The superficial ones, fig. 131, *x*, arising from the skin, are inserted into the sides of the base of the dermoneural or dermo-hæmal spine. The deep ones, *ib. y*, arise from the interneural or interhæmal spine, and are inserted into the base of the dermoneural or dermo-hæmal spine: the anterior of these, fig. 137, 3, erects the spine; the posterior, *ib. 4*, depresses it. The myocommas answering to the neural and hæmal spines of the coalesced or suppressed centres of the terminal caudal vertebræ, change their direction like those spines, slightly diverging from the axis of the trunk to be inserted into them: these modified terminal segments, by their connection with the interlocked myocommas of the great lateral masses, concentrate the chief force of those muscles upon the caudal fin. The rays of this important fin are moved by three series of muscles, the one superficial, the second deep-seated, the third interspinous. The

superficial muscle, arising from the terminal aponeurosis of the 'lateral muscle,' expands and separates fan-wise, fig. 131, *z*, to its insertion into the bases of the caudal rays. The deeper-seated fascicles are exposed by the removal of the foregoing and their aponeurotic origin, and arise from the coalesced terminal centrams of the caudal vertebræ, to be inserted further from the basal joints of the rays, and more advantageously for effecting the movements which alter the spread of the tail-fin. Slender longitudinal muscles, *supra-carinales*, extend along the mid-line of the back from the occiput to the first dorsal, and along the interspaces of the dorsal fins in the Cod : similar muscles, fig. 131, *u*, extend from the last dorsal to the caudal fin in the Perch ; and *infra-carinales*, ib. *v*, extend from the anal to the caudal along the keel of the tail. In the *Gymnotus* the *supra-carinales* form a single pair, which extends from the occiput to the end of the tail. The modified cranio-dermal spines, which constitute the oval sucking-disc of the *Remora*, have a complex series of minute muscles, which raise or depress the transverse lattice-work ; and thus become the means of giving the little feeble fish all the advantage of the rapid course of the whale or the ship to which it may have attached itself. The muscular and membranous webs of the coalesced pectorals and ventrals of the Lump-fish, form a sucker on the opposite surface of the body, by which it may safely anchor itself to the rock, in the midst of the turbulent surf or storm-tossed breaker.

There are many modifications of the muscular system in the orders at the two extremes of the class.

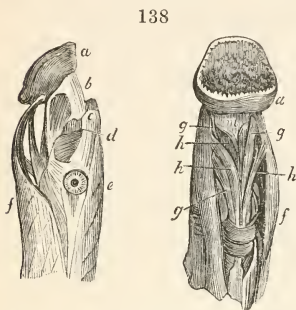
The segmental disposition of the muscular masses is most simple, most distinct, most like the annulose type, in the *Cyclostomi* : yet it is considerably specialised for the due working of the suctorial apparatus. In the Lamprey, fig. 138, slips are continued or derived from the anterior part of the myocommas, for drawing back, bending in different directions, and expanding the mouth. Of these, the superior, *e*, is inserted into the cartilage, fig. 24, 20 ; raises and fixes it, giving a fulcrum and favourable direction for the muscle, fig. 138, *b*, which directly retracts and raises the sucker, *a* : the inferior slip, *f*, is inserted into the process, fig. 24, *q*, and into the lower border of the gristly base of the sucker, ib. 22 : it retracts and depresses the sucker. An intermediate lateral slip, inserted a little higher upon the margin of *q*, fig. 24, retracts and draws outward the sucker. All these retractors, co-operating, serve to expand the sucker ; or, if duly antagonised by the *sphincter oris*, pull back the object seized by the sucker, or draw the body of the fish towards it, according to the fixed point.



Shorter muscles arise, above, from the cranial cartilage, fig. 24, *d*, and below, from the hyoid cartilage, to act upon parts of the sucker; the latter, *g*, *h*, diverge to their insertions. Part of the deep-seated longitudinal *expansor oris*, more directly antagonising the circular *sphincter oris*, *a*, is seen at *m*, fig. 136.

Details of the myology of the Myxinoids with a comparison of the muscular system of Fishes with that of higher Vertebrates, will be found in XXI. pp. 179–249.

In the Trunk-fish (*Ostracion*) flexion of the trunk is abrogated by the case of ganoid armour, fig. 16, *dn*, *dh*, inclosing the body, and which leaves only the jaws and fins free. The myocommas are accordingly reduced to a thin layer of longitudinal fibres, modified posteriorly for insertion into the moveable part of the tail and its fin.



Muscles of head and sucker; Lamprey, XLIII.

In another plectognath, the odd-shaped Sun-fish (*Orthogoriscus*) the muscles of the continuous vertical fins take the place of the ordinary myocommas: those of the lofty dorsal commencing behind the occiput; those of the deep anal behind the short abdomen: the *dermoneurales* arise from the integument, especially the fibrous septum of the lateral line; the deeper-seated *interneurales* from the neural and interneural spines. Each series is more or less blended together, conformably with the degree of confluence of the interneurals, upon the expanded ends of which the spines of the dorsal fin move as one body, the anal fin having a similar structure. Nevertheless, towards their insertion, the fasciculi of the fin-rays become, like them, distinct; each one behind being sheathed by the one in front, and their long tendons passing through lubricated grooves or sheaths to their insertions. On the sides of the abdomen the muscles are reduced to two fasciculi, expanding, the one from the clavicle, the other from the coracoid, upon the peritoneum.<sup>1</sup>

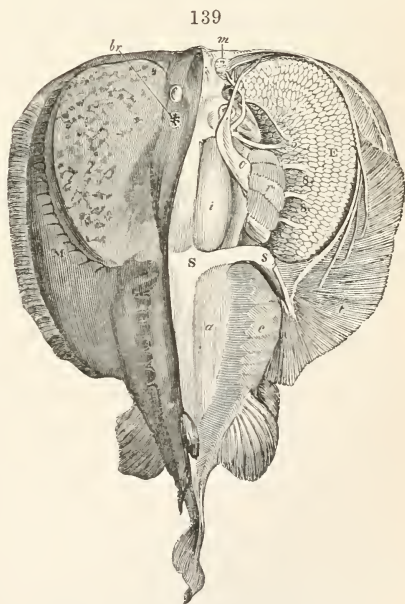
Amongst the *Plagiostomi*, the Sharks are the most active and powerful, and in them the muscular system is most developed, and in certain parts most specialised. The more acute angles formed by the intermyocommal septa have already been noticed, fig. 132. A fasciculus continued from the upper portion is inserted, by a strong aponeurosis into the upper part of the cranium, ib. *a*, *a*.

<sup>1</sup> XLVI. and CXCVII.

The muscles of the jaws are very powerful, as might be expected in these fierce and predatory fishes. One, analogous to the 'temporal,' fig. 132, *m*, arises from the lateral and posterior ridge of the cranium, and its fibres converge as they pass obliquely downward and forward to their insertion into the mandible. They are covered in great part by the stronger muscle *ib. l*, analogous to the 'masseter,' which arises from the under part of the postfrontal ridge, passes over the maxillo-mandibular joint, as over a pulley, and expands to its insertion in the lower side and ridge of the hinder two-thirds of the mandible. Smaller muscles, 'maxillo-mandibulares,' *ib. g*, pass from the upper to the lower jaw, and directly close the mouth. The openers are chiefly the muscles, *p*, which have their chief fulcrum in the coracoids, and expand to be inserted into the symphysis mandibulæ. The gill-apertures are contracted by the muscles, *q, q*, and dilated by others passing obliquely from above to their front boundaries. The muscular invest-

ment of the branchial chamber of the Torpedo fig. 139, *r*, receives a fasciculus from the scapula, and sends another, *ib. o*, forwards to the cranium, from which the constrictor of the electric battery, *E*, is continued. The *protractor scapulae* in the Skate and Torpedo is of considerable length, in consequence of the backward displacement of the scapular arch, and is of great strength, by reason of the enormous pectoral appendage which the arch sustains. The myocommas of the trunk are fused into four great longitudinal masses. The *neuro-medial* mass, fig. 139, *a*,

arises from the scapula, *s*, and by strong carneous fasciculi from the vertebræ behind the scapular attachment: above the pelvis they divide into tendinous slips, which pass backward in separate sheaths, to be successively inserted into each vertebra as far as the end of the tail. The *neuro-lateral* mass or muscle,



Muscles and electric batteries of the Torpedo.  
XLIII.

ib. *c*, arising from the outer part of the scapula and from the parapophyses of succeeding vertebræ, is inserted by similarly disposed, but more slender tendons. At their termination, each tendon bifurcates, allowing that appropriated to the succeeding vertebra to pass through it, so that all, save the last, are both *perforati* and *perforantes*. The *protractor scapulae*, ib. *i*, becomes, when antagonised by the two foregoing muscles, the chief elevator of the head. Of the two muscles of the rostrum in the Ray, the superior, *levator rostri*, arises from the scapula by a short fleshy belly ending in a slender round tendon which runs above the branchiæ in a synovial sheath to the rostral cartilage, which it serves to raise: the inferior, *depressor rostri*, arises from the lower part of the coalesced anterior vertebræ, runs obliquely outward, and then curves inward to its insertion into the lower part of the base of the rostrum. The muscles of the jaws in the Rays include, with *maxillo-mandibulares*, those answering to *l* and *m* in the Shark, fig. 132. The *depressor mandibuli* is a large oblong mass of parallel longitudinal fibres, arising from the lower (coracoid) part of the scapular cincture, and passing forward to be inserted into the mid part of the mandible. Two small muscles, one on each side, contribute to depress the mandible: they are attached in front near the commissure of the lips, and, running inward, almost cross each other beneath the great depressor. A third muscle has its fibres remarkably interlaced, but divisible into three chief fascicles, two of which are anterior and one posterior: this is derived from the end of the upper jaw and joins the hinder margin of the second mass. The first portion is situated in front and above the maxilla, near its commissure, and runs obliquely to join the outer edge of the second fascicle: all co-operate in firmly closing the mouth. The *protractor oris* forms a pair of long and slender muscles passing from the rostrum between the cranial base and the palate to be inserted into the maxilla. The muscles of the vast pectoral fins form two thick fleshy layers, covering its cartilages above, fig. 139, *t*, and below, and dividing into as many fasciculi as there are fin-rays, into which they are inserted. A similar arrangement obtains in the muscles of the ventral fins, ib. *v*.

The muscles, in Fishes, of the eye-ball, the air-bladder, and of some other special organs, will be described with the parts they move.

The muscular tissue (myonine) of fishes is usually colourless, often opaline, or yellowish; white when boiled: the muscles of the pectoral fins of the Sturgeon and Shark are, however, deeper coloured than the others; and most of the muscles of the Tunny

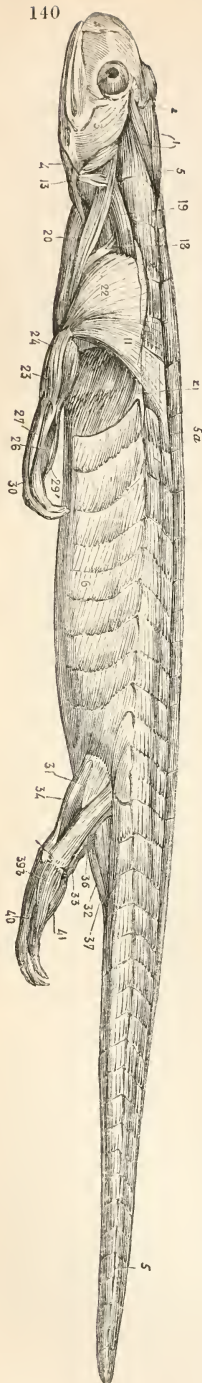
are red, like those of the warm-blooded classes. The want of colour relates to the comparatively small proportion of red blood circulated through the muscular system,<sup>1</sup> and the smaller proportion of red-particles in the blood of fishes: the exceptions cited seem to depend on increased circulation with great energy of action; and, in the Bonito and Tunny, with a greater quantity of blood and a higher temperature<sup>2</sup> than in other fishes. The deep orange colour of the flesh of the Salmon and Char depends on a peculiar oil diffused through the cellular sheaths of the fibres. The muscular fasciculi of Fishes are usually short and simple: and very rarely converge to be inserted by tendinous chords.<sup>3</sup> The proportion of myonine is greater in Fishes than in other Vertebrata; the irritability of its fibres is considerable, and is long retained. Fishermen take advantage of this property, and induce rigid muscular contraction, long after the usual signs of life have disappeared, by transverse cuts and immersion of the muscles in cold water: this operation, by which the firmness and specific gravity of the muscular tissue are increased, is called 'crimping.'

§ 47. *Myology of Reptiles*.—The myonine of the air-breathing Hæmatoerya is always pale in colour, and the fibres are tenacious of their irritability: the energy of the muscular contraction is in some instances, and on some occasions, great; but cannot be excited in frequent succession, such power being soon exhausted.

In the ichthyomorphous Batrachia the recent myonine presents a pearly clearness, as in some fishes, and the chief bulk of the tissue is arranged in transverse segments, of which, however, the progress of massing into longitudinal groups is greater than in the Sharks. In the Salamander, figs. 140, 141, the neural or upper halves of the myocommas, separated at the midline of the back by a furrow lodging cutaneous follicles, have a tendency to group themselves into distinct longitudinal tracts, as they advance forward: just as their homologue — the common 'erector spinæ' in man — subdivides into the longitudinal masses called 'sacro-lumbalis,' 'longissimus dorsi,' and 'spinalis dorsi,' &c., in its corresponding course. The median portion, fig. 140, 5 a, in *Salamandra*, representing the *spinalis dorsi* in the trunk, has its anterior insertions in the neural arches and spines of the cervical and occipital vertebræ; and there answers to the 'spinalis' and 'semispinalis' colli, and to the 'biventer cervicis' and 'complexus.' The lateral portion, answering to the *longissimus dorsi* and *sacro-lumbalis* in the trunk, represents, by its insertions, the 'transversalis colli' and trachelo-mastoideus, fig. 140, 5, in the neck. The hæmal

<sup>1</sup> XLVIII. pp. 4, 16.<sup>2</sup> L.<sup>3</sup> XLIX. p. 3.





Muscles of *Salamandra terrestris*.  
CLXXXVII.

or lower half of the myocommas in the trunk, fig. 140, 6, has been held to represent the *obliquus externus abdominis*; but, as it is segmented by aponeurotic prolongations of the short pleurapophyses, both in the abdominal and caudal regions, it is more like a series of intercostals. The broad, thin, carneotendinous sheets, called 'external' and 'internal oblique' muscles in Mammals, having their fibres running in opposite directions, may, indeed, be referred to the same system of segmental trunk-muscles; but this grade of differentiation is not reached in Fishes and fish-like Batrachians. The medial parts of the hæmal myocommas are more distinct, and show more of the character of a longitudinal muscle with tendinous intersections, like the 'lineæ transversæ' of the human 'rectus abdominis;' and this muscle is one of the determinable homologues of a recognisable tract of the myocommas of the fish and newt. In the Salamander, however, the tract, fig. 141, 8, is as superficial as that part of the sheath of the 'rectus abdominis' in Mammals; and it forms a corresponding part of the sheath of a deeper-seated longitudinal muscle, fig. 141, 7. Both 7 and 8 are specialisations of the lowest hæmal portions of the myocommas: they are anteriorly resolved, or continued, as in Fishes, into muscles acting upon the scapular, hyoidean, and mandibular arches. The *pubohyoideus*, 7, arises from the pubis and outer part of the gristly hæmapophysis, or Y-shaped cartilage, fig. 113, *d*; it runs forward in a sheath, analogous to that formed by the aponeurosis of the external and internal oblique muscles of Mammals, and is inserted into the ceratohyal. The muscle, 8, called *rectus abdominis*, by Funk,<sup>1</sup> has its attachment to the pubis through the medium of the Y-shaped cartilage, which represents the marsupial bones and tendinous 'pillars of the abdominal ring' in Mammals: it is

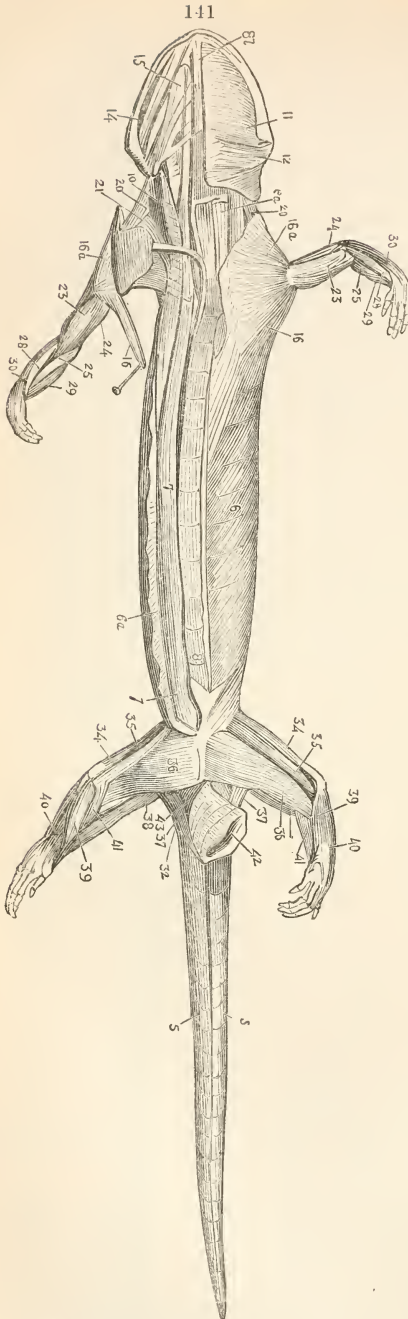
<sup>1</sup> CLXXXVII.

attached anteriorly in part to the triangular short sternum, extending beyond it to the transverse part of the episternum, and is thence continued (as in fig. 135, 27), to the symphysis mandibulæ, representing the *geniohyoideus*. A small fasciculus, fig. 141, 10, is also sent to the coraco-scapular joint.

The upper jaw is fixed. The muscle which, by its insertion into the lower jaw, acts as a *temporalis*, is divided into two fasciculi; one, fig. 140, 2, has the normal origin from the side of the cranium; the other, ib. 1, *atlanto-mandibularis*, acts with greater force by deriving its origin from the neural arch and spine of the atlas. The *masseter*, ib. 3, arises from the mastoid and epitympanic, and is inserted into the outer surface of the hinder half of the mandible. The *occipito-mandibularis*, or *digastricus*, ib. 4, arises from the paroccipital and back part of the epitympanic, and is inserted into the angular element behind the tympano-mandibular joint whereby it opens the mouth. In this action it is aided by the strip, ib. 13, which passes from the angle of the jaw upward to the skin. Some amount of lateral movement of the mandible is effected by a *pterygoid* muscle. The retraction of the mandible is provided by the muscle, ib. 13, although it seems lost in the skin, as it passes backward from the angular process. A *mylohyoideus*, fig. 141, 11, passes from one ramus to the other, external to the *geniohyoideus*, ib. 81, and to the following muscles of the hyoid arch. The *genio-ceratoideus*, ib. 14, arises from near the symphysis mandibulæ, and is inserted into the ceratohyal. The *hyobranchialis*, ib. 15, passes from the base of the ceratohyal to the hyobranchial cornu.

With the growth and specialisation of the segments of the limbs the muscles became larger, more numerous, and more distinct. The *pectoralis*, fig. 141, 16a, 16, has its origin extended from the fore part of the coracoid and episternum to the linea alba, or aponeurotic continuation of the sternum, half an inch beyond the coracoid; the fibres converge to their insertion into the pectoral ridge of the humerus; but so that the coracoid portion is almost a distinct muscle. This muscle suspends the fore part of the trunk upon the fore-legs, and besides depressing the humerus, rotates it in the plane of the body's axis as different portions of the muscle come into action.

A muscle, fig. 140, 11, arising from scattered fibres by a longitudinal tract of the aponeurosis, covering the *longissimus* and *spinalis dorsi*, collects those fibres and contracts as it descends over the hind part of the scapula to be inserted into the back part of the pectoral ridge. An anterior part, ib. 22, of the same



Muscles of Salamandra terrestris. CLXXXVII.

system of converging fibres takes its origin from the scapula itself, and converges to an insertion close to that of the preceding. The entire mass of the muscles 22 and 11 antagonise that, 16, 16a, below; one raises, the other depresses, and both rotate, the humerus to and fro. As the fore-limb gains size and power in higher air-breathers, the muscle 11 seeks a more extended origin, covers a greater proportion of the segmental system of trunk-muscles, acquires the name of *latissimus dorsi*, and, in Anthropotomy, is classed amongst the 'first layer of the muscles of the back.' The muscle 22, becomes developed into 'supra-' and 'infra-spinatus,' and, perhaps, also *deltoides*. The *protractor scapulae*, arising, as in Fishes, from the paroccipital, now also derives fibres from the transverse processes of the first and second trunk-vertebrae, and divides into two distinct fasciculi; one, fig. 140, 19, is inserted into the base of the scapula; the other, ib. 20, into the humeral end of that bone. A small strip, 18, which tends more directly to raise the scapula, arises from the transverse processes of the third vertebra; but the muscle, 19, is that which best answers to the *levator scapulae* of Mammals. Two

strips from the second and third cervical diapophyses, inserted into the under part of the scapula, indicate the commencement of the *serratus magnus anticus*, fig. 141, 21. The mass of muscle, figs. 140, 141, 23, which protracts or 'flexes' the fore-arm, arising from the fore and inner part of the glenoid cavity and from the fore part of the humerus, represents the *biceps* and *brachialis internus*. The retractor or extensor mass, ib. 24, answers to the divisions of the triceps. On the antibrachium the flexor of the wrist is divided into a 'radial,' fig. 141, 25, and 'ulnar,' fig. 140, 26, portion; as is likewise the extensor, of which, 27, fig. 141, represents the *extensor carpi ulnaris*, and 28 the *extensor carpi radialis*: 29 is the *flexor digitorum communis*, and 30 the *extensor digitorum communis*.

The *pectoralis*, fig. 141, 16, is represented in the pelvic limb by the muscle, ib. 36, which arises from the ischiopubic symphysis, and is inserted into the front and inner part of the head of the tibia. This mass in higher reptiles becomes differentiated into the *pectineus*, the *adductors*, and the *gracilis*; it depresses and adducts the pelvic limb. Its chief antagonist is marked 36 in fig. 140. It rises from the ilium, and is inserted into the lower and outer part of the femur, and also into the outer part of the head of the tibia; it corresponds by its origin with 22 in the fore limb, and becomes developed into *gluteus externus* and 'tensor fasciæ femoris' in Mammals. The fasciculi which correspond with 11, in the fore-limb are 37 and 32, fig. 140; they arise from fascia connected with the transverse processes of the third and fourth caudal vertebræ, and are inserted into the middle and back part of the femur. The muscle, 31, which arises from the fore part of the ilium, and is inserted into the upper third of the femur, repeats the anterior fibres of 22 in the scapular limb. The chief difference is that the protractors, 31, and retractors, 32 and 37, of the thigh are more distinct from the abductor and levator, 36; and that this has a more advantageous insertion for its office by being extended to the second segment of the limb. The retractors, 32, 37, act like the *latissimus dorsi* 11: their origin is in connection with the vertebral or axial system: they become developed in the pelvic limb of higher animals into parts of the 'glutei' and 'pyriformis.'

The protractors or flexors of the thigh, 34, 35, which answer to those of the arm, 23, arise from the fore and under part of the ilium, and are inserted into the fore and upper end of the tibia. The muscle, fig. 141, 35, which passes to the inner side of the head of the tibia, answers best to the *sartorius*; the larger mass on its



outer side, 34, to the *triceps extensor cruris*, and more especially to the *rectus femoris*, as having its chief origin from the ilium; whilst its tendon expands over the fore part of the knee joint, as that of 23 passes over the fore part of the elbow joint; and both without having any sesamoid lever developed therein.

The retractors or extensors of the thigh and leg, ib. 33, answering to the retractors of the arm and fore-arm, 24, arise from the hinder and outer part of the ilium, and are inserted partly into the femur, partly into the outer part of the head of the tibia. A muscle, fig. 141, 38 (*sacro-plantaris*), forming part of this system, has a special extent and disposition, favouring the effective backward stroke of the foot in swimming: it arises from the sacral rib and is inserted into the plantar fascia. It is a 'flexor' of the leg, like the 'biceps flexor cruris:' it is an 'extensor' of the foot, like the 'plantaris.' And here a few remarks may be offered on the terms 'flexion' and 'extension,' as applied to the 'fore-arm' and 'leg' in higher air-breathing Vertebrates and in Man.

The fore and hind limbs of the Salamander are figured extended in corresponding positions, in fig. 140, as those of the Plesiosaurus are represented in fig. 45. The ulna is external or posterior in the arm, the fibula in the leg. If, in the dead newt, the fore-arm be moved upon the arm to and fro, in the direction of the trunk's axis, it can be bent at an angle with the arm either way; and the like would most probably be the case in the Plesiosaur: there is no bony configuration of the elbow-joint to prevent this in either reptile; only the ligaments favour the forward bend more than the hinder one, in the batrachian. In the hind limb the leg can be bent at an angle with the thigh, both forward and backward; but the ligaments of the joint offer more resistance to the forward than to the backward bend. As we ascend the vertebrate scale in the comparison of limbs, a bone of the fore-arm sends a process across the back part of the elbow-joint which fits into a cavity in the bone above the joint when the two are brought into the same line; and the fore-arm cannot be bent back at an angle with the arm without fracture of the interlocking bar or 'olecranon.' In the leg the contrary bend, at an angle forward upon the thigh, is prevented by configuration of the knee-joint, with interarticular cartilages and ligaments.

Thus the forward bend is favoured in the fore-limb; the backward bend in the hind limb.

In quadrupeds the limbs are habitually retained with the first and second segments more or less bent in the directions favoured by the configuration of the elbow-joint and knee-joint respec-

tively, to which the muscles conform in relative size and position. These opposite bends are shown in the skeleton of the Crocodile, fig. 57.

When the leg, 66, is brought forward (protracted), widening the angle between it and the thigh, *v*, and when the fore-arm, 55, is brought forward, contracting the angle between it and the arm, 53, the motions are the same, or homologous in both limbs. But in one case such motion is called 'flexion;' in the other 'extension:' these terms relating not to the absolute line or direction of motion of the limb, but to the resulting relative position of one segment of the limb to another. The protractor muscles drawing forward the second segment of the limb *to* an angle with the first, are called 'flexors;' those drawing forward the second segment *from* an angle with the first, are called 'extensors.' The same distinction is made with the 'retractors,' according as, in drawing back the second segment, they rotate it from an angle to a straight line with the first segment, or from a straight line to an angle. Thus the homologous movements are signified by different terms, and the homotypy of the muscles has been masked by the same artificial verbal distinctions. The 'flexors' of the fore-arm answer to the 'extensors' of the leg in serial homology. The 'biceps flexor cubiti,' with the 'brachialis anticus,' is the homotype of the 'triceps extensor cruris,' not of the 'biceps flexor cruris;' while this muscle, with the semitendinosus, is the homotype of the 'triceps extensor cubiti.' Much of the difficulty of comprehending the true serial homology of the parts of the fore and hind limb has arisen from regarding the flexors in the one limb to be the homotypes of the flexors of the other, and vice versâ. The pertinacity with which the idea of the patella being the homotype of the olecranon is maintained, depends in a great degree upon the error of supposing the 'triceps extensor cubiti' and the 'biceps extensor cruris' to be homotypes or serial homologues.<sup>1</sup>

Returning to the Newts, we find the chief retractor or extensor, fig. 141, 39, of the foot answering to the retractors or flexors of the carpus, 25 and 26. But, as regards the toes, since their joints are so arranged as to allow them to be most easily and extensively

<sup>1</sup> Some anatomists assuming this to be a matter determined and unquestionable, make it the basis for impugning the opinion that the patella answers serially to the tendon of the biceps brachii, and especially to the sesamoid sometimes developed therein. "Unless we are entirely to disregard the guidance of muscular relations in determining homology, we must admit that the ossicle upon the olecranon is the homotype of the patella," &c. CLXXI. p. 21, and CLX. *passim*. The muscular concur with the osseous relations in showing that the ossicle upon the olecranon is the homotype of that upon the peronecranon, or produced head of the fibula in certain marsupial and other mammals. CLXI. pl. 1, fig. 16.

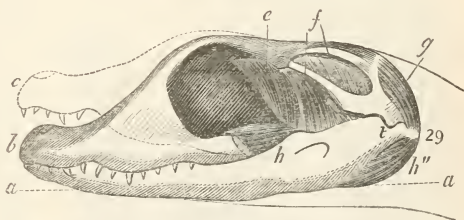
moved in the direction of 'retraction,' as the limbs hang in fig. 140, the 'flexors' of the fingers have their homotypes in the hind limb called 'flexors of the toes,' and the muscles effecting the opposite movements of the digits are termed 'extensors' in both fore and hind limbs. The muscle, 40, arising from the fascia of the knee, becomes by its insertion the *extensor longus digitorum pedis*. The muscle, 41, is the *flexor longus digitorum pedis*. A *short extensor* arises from the fore part of the tarsus; its tendons unite with those of the long extensor. A *short flexor* from the opposite side of the tarsus divides, to be inserted by fleshy fibres into the tendons of the flexor longus. The hallux has a special extensor and abductor: the fifth toe has also an abductor: these combining in action, enlarge the breadth of the foot.

In the higher reptiles, of the order *Crocodylia*, chiefly affecting the watery element, and with frame and limbs proportioned for natation, the primitive segmental structure continues to be shown by the vertical aponeuroses passing outward from each successive vertebra, especially from the di- and pleur-apophyses; they divide the mass of muscles answering to the caudal myocommas of Fishes and fish-like Batrachia in the tail; to the *spinalis dorsi*, *longissimus dorsi*, and *sacrolumbalis* of higher Vertebrates in the back; and to the *cervicalis ascendens*, *splenius capitis*, and *transversalis colli* in the neck. The posterior attachment of the *sacrolumbalis* is to the fore part of the ilium by a slender tendon: that of the *longissimus dorsi* is to the sacral ribs. External to the longissimus dorsi is the *trachelomastoideus*, originating behind from the diapophyses of the second or third dorsal vertebra, passing forward between the di- and zyg-apophyses of the cervical vertebrae, deriving slips therefrom, and inserted into the mastoid. The *complexus* rises from the sides of the neural spines of the middle cervical vertebrae, and is inserted into the paroccipital. The *splenius capitis* arises from the neural spines of the anterior dorsals, and is partly a continuation of the spinalis dorsi: it is inserted into the superoccipital, and shows traces of the segmental structure. The powerful muscles of the tail are more decidedly divided by aponeurotic septa into segments, corresponding with the vertebrae; but they are grouped together, by Cuvier, into three pairs of longitudinal muscles. The first is neural in position, and chiefly a backward prolongation of the spinalis dorsi; the myocommal septa form an angle directed forward. The second is lateral, and begins by a strong tendon from the upper and back part of the ilium, and by a second tendon from the ischium: it is also connected with fleshy flattened fasciculi from the pubis

and abdominal ribs: its myocommal septa describe an acute angle directed backward. At the base of the tail it descends to the lower border, and covers part of the third muscular column. This derives a tendinous origin from the inner trochanterian ridge of the femur, and from a ligament thence extending to the femoro-fibular articulation: from these attachments the muscle passes backward to the hæmal arches and spines related thereto by alternating origins and insertions, and there assumes the myocommal character of the lowest or hæmal tract in the tail of the Newt and Fish. By its anterior attachments in the Crocodile, this series of muscles—the *femoro-peroneo-coccygius* of Cuvier—closely associates the pelvic limbs with the tail in the natatory actions and evolutions of the amphibious carnivore.

The mandibular muscles are strongly developed in the Crocodile in comparison with other Saurians; although they seem, after a comparison with those of carnivorous mammals, small in proportion to the length and massiveness of the jaws. The temporal is represented by two muscles, one of which, the *pretemporalis*, fig. 142, *e*,

142



Mandibular muscles, Crocodile

has its origin extended forward into the orbit from beneath the postfrontal, whence its fibres pass obliquely backward: the larger *temporalis*, ib. *f*, is attached to the parietal, the mastoid, and tympanic, and its fibres pass vertically external to those of the pretemporal, to be inserted into the coronoid and surangular. The *pterygoidei* are larger muscles than the temporales; the one from the ectopterygoid, fig. 142, *h*, receives an accession of fibres from the long pterygoid bone, and, passing obliquely backward, swells out into almost a hemispheric prominence at its insertion into the outer side of the angular elements at *h*. The apertor oris, or *digastric*, ib. *g*, arising from the back part of the prominent mastoid, descends obliquely backward to the projecting angular process behind the tympano-mandibular joint. When the mandible rests on the bank, as at *a*, *a*, supporting the head of the crocodile, and makes its angles, ib. 29, the fixed point, the *digastrici*, *g*, acting upon the lever of the mastoid, *s*, open the mouth by rotating the cranium and upper



jaw from *b* to *c*, upon the tympano-mandibular joints, *t*. Observation of this action engendered the notion that the upper jaw was moveable, and that this was a peculiarity of the Crocodile; but it moves only as part of the entire cranium.

As the muscles of the limbs reach their maximum of number and variety in the *Chelonia* and saltatory *Batrachia*, they will be specified in those groups; and the myology of the trunk will be resumed, as it is seen in the *Ophidia*.

In these reptiles, as might be expected from the functions of the spinal column, specialisation of the muscles of the vertebræ and ribs reaches its maximum. The coalescence of the upper or neuromesial and neurolateral parts of the myocommas into longitudinal tracts is more complete and distinct than in the fish-like

*Batrachia*, or the *Crocodylia*; the primitive distinction or segmentation being preserved only at the points of attachment.

In the neuromesial tract, fig. 143, A, those which may be called 'origins' are in two series, one from the bases of the neural spines, the other by short tendons from the diapophyses: the fleshy fibres from each origin converge and coalesce as they pass forward, and terminate in a long slender tendon: these tendons are attached to the summits of the neural spines. We have here the characters of *semispinalis* and *spinalis dorsi*. The column external to the preceding answers to the *longissimus dorsi*; it arises by a series of fleshy origins from the transverse processes, and by tendons from the contiguous parts of the ribs; the fleshy fibres



Muscles of the vertebræ and ribs. Python, cxci.

pass forward and outward partly to the fascia covering the

semispinalis dorsi, and partly to its insertions into the neural spines; its foremost attachment is to the superoccipital. The third (neurolateral) tract derives fibres from the tendinous origins of the longissimus dorsi, and detaches from its outer side thin slips, each inserted by a slender tendon into a rib; it represents the *sacrolumbalis*. A muscle deriving slips of origin from the zygapophyses of four or six anterior vertebræ passes forward to be inserted into the mastoid, fig. 145, *r*, and represents the *trachelomastoideus*. On the under part of the vertebral centrum are a series of oblique fasciculi, extending and converging in pairs from the diapophysis of one vertebra to the hypapophysis of the second or third vertebra in advance. The *longus colli* at the fore or upper part of the spinal column in Mammals and Man is a repetition of this series; the greater extent and development of which in Ophidians is indicated by the number and length of the hypapophyses, *hy*, figs. 46, 47: and of the subdiapophyses, *d'*, fig. 47 *a*; and these are maximised in *Crotalus* and *Naia*; the co-related muscle, having its foremost insertion into the occipital hypapophysis, fig. 146, *p*, brings down the head in the blow inflicted by the venom-fangs with proportionate force.

On removing the semispinalis dorsi, muscles appear which pass obliquely between the transverse and spinous processes, like the series called *multifidus spinæ* in Man. Beneath these are *interspinales* and *intertransversales*. External to the multifidus spinæ is a series of *levator costarum breviores*, fig. 143, *B*, arising from the diapophyses, and respectively inserted into the rib of the succeeding vertebra. At their insertion arise the *pretrahentes costarum*, *ib. C*, which run more obliquely backward, and terminate each in the eighth (*Naia*) rib beyond that from which it arose; being attached also to the intermediate ribs and intercostal fasciæ. In *Python* they are continued on to the tenth or twelfth rib, fig. 143, *D*, and these continuations have been described as a distinct series. Beneath them is a shorter series, the *pretrahentes breviores*, *ib. E*. The *retrahentes costarum*, fig. 144, *C*, arise from the lower part of the diapophysis, and pass obliquely forward and outward along the internal surface of the ribs to be inserted into the fourth rib in advance. Where these muscles terminate, the *transversalis abdominis*, *ib. D*, takes its serrated origin; its fibres descend obliquely forward and terminate, with those of the opposite side, in the raphé, or medial tendinous line; which closely adheres to that part of the inserted border of the ventral scutes. The *retrahentes inferiores*, *ib. B*, interdigitate at their origins (in *Python*) with

those of the *transversalis abdominis*, and pass forward to be inserted at the end of the bony part of the fourth rib in advance. The muscle answering to the *rectus abdominis*, ib. A, has the short rib-cartilages for its intersections, instead of the fibrous 'lineæ transversæ,' as in Man.

The *intercostales*, fig. 143, F, have their usual position and decussating arrangement in two planes. The *squamo-costales*, figs. 143, 144, I, I, arise from the ribs near the insertions of the *levatores costarum*, B: these origins have been detached and the muscles reflected; in the figures they pass obliquely backward,

and are inserted into the skin near the outer margins of the ventral scutes,

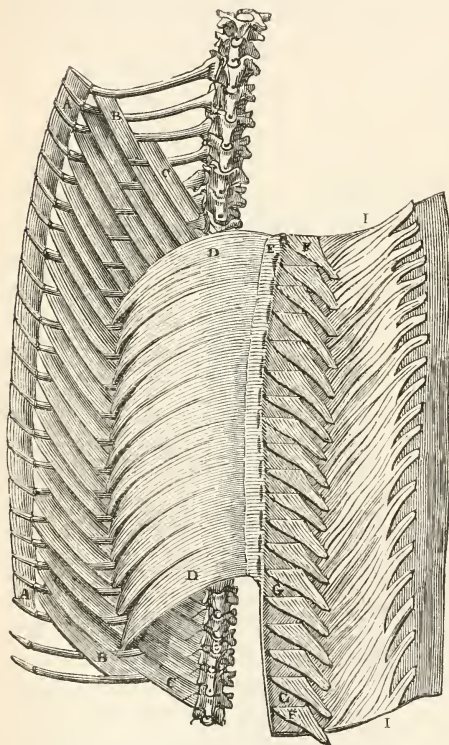
The *scuto-costales*, fig. 143, H H, rise from the fore part of the end of the rib, and are inserted into the edge of the scute.

The *interscutales*, figs. 143, 144, F, G, K, are in two layers, which decussate each other, and cooperate with the *scuto-costales* in alternately erecting and depressing the scutes.<sup>1</sup> The fixed point of one series is the 'linea alba,' ib. E; of the other, the line of insertion of the *squamo-costales*, ib. I. The co-ordinate effects of the foregoing muscles of the ribs and scutes produce deter-

minate movements, to and fro, of the ribs, with alternate erection and depression of the broad transverse ventral scutes.

The tympano-mandibular arch has unusual mobility in Ser-

144



Muscles of the ribs and scutes, *Python*. cxci.

<sup>1</sup> xx. vol. i. pp. 69-72.



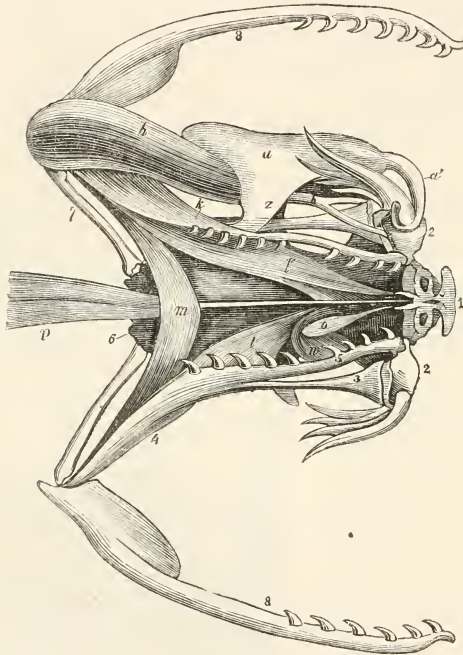




process of the mandible. From fascia attached to the neural spines of some of the anterior vertebræ there extends a flattened muscle, *neuro-mandibularis*, fig. 145, *t*, which unites with a smaller strip from fascia connected with the ribs of those vertebræ, *costo-mandibularis*, figs. 145, 147, *u*, to be inserted into the lower border of the mandible. These muscles depress and retract the lower jaw.

A powerful muscle, *ectopterygoideus*, fig. 146, *h*, which in its mandibular relations resembles the external pterygoid, advances

146



Muscles of the ptergo-palatine apparatus of the *Crotalus*. excii.

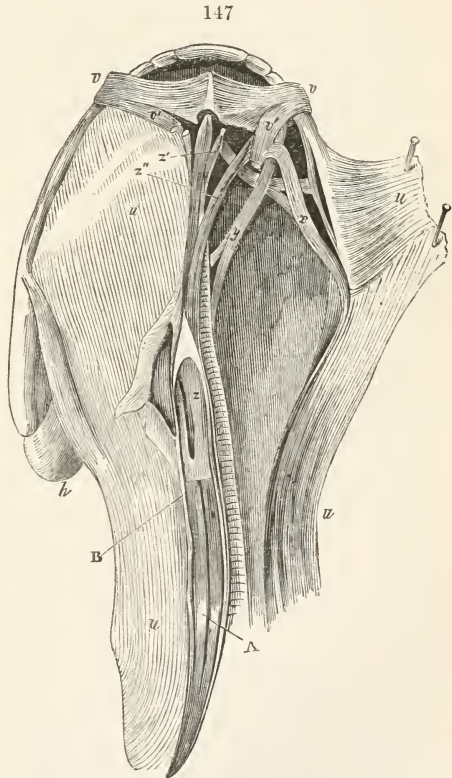
forward to the fore part of the ectopterygoid, and to the back part of the maxillary in *Python*. In *Crotalus* it expands into a fascia, spread over the pouch lodging the venom-fangs, preserving a tract of tendinous strength for insertion into the lower part of the hinder process of the maxillary. It cooperates with the erector of the fang in fixing the moveable maxilla during the blow, and retracts the fang on the relaxation of the erector. When its fore part is the fixed point, the ectopterygoideus spreading its man-

dibular attachment over the articular capsule to the back part of the angular process, protracts the lower jaw.

The *entopterygoideus*, fig. 145, *k*, is attached anteriorly to the pterygoid bone, ib. 4, whence its fibres pass outward and backward to the inner surface of the angular and surangular elements, covered by the ectopterygoideus. It retracts and divaricates the palato-pterygoid jaws, protracts and approximates the back parts of the mandibular rami. The fore parts of those bones which, through their loose elastic symphysial connection, yield laterally to the pressure of the prey when seized, are brought together, after

it is swallowed, by an *intermandibularis*, answering to 21, fig. 137, in fishes: it is shown in fig. 147, passing from the end of one ramus to that of the other, at *v, v*, with a median raphé, as in the mylohyoideus; and sending a slip *v* from each attachment, which expands upon the intermandibular integument, restoring and corrugating it after its great occasional stretching. In this it is aided by a thin layer of fibres internal to and in close connection with the insertion of the costomandibularis exposed by the outward reflection of that muscle at fig. 147, *a*.

In Fishes the fore part of the levator tympani, fig. 136, 22, is inserted into the pterygoid: in Serpents the origin of the answerable part, *presphenopterygoideus*, is advanced forward to the pre-sphenoid, whence its fibres, fig. 146, *l*, pass outward and backward to their insertion into the pterygoid, 4, and ectopterygoid, 3, at their junction. In protracting the pterygoid it pushes forward the maxillary, rotating it outward in the Constrictors; but, by



Muscles of the throat of the Rattlesnake. (*Crotalus*.) CXCII.

its fibres, fig. 146, *l*, pass outward and backward to their insertion into the pterygoid, 4, and ectopterygoid, 3, at their junction. In protracting the pterygoid it pushes forward the maxillary, rotating it outward in the Constrictors; but, by

the modification of the bones peculiar to venomous serpents, as shown at 3 and 2, fig. 146, the muscle rotates the short maxillary vertically through the ectopterygoid, so as to bring the venom-fang from the recumbent to the vertical position ready for the blow.

The *presphenopalatine* muscle arises from the side of the fore part of the presphenoid and passes outward to its insertion along the inner surface of the palatine. From the side of the presphenoid rises the small *prespheno-vomerine* muscle, fig. 146, *v*, which sends forward a slender tendon to the half of the divided vomer, and through that bone depresses and retracts the pre-maxillary, ib. 1, after the displacement of all the bones of the mouth caused by the engulfing of the prey.

The hyoid arch is reduced to a pair of slender cartilaginous ceratohyals, running forward, almost parallel, fig. 147, B, beneath the sheath of the filamentary tongue, before their anterior membranous union. The raphé of the muscles *v* and *u*, fig. 147, is so far attached to the hyoid and lingual sheath, that by their contraction they raise the tongue after it has been pushed down: the fibres of the costomandibularis, *u*, attached to the foremost part of the mandible, through the same medial attachment protract the lingual sheath; the posterior part of the costomandibularis can retract the lingual sheath, and these actions are analogous to those of the 'sternohyoid' and 'geniohyoid' muscles in higher vertebrates. On reflecting the costomandibularis from the raphé outward, the *genioglossi* are exposed: their antero-median attachment, fig. 147, *z'*, *z'*, is to the raphé of the intermandibularis, *v*; their antero-lateral attachment, *z''*, is to the fore end of the mandibular ramus. The muscle formed by their union, *z*, extends backward along the lingual sheath to its extremity: it is the chief pro-truder of the tongue. The retractors, answering to *hyoglossi*, ib. A, arise from the hinder ends of the ceratohyals, run forward, enter the lingual sheath, and seem to coalesce in forming the main substance of the cylindrical tongue; but they again separate to terminate in its forked extremity. The fore part of the trachea is closely connected with the lingual sheath, and advances so far forward to terminate in the mouth, as to be subject to the stretchings and displacements of the elastic floor of that cavity. A special muscle, *geniotrachealis*, fig. 147, *y*, arises from the fore end of the mandibular ramus, and passes inward and backward to expand upon the sides of the fore part of the trachea. The pair draw forward the glottis; its retraction is effected through the medium of the lingual sheath and its muscles.

There are small modifications of the muscles of the long anterior outstretched ribs of the Cobra, fig. 46, *pl*, which sustain the peculiar folds of integument forming the conspicuous 'hood' of that poisonous snake. These ribs are protracted or raised by the levatores breviores, and by two sets of pretrahentes, one passing over two ribs to the third behind, the others passing over one rib to the second, and by the intercostales externi. The muscles passing from the hood-ribs to the skin come off about four lines from the head by a short tendon, the fleshy band extending between one and two inches, outward and backward to its insertion into the skin.

The muscular system of the trunk reaches, in Reptiles, its maximum in Serpents; it is reduced to a minimum in Tortoises: yet, where it has to act on the only moveable part of the vertebral column of these slow and heavy house-bearers, it is specially and in some parts largely developed.

Homology can seldom be determined or discerned, save in a general way, in the fleshy parts of *Chelonia*; as, e. g., that the muscles upon or about the trunk-vertebræ answer to those so situated in lower or higher Vertebrates; and that the primitive segmental character of such muscles is still indicated by distinct and successive attachments to a consecutive series of bony segments, as is shown, e. g., in fig. 148, 37, 39, fig. 149, 27. Where a more special determination has been attempted it has usually rested on a similarity of attachment of one end of a muscle, with acknowledged discrepancy at the other end; as when Cuvier<sup>1</sup> compares 27, fig. 148, to the *sacro-lumbalis* and *longissimus dorsi*; and when Bojanus<sup>2</sup> gives the latter name to the portions of myocommas at the opposite side of the back-bone, fig. 148, or calls the muscle, fig. 152, 91, which arises from the pubis, the *iliacus internus*. It will be understood, therefore, that in applying to the muscles of the Box-tortoise (*Emys Europæa*), the names assigned to them by the author of the exemplary and beautiful monograph<sup>3</sup> from which the illustrations, figs. 148—159, have been copied, they are to be taken more or less in an arbitrary sense, and that the characters of the muscles mainly exemplify the greater degree in which the adaptive principle prevails over the archetypal one in the soft than in the hard parts of the frame.

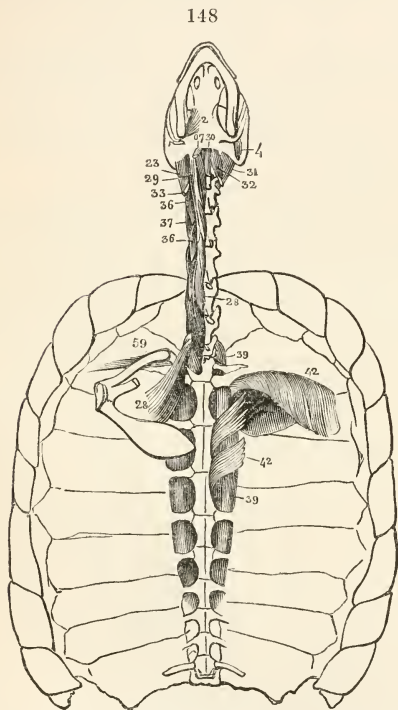
On the dorsal aspect of the vertebræ of the back, the muscular system is restricted to the '*spinalis dorsi*,' fig. 148, 39; it rises from the neural and beginning of the costal plates, neural arch

<sup>1</sup> XIII. i. p. 292.<sup>2</sup> XXXVIII.<sup>3</sup> *Ib.*



and rib of the seventh to the third dorsal vertebra inclusive, occupying the interspaces between those parts; it is inserted into the neural arch of the last cervical, and into the postzygapophysis of the next vertebra in advance.

The series of muscles called 'longus colli,' ib. 28, 28, commences by the broad origin from the under part of the first and second costal plates, and is continued by eight narrower slips from the hypapophyses of the first dorsal, and seven antecedent cervical vertebræ. These fasciculi incline forward and inward,



Muscles of the dorsal, cervical, and occipital vertebræ,  
*Emys Europæa*. XXXVIII.

overlapping each other, to be inserted successively into the parapophyses of the eighth and lower part of the centrum of the antecedent cervicals, with interposed sesamoids at the sixth, fifth, and fourth vertebræ; the foremost insertion being into the basioccipital.

Six or seven lateral portions of cervical myocommas, called *intertransversarii colli*; ib. 36, pass from the diapophyses of the eighth to the second cervicals, and are inserted along with the corresponding insertions of the longus colli from the sixth to the centrum of the atlas, or odontoid. The *intertransversarii obliqui*, figs. 148, 149, 37, are four strips from the diapophyses of the sixth,

fifth, fourth, and third vertebræ, which pass forward and downward to the parapophyses of the fourth, third, second, and first cervicals respectively. There are *interspinales* between the neural spines of the first three cervicals.

The *transversalis cervicis*, fig. 151, 33, arises from the postzygapophysis of the fifth, fourth, and third cervicals; these blend outwardly, and detach inwardly insertions to the postzygapophyses of the fourth, third, and second cervicals, and into the

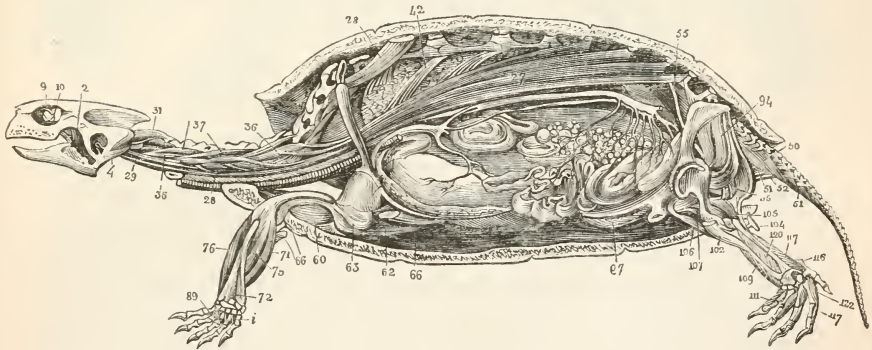
diapophysis of the atlas: the tendon so inserted is shown at 33, fig. 148.

The *complexus*, fig. 148, 23, arises from the diapophyses of the first three cervicals, and is inserted into the paroccipital: in fig. 150, the hindmost origin of this muscle is marked 25.

The *rectus capitis anticus longus*, fig. 148, 29, arises from the hypapophyses of the third and second cervicals, and is inserted into the side of the basioccipital. The *rectus capitis anticus brevis*, fig. 152, 30, arises from the atlantal hypapophysis, and is inserted into the basioccipital. The *rectus capitis posticus major*, fig. 148, 31, arises from the neural spines of the axis and atlas, and is inserted into the paroccipital. The *rectus capitis posticus minor*, ib. 31, arises from the neural arch and diapophysis of the atlas, and is inserted into the base of the exoccipital.

The largest and most remarkable portions of muscular segments of the trunk are those which are combined to effect the retraction beneath the carapace of the head and neck. The *retrahens*

149



Side view of trunk-muscles and deeper seated limb-muscles, *Emys Europæa*. XXXVIII.

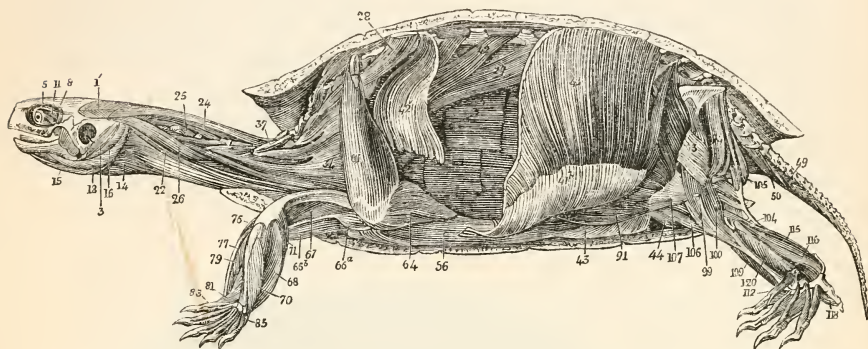
*capitis collique*, figs. 149, 150, 27, arises by six fleshy fasciculi from the neural arches and spines of the eighth to the fifth dorsals inclusive; these pass forward, blending together, and then detach four tendinous insertions: of these, the anterior and longest, as well as strongest, is into the basioccipital fossa; the other three are into the diapophyses of the fourth, fifth, and sixth cervicals. It is not difficult to sever the part of the great retractor connected with the cervical insertions, as a distinct muscle from that inserted into the occiput. The *biventer cervicis*, figs. 150, 151, 24, arises from the neural spines of the fifth, fourth, and

third cervicals, and is inserted into the same part of the occipital vertebra.

The *trachelomastoideus*, fig. 150, 26, arises from the hypapophyses of the third and second cervicals, and ascends obliquely to be inserted into the mastoid.

The *scalenus*, fig. 150, 34, arises from the inner border of the lower three-fourths of the scapula; its fibres emerge as it advances, and deliver strips of insertion to the diapophyses of the eighth to the second cervical inclusive.

150



Side view of muscles of the trunk, head, and limbs, *Emys Europaea*. XXXVIII.

The *sternomastoideus*, fig. 150, 22, arises from the middle of the inner surface of the entosternum, and is inserted into the mastoid.

The *diaphragmaticus*, figs. 148, 149, 150, 42, 42, arises by three sheets from the bodies of the fifth and fourth dorsals, and from the rib of the third dorsal; the two posterior unite to apply themselves and adhere to the mesial surface of the lung; the third sweeps over to the outer surface, 42, fig. 150, and 42, fig. 151, and is reflected from its lower border upon the peritoneum.

The *transversalis abdominis*, figs. 150, 151, 41, arises along a curved line on the inner surface of the fourth, fifth, sixth, and seventh costal plates, extending from the end of the fourth to the beginning of the seventh; also by a separate fasciculus from the eighth rib; and by three slender tendons from near the cardinal border of the hyposternal; it is inserted by a broad tendinous sheet into the mesial border of the same plastral element, which is the homologue of the abdominal hæmapophyses and spine receiving the same insertion.

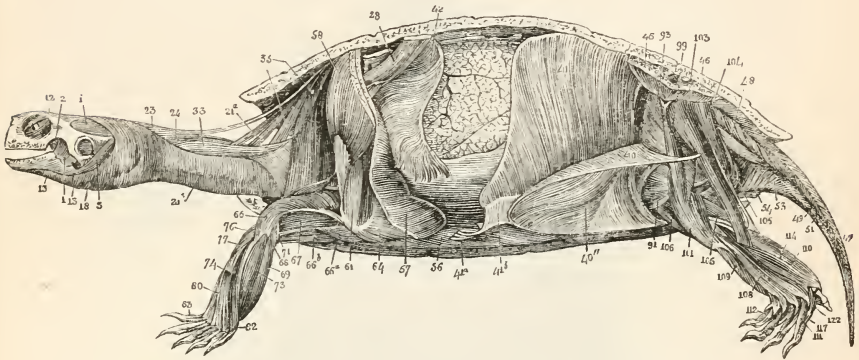
The *obliquus externus*, fig. 151, 40, arises from the inner side of the extremities of the last four costal plates, and adherent



marginal ones; it is inserted along a sigmoid line extending from the postero-external angle of the hyposternal to the middle of the xiphisternal and by a special fasciculus and tendon into the lateral process of the pubis.

The *latissimus colli*, figs. 151, 152, 21, consists of two parts; both are attached, above, to aponeuroses connecting them with the cervical diapophyses; the fibres of the posterior division, fig. 149, 21 *a*, pass down and rather backward, over the muscles of the base of the neck, and are inserted into the midline of the

151



Side view of superficial muscles of trunk, head and limbs, *Emys Europæa*. XXXVIII.

epi- and ento-sternals: the fibres of the longer anterior portion sweep transversely across the lateral and lower parts of the neck, fig. 152, 21.

The *extensor caudæ*, fig. 151, 47, includes the neural portions of the myocommas of this region from its base, where the foremost has a sacral origin, to near the tip. The *flexor caudæ lateralis*, ib. 48, consists of the lateral parts of the same muscular segments. The *flexor caudæ inferior* is shown at ib. 49: the *flexor caudæ lumbalis* in fig. 150, 50: the *flexor caudæ obturatorius* in figs. 151 and 156, 51.

The following are muscles of the tympano-mandibular arch.

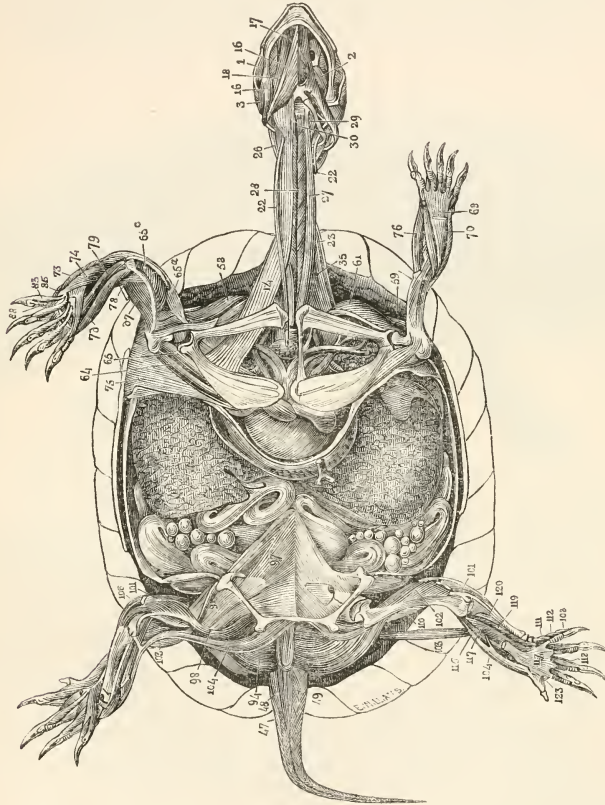
The *temporalis*, figs. 151, 152, 1, arises from the parietal and superoccipital spines, and is inserted into the coronoid part of the mandible. The *pterygoideus*, figs. 148, 149, 152, 4, arises from the outer surface of the pterygoid, and is inserted into the internal tuberosity of the articular element of the mandible. The *apertor oris*, or digastricus, figs. 150, 153, 3, arises from the mastoid, and is inserted into the angular process of the mandible. The *dilatator*



*tuba*, figs. 148, 149, 4, arises from the mastoid, and is inserted into the postero-inferior angle of the tympanic and into the beginning of the eustachian tube.

The following are muscles of the hyoidean arch and appendages. The *mylohyoideus*, fig. 153, 13, extends transversely between the mandibular rami, and is attached to the hyoid by its median

152

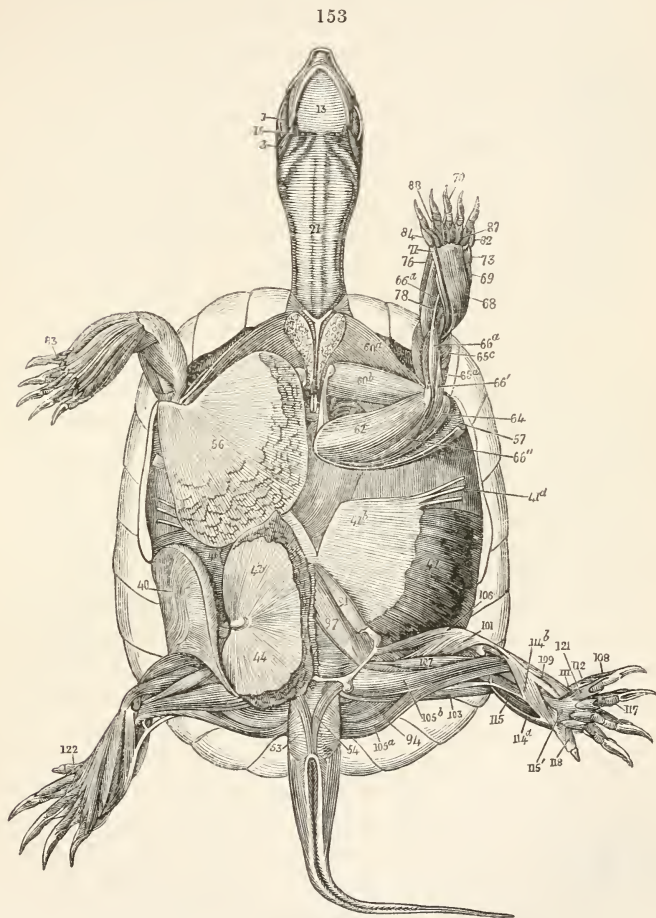


Muscles and viscera *in situ*, from below, *Emys Europaea*. XXXVIII.

raphé. The *omohyoideus*, figs. 150, 152, 14, arises from the coracoid, and is inserted into the basi-, cerato-, and thyro-hyals. The *geniohyoideus*, figs. 150, 152, 15, 16, arises from the back part of the symphysis mandibulæ; is united to its fellow as far back as the basihyal, and there diverges to its insertion into the ceratohyal. The *hyomaxillaris*, fig. 150, 16, arises from the articular element and is inserted into the ceratohyal. The *genioglossus*,

fig. 152, 17, arises from the dentary and is inserted into the outer angle of the basihyal and into its triangular appendage. The hyoglossus, fig. 151, 18, passes from the basihyal and its appendage to the ceratohyal, which it covers on the left side of fig. 152.

The proper muscles of the scapular arch are very few, by



Muscles of trunk and limbs, from below, *Emys Europæa*. XXXVIII.

reason of its fixity, although it gives origin to many which act upon other more moveable parts.

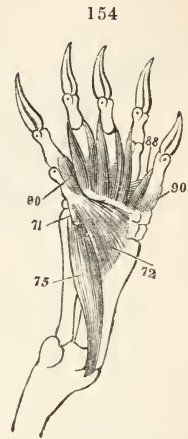
The *subclavius*, fig. 148, 59, arises from the under part of the first costal plate, and is inserted into the suprascapula and contiguous part of the scapula. The *serratus magnus*, fig. 152, 75,

fig. 153, 57, arises from part of the outer margins of the first and second costal plates and from the same margin of the cardinal process of the hyosternal and contiguous part of the hyposternal: it is inserted into the upper surface of the coracoid. The *latissimus dorsi*, fig. 152, 58, arises from the inner surface of the first costal plate, and is inserted into the neck of the humerus. The *deltoides*, fig. 153, 60, arises by three heads; one, ib. 60 *a*, from the inner surface of the ento- and epi-sternals; another, ib. 60 *b*, from the clavicular process of the scapula; and the third from the angle between that process and the body of the scapula: it is inserted into the lesser tuberosity of the humerus. The *claviculobrachialis*, fig. 152, 61, arises from the clavicle, and is inserted into the outer tuberosity of the humerus. The *subcoracoideus*, fig. 153, 62, arises from the under surface of the coracoid, and is inserted into the inner tuberosity of the humerus. The *supercoracoideus*, figs. 151, 152, 64, arises from the upper surface of the coracoid, and is inserted into the outer tuberosity of the humerus. The *teres minor*, fig. 152, 65, arises from the posterior border of the coracoid and is inserted into the pit between the humeral tuberosities, with an attachment to the capsule of the shoulder-joint. The *triceps brachii*, figs. 152, 153, 65 *a c*, arises from above the glenoid margin of the scapula, 65 *a*, and from the humerus, 65 *c*: it is inserted into the olecranon. The *biceps brachii*, fig. 153, 66, arises from the back part of the coracoid, 66'': it is inserted, with the brachialis internus, into the ulna, and by a slender tendon, 66 *a*, into the radius. The *brachialis internus*, fig. 152, 67, arises from the inner tuberosity and concave surface of the humerus and is inserted into the proximal ends of both the radius and ulna. The *palmaris*, figs. 150, 153, 68, arises from the outer condyle of the humerus, and is inserted into the palmar aponeurosis. The *flexor sublimis*, figs. 151, 153, 69, arises from the outer condyle of the humerus and is inserted into the metacarpal of the fifth digit and into the tendon of the ulnaris internus. The *flexor profundus*, figs. 150, 151, 70, arises from the concave side of the ulna, and is inserted into an aponeurosis splitting into five tendons for the last phalanges of the five digits. The *pronator teres* arises from the outer condyle of the humerus: its insertion, shown in fig. 154, 71, is into the radial side of the carpus, with that of the *pronator quadratus*, ib. 72. The *ulnaris internus*, figs. 151, 153, 73, arises from the tubercle above the outer angle of the humerus, and is inserted into the ulnar side of the carpus and contiguous end of the fifth metacarpal. The *ulnaris externus*, figs. 151, 152, 74, arises from the tubercle above the inner condyle of the

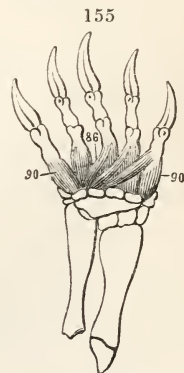
humerus, and is inserted into the carpus near the ulna. The *radialis internus*, fig. 154, 75, arises from the tuberosity above the outer condyle of the humerus, and is inserted into the distal end of the radius. The *radialis externus longus*, fig. 152, 76, arises from the tuberosity above the internal humeral condyle, and is inserted into the radial margin of the carpus; the muscle converging towards 76, in the same figure, is the *radialis internus*. The *radialis externus brevis*, fig. 150, 77, arises from the tuberosity above the internal humeral condyle, and is inserted into the back of the carpus. The *supinator longus*, figs. 152, 153, 78, arises above the internal humeral condyle, and is inserted into the radial side of the carpus and the same border of the radius. The *supinator brevis*, fig. 152, 79, arises from the tubercle above the inner humeral condyle, and is inserted into the back of the radius. The *extensor communis digitorum*, fig. 151, 80, arises from the tuberosity above the inner humeral condyle, and is inserted into the five metacarpals. The *extensor proprius pollicis*, fig. 150, 81, arises from the ulna, and is inserted into the metacarpal of the pollex. The *extensor proprius digiti minimi*, fig. 152, 82, arises from the ulnar side of the carpus and is inserted into the metacarpal and first phalanx of the fifth digit. The *extensores breves digitorum*, figs. 151, 153, 83, arise from the back of the carpus and metacarpus, and are inserted into the distal phalanges. The *abductor pollicis*, fig. 153, 84, arises from the inner side of the carpus, and is inserted into the first phalanx of the pollex. The *flexores breves digitorum*, fig. 153, 88, arise from the palmar sesamoids and fascia, and are inserted into the phalanges. There are also, *interossei*, both external and internal; the latter are shown at 90, figs. 154 and 155. The *adductores digitorum*, fig. 155, 86, are limited to the first, second, and third fingers, to the metacarpals of which the muscles incline, radiad, from the second row of carpals.

The following are the muscles of the pelvic arch and limb:—

The *attrahens pelvim*, figs. 150, 153, 43, arises from contiguous



Muscles of fore foot, *Emys Europæa*. XXXVIII.

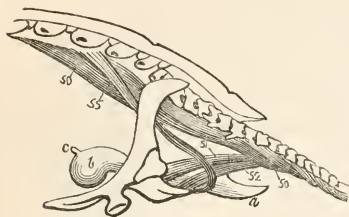


Muscles of fore-foot, *Emys Europæa*. XXXVIII.



parts of the hypo- and xiphi-sternals, and is inserted into the outer process of the pubis. The *retrahens pelvim*, ib. 44, arises from the posterior half of the xiphisternal, and has a similar insertion.

156

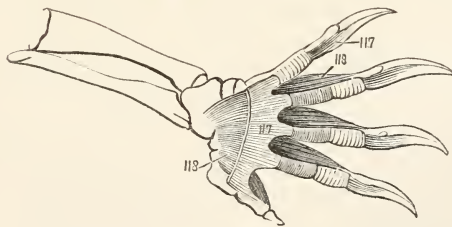


Muscles of pelvis, *Emys Europaea*. XXXVIII.

More direct retractors of the pelvis are the muscle called *flexor caudæ obturatorius*, which arises from the caudal hæmapophyses, and is inserted into the front border of the obturator foramen; and the *flexor caudæ ischiadicus*, ib. 52, with a similar origin, but inserted into the ischial symphysis. The *pectineus* (iliacus internus, *Boj.*), figs. 150, 152, 153, 91, arises from the upper surface and outer process of the pubis, and is inserted into the inner trochanter of the femur. Its insertion receives also a small fasciculus from the ninth dorsal centrum, and the tenth pleurapophysis, which may represent the *psaos*. A *glutæus*, figs. 150, 151, 93, arises from the ninth and tenth pleurapophyses, and from the ilium. A second *glutæus*, figs. 150, 151, 152, 94, arises from the sacral and anterior caudal pleurapophyses. Both are inserted into the outer trochanter, together with a fasciculus, representing an *obturatorius*, from the inner surface of the obturator fascia, and from the ischial symphysis. The *triceps adductor*, figs. 152, 153, 97, arises from the inferior surface of the pubis, and is inserted into the inner trochanter, crossed by the ischio-pubic ligament. The *quadratus*, fig. 152, 98, arises from the tuber ischii, and is inserted into the back interspace of the trochanters. The *rectus femoris*, fig. 151, 99, arises by a bifid tendon from the upper end of the ilium, and is inserted, with the *vastus externus*, fig. 150, 100, *vastus internus*, fig. 151, 101, *cruræus*, fig. 152, 102, and *sartorius*, fig. 153, 106, into the fore-part of the head of the tibia. The *semitendinosus*, figs. 150, 152, 104, has three origins, one from the back part of the upper end of the ilium and contiguous part of the sacrum, a second from the tuber ischia, a third from the back part of the ischial symphysis; they join a common tendon which passes behind the knee-joint, and then bifurcates to be inserted into the outer proximal tuberosity of the tibia, and into the gastrocnemius, 114 *b*. The *semimembranosus*, fig. 153, 105, has two origins, one, 105 *a*, from the first caudal vertebra; the other, 105 *b*, from the tuber ischii and ischio-pubic ligament. It is inserted into the upper part of the tibia. The *gracilis*, fig. 153, 107, arises from the middle of ischiopubic ligament, and is inserted into the upper and outer part of the tibia. The *extensor communis digitorum*, fig. 151, 108, arises from

the ridge anterior to the outer femoral condyle, and is inserted into the distal phalanx of the hallux and into the proximal phalanges of the other toes. The *tibialis anticus*, figs. 150, 153, 109, arises from the antero-internal margin of the tibia, and is inserted into the tibial side of the tarsus and first metatarsal. The *peroneus*, fig. 151, 10, arises from the fore part of the fibula, and is inserted into the cuboid, and fourth and fifth metatarsals. The *digit-extensores breves*, figs. 149, 151, 111, arise from the dorsal aspect of the second row of tarsals, metatarsals, and proximal phalanges, and are inserted into the unguis phalanges. The *extensor proprius hallucis*, figs. 152, 153, 112, arises from the lower end of the fibula, and is inserted by a bifurcate tendon into the sides of the first phalanx of the hallux. The *abductor hallucis* arises from the tendon of the *tibialis anticus*, and from the first metatarsal, and is inserted into the base of the proximal phalanx of the hallux. The *gastrocnemius*, figs. 151, 153, 114, has two heads, one, 114 *a*, from the outer femoral condyle; the other, 114 *b*, from the outer margin of the tibia, and this receives also the tendon from the semitendinosus: it is inserted into the calcaneum and expanded metatarsal of the fifth digit, and is continued into the plantar fascia. The *plantaris*, fig. 153, 115, arises above the outer femoral condyle, and coalesces with the *soleus*, fig. 152, 116, and the *digitiflexor longus*, 117, to terminate in a common aponeurosis, attached to both sides of the tarsus, and dividing, as in fig. 157, 117, to be inserted into the unguis phalanges. The *digitiflexores breves*, fig. 157, 118, are four in number, arise from the tarsus, and are

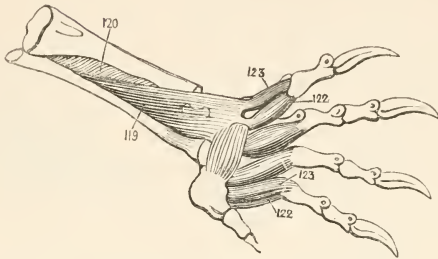
157

Muscles of hind-foot, *Emys Europæa*. XXXVIII.

inserted into the sides of the middle phalanx, and by a slender tendon into the unguis phalanx, of the four outer toes. The *tibialis posticus*, figs. 152, 158, 119, arises from the inner and back part of the fibula, and expands into an aponeurosis, including a sesamoid, which divides to be inserted into the second row of tarsals, and the metatarsals of the hallux and fifth digits. The

*interosseus cruris*, fig. 158, 120, extends obliquely between the opposite margins of the leg-bones. The *interossei digitorum*

158



Muscles of hind-foot, *Emys Europæa*. XXXVIII.

*dorsales*, are shown at 122, and those of the plantar surface at 123, fig. 158.

The highest faculty of terrestrial locomotion in the reptilian class, is manifested by the saltatory batrachians.

In the hind limb of the frog there is a muscle which extends from the diapophysis of the third vertebra to the ilium, which it tends to protract, and acting from which it may slightly bend the back. The *ectogluteus* receives an accessory strip from the coccygeal style. The *mesogluteus* is a strong muscle. The *entogluteus* and *iliacus* are united. The *obturator externus* has a semi-circular form. The *quadratus femoris* is in two strata. There are two *pectinei* and four *adductores femoris*. The *extensor cruris* consists of a *vastus internus* and a *vastus externus* with a coalesced *cruræus*; there is no *rectus femoris*. The *flexor cruris* has but one head or origin from the lower and back part of the ilium. The *semitendinosus* has two heads, one from the fore part, the other from the back part of the ischio-pubic symphysis. The *semimembranosus* and *gracilis* have the usual attachments. The *sartorius* resembles the *rectus* in its position and course in front of the thigh: it is united to the *tensor fasciæ latæ*. The *gastrocnemius* is represented by its external moiety, which is so large as to give the appearance of a 'calf' to the leg: its tendon glides behind the tibio-tarsal joint, and expands as it descends along the tarsal segment into a plantar fascia. The *tibialis anticus* arises by a strong tendon from the femur, and divides at the middle of the tibia into a fascicle inserted into the astragalus, and a second inserted into the calcaneum; in both at the proximal end. A *cruro-tibialis* rises from the lower end of the femur, and

is inserted into the fore part of the lower three-fourths of the tibia. The *tibialis posticus*, with the usual origin, is inserted into the astragalus, fig. 44, *a*. A *peroneus* arises from the outer femoral condyle, and from the outer side of the leg-bone; its tendon bifurcates, one part being attached to the outer malleolus, the other to the base of the calcaneum, *ib. d*. An *extensor longus digitorum* arises from the outer malleolus, passes between the two portions of the *tibialis anticus*, and, after sending an insertion to the astragalus, is continued to the three middle toes. The *extensor brevis* arises from the whole length of the calcaneum, and divides into six parts, an external to the metatarsal of the hallux, an internal to that of the minimus, and the intermediate four to the phalanges of the four outer toes; these unite with the tendons of *interossei externi*, to which might be referred the extensor of the hallux. Both this toe and the outermost have their abductors for spreading the web. There is also an abductor of the entocuneiform, fig. 44, *ci*, which resembles a small accessory digit. The plantar aponeurosis, which receives a fleshy fascicle from the tibio-tarsal capsule, gives origin to a muscle inserted into the whole length of the astragalus, divides into six fascicles, which form sheaths for the flexor tendons, two of which belong to the fourth toe; and, finally, is resolved into three tendons, of which two go to the fifth toe, and one to the fourth. The *flexor longus digitorum* arises from the tibio-tarsal capsule, and is expended upon the three outer toes. The several insertions of the foregoing digital flexors give one tendon for the unguis phalanx, and two for the other phalanges.

§ 48. *Locomotion of Fishes*.—Hitherto the osteology and myology of the cold-blooded Vertebrates have been considered chiefly from a homological point of view. I have aimed at relieving the dryness of descriptive detail, and at connecting the multifarious particulars of this difficult part of Comparative Anatomy in natural order, so as to be easily retained in the memory, by referring to the relations which the bones and muscles of Fishes and Reptiles bear to the general plan of vertebrate organisation, and by indicating their analogies to transitory states of structure in the embryo of higher animals, and to those answerable conditions of the mature skeleton which, in longer lapse of time, have successively prevailed and passed away in the generations of species that have left recognisable remains in the superimposed strata of the earth's crust.

To determine the parts of the vertebrate structure which are most constant — to trace their general, serial, and special homo-



logies, under all the various modifications by which they are adapted to the several modes and spheres and grades of existence of the different species — should be the great aim of anatomical science ; as being that which reduces its facts to the most natural order, and their exposition to the simplest expressions.

It is impossible, in pursuing the requisite comparison upward through the higher organised classes, not to recognise resemblances between the ultimate states and forms of ichthyic organs, and the transitory condition of the same parts, in the higher species. But these resemblances have been sometimes overstated, or presented under unqualified metaphorical expressions, calculated to mislead the student and to obstruct the attainment of complete conceptions of their nature. We should lose most valuable fruits of anatomical study were we to limit the application of its facts to the elucidation of the unity of the vertebrate type of organisation, or if we were to rest satisfied with the detection of the analogies between the embryos of higher and the adults of lower species in the scale of being. We must go further, and in a different direction, to gain a view of the fruitful physiological principle of the relation of each adaptation to its appropriate function, if we would avoid the danger of resting in speculations on the mode of operation of derivative secondary causes, and of blinding the mental vision to the manifestations of Design which the various forms of the Animal Creation offer to our contemplation.

To revert, then, to the skeleton of Fishes, with a view to the teleological application of the facts determined by the study of this complex modification of the animal framework. No doubt there is analogy between the cartilaginous state of the endoskeleton of Cuvier's Chondropterygians, and that of the same part in the embryos of air-breathing Vertebrates ; but why the gristly skeleton should be, as it commonly has been pronounced to be, absolutely or teleologically inferior to the bony one is not so obvious. The ordinary course of age, decrepitude, and decay of the living body is associated with a progressive accumulation of earthy and inorganic particles, gradually impeding and stiffening the movements, and finally stopping the play of the vital machine. And I know not why a flexible vascular animal substance should be supposed to be raised in the histological scale because it has become impregnated, and as it were petrified, by the abundant intus-susception of earthy salts in its areolar tissue. It is perfectly intelligible that this accelerated progress to the inorganic state may be requisite for some special office of such calcified parts in

the individual economy; but not, therefore, that it is an absolute elevation of such parts in the series of animal tissues.

It has been deemed no mean result of Comparative Anatomy to have pointed out the analogy between the shark's skeleton and that of the human embryo, in their histological conditions; and no doubt it is a very interesting one. But the perception of such analogy is not incompatible with the endeavour to gain insight into the purpose of the Creator, in so arresting the ordinary course of osteogeny in the highly organised fish. No law of human intelligence condemns it to restrict its cognizance of the phenomenon, as solely those of an unfinished, incomplete stage of an hypothetical serial developement of organic forms.

The predaceous Sharks are the most active and vigorous of fishes; like birds of prey, they soar, as it were, in the upper regions of their atmosphere, and, without any aid from a modified respiratory apparatus, devoid of an air-bladder, they habitually maintain themselves near the surface of the sea, by the action of their large and muscular fins. The gristly skeleton is in prospective harmony with this mode and sphere of life, and we shall subsequently find as well-marked modifications of the digestive and other systems of the shark, by which the body is rendered as light, and the space which encroaches on the muscular system as small, as might be compatible with those actions. Besides, lightness, toughness, and elasticity are the qualities of the skeleton most essential to the shark: to yield to the contraction of the lateral inflectors, and aid in the recoil, are the functions which the spine is mainly required to fulfil in the act of locomotion, and to which its alternating elastic balls of fluid, and semi-ossified biconcave vertebræ, so admirably adapt it. To have had their entire skeleton consolidated and loaded with earthy matter would have proved an encumbrance altogether at variance with the offices which the Sharks are appointed to fulfil in the economy of the great deep.

I suspect that those who see in a modification of the skeleton, so beautifully adapted to the exigencies of the highest organised of fishes, nothing more than a foreshowing of the cartilaginous condition of the reptilian embryo in an enormous tadpole, arrested at an incomplete stage of typical developement, have been misled by the common name given to the Plagiostomous fishes. The animal basis of the shark's skeleton is not cartilage; it is not that consolidated jelly which forms the basis of the bones of higher Vertebrates: it has more resemblance to mucus; it requires 1000 times its weight of boiling water for its solution, and is neither

precipitated by infusion of galls, nor yields any gelatine upon evaporation.

In like manner the modifications of the dermal skeleton of fishes have been viewed too exclusively in a retrospective relation with the prevalent character of the skeleton of the Invertebrate animals. Doubtless it is in the lowest class of Vertebrata that the examples of great and exclusive developement of the exoskeleton are most numerous; but some anatomists, in their zeal to trace the serial progression of animal forms, seem to have lost sight of all the vertebrate instances of the bony dermal skeleton, except those presented by the ganoid and placoid fishes. He must have sunk to the low conception that nature had been limited to a certain allowance of the salts of lime in the formation of each animal's skeleton, who could affirm that in the higher Vertebrata 'the internal articulated skeleton takes all the earthy matter for its consolidation,'<sup>1</sup> forgetting that the bulky *Glyptodon*, and its diminutive congeners the *Armadillos*, have their internal skeleton as fully developed and as completely ossified as in any other mammal. The organising energies which perfect and strengthen the osseous internal skeleton do not destroy nor in any degree diminish the tendency to calcareous depositions on the surface, when the habits and sphere of life of the warm-blooded quadruped require a strong defensive covering from that source. Neither do we find in the cold-blooded series that the endoskeleton of the alligator or seelidosaur was consolidated by a minor amount of earthy matter than that of the naked frog or horn-scaled lizard.

The moment that the observations of the naturalist bring to light the mode of life of any of those fishes which are said to retain an unusual proportion of the external shell of the Invertebrata, we are in a condition to appreciate the adaptation of that external defensive covering to such mode of life. The Sturgeons, for example, were designed to be the scavengers of the great rivers; they swim low, grovel along the bottom, feeding, in shoals, on the decomposing animal and vegetable substances which are hurried down with the debris of the continents drained by those rapid currents; thus they are ever busied reconverting the substances, which otherwise would tend to corrupt the ocean, into living organised matter. These fishes are, therefore, duly weighted by a ballast of dense dermal osseous plates, not scattered at random over their surface, but regularly arranged, as the seaman knows how ballast should be, in orderly series along the

<sup>1</sup> XXVII. p. 527.

middle and at the sides of the body. The protection against the water-logged timber and stones hurried along their feeding grounds, which the sturgeons derive from their scale-armour, renders needless the ossification of the cartilaginous case of the brain or other parts of the endoskeleton; and the weight of the armour requires that endoskeleton to be kept as light as may be compatible with its elastic property and other functions. The sturgeons are further adjusted to their place in the liquid element, and endowed with the power of changing their position and rising to the surface, by a large air-bladder.

These teleological interpretations of the dermal bony plates may give some insight into the habits and conditions of existence of those Ganoid and heavily-protected Placoid Fishes which so predominated in the earlier periods of animal life in our planet, which Ganoids and Placoids have hitherto been viewed almost exclusively by the light of the analogy of an embryonic 'Age of Fishes,' or explained as arrested stages in the transmutation of Crustacea. I long ago demonstrated that both placoid plates and ganoid scales, in the extinct (*Lepidotus*<sup>1</sup>) as well as existing (*Lepidosteus*) fishes, differed from the superficial shells of the Invertebrata<sup>2</sup> in presenting the same organisation for growth and repair, the same essential microscopic structure, as the ossified parts of the endoskeleton which they serve to protect.

The *Coccosteus*, fig. 127, of the Old Red Sandstone, like the *Pimelodus* of the Ganges, had a half suit of such organised armour; and, as Hugh Miller<sup>3</sup> suggests, the habits of the modern sheat-fish may have been foreshown in primeval times by the placoganoid, burying the undefended part of its body in the mud, and exposing only its helm and cuirass, to arrest, as they passed, the smaller animals on which it preyed.

Nevertheless, the degree in which the exoskeleton predominates over the endoskeleton as we penetrate into past time, descending into the fossiliferous strata of the earth for evidence of ancient life, is highly interesting and suggestive.

At the present day only two lepidoganoid genera of fishes are known—the *Lepidosteus* of North America, and the *Polypterus* of Africa—both restricted to fresh waters. Other existing fishes of cognate organisation (*Amia*, *Sudis*, e. g.) have soluble and flexible scales. As we descend to the older tertiary beds the number of Lepidoganoids increases, their geographical relations expand, and their sphere of life embraces the salt waters of the ocean. At the present day the placoganoid and placoid, or plagiostomous,

<sup>1</sup> v. p. 14.<sup>2</sup> xxvii. p. 337.<sup>3</sup> cxcvi. p. 288.



fishes, form a small minority of the class. In the chalk formations the number of the species of Placoids and Ganoids rapidly increases, and soon preponderates; in all the older fossiliferous strata they exclusively represent the class of Fishes. The predominance of osseous matter deposited in the tegumentary system in these ancient extinct Fishes is not unfrequently accompanied by indications of a semi-cartilaginous state of the endoskeleton, like that in the *Lepidosiren* of the present day; the total absence of any trace of vertebral centres, and the vacant tract, where they should have been, between the bases of the neur- and ham-apophyses which have been little disturbed, as in fig. 127, show plainly enough that the primitive gelatinous notochord has been persistent.<sup>1</sup> In not one of the extinct Fishes of the Devonian and Silurian systems has a vertebral centrum been discovered; but the enamelled dermal osseous scales and plates are richly developed, and most remarkable for their beautiful and varied external sculpturing, and often for their great size.

In the mesozoic strata ganoid species exhibit a progressive expanse and downward growth of the neurapophyses, converting the notochordal capsule into distinct bony segments; the terminal cups of bone are subsequently added, and the centrum is completed.

At the present day the *Lepidosiren* repeats the notochordal condition of the endoskeleton, but without the compensating ganoid or placoid developments of the skin; and the Sheat-fishes (*Siluridæ*) combine the large tuberculated osseous dermal plates with a well ossified internal skeleton. The existing sturgeons alone manifest contrasted conditions of the endo- and exo-skeletons, like those in the ancient placoganooids; but what is now a rare and exceptional instance of analogy to the testaceous and crustaceous Invertebrates was the rule in the first-born fishes of our globe. Those fishes, which from the determination of the ossifying energies to the endoskeleton have been termed *Teleostei*, constitute the bulk of the tertiary and existing species of this class. But gradations of endoskeletal ossification are still indicated. A great proportion of the primitive cartilage is retained in the skull of many of the *Teleostei*, the Salmon and Pike, for example; and the greater proportion of the animal to the earthy matter in all the bones, their coarse texture, the radiating fibres of the flat cranial bones, and the general absence of dentated sutures, are characters in all Osseous Fishes, which remind the Anthropotomist of transitional ones in the human fœtus; but the light of teleo-

<sup>1</sup> See also the beautiful illustration of this fact in the *Microdus radiatus*, No. 626, of the Hunterian Series of Fossil Fishes in the Museum of the London College of Surgeons; cxciii. p. 155.

logy demonstrates the perfection of such conditions, in relation to the atmosphere and movements of the Fish. It is generally in fresh-water abdominal Fishes that the semi-osseous condition of the skull is found, and the diminution of the quantity of heavy earthy particles may be connected with the less dense quality of their medium, as compared with sea-water, and with the usually more posterior position of the ventral fins.

In the form of a fish, the head is disproportionately large, as it is in the mammalian embryo. But the head of a fish must needs be large to meet and overcome the resistance of the fluid, in the mode most favourable for rapid progression: it must therefore grow with the growth of the fish. Hence the large cranial bones always show the radiating osseous spiculæ in their clear circumference, which is the active seat of growth; hence the number of overlapping squamous sutures, which least oppose the progressive extension of the bones. The cranial cavity expands with the expansion of the head: the absorbents remove from within as the arteries build up from without; but the brain undergoes no corresponding increase; it lies at the bottom of its capacious chamber, which is principally occupied by a loose cellular tissue, situated, like the arachnoid, between the pia mater and the dura mater, and having its cells filled with an oily fluid, or sometimes, as in the Sturgeon, by a compact fat.<sup>1</sup> Now, this condition of the envelopes of the brain is not only, like the fibrous tissue and squamous sutures of the ever-growing cranial bones, related to the requisite proportions of the fore-part of the fish for facilitating its progressive motion, but it is one which no embryo of a higher animal ever presents: it is as peculiarly piscine, as it is expressly adapted to the exigencies of the fish.

It has been held that confluence of distinct bones is a consequence of high circulating and respiratory energies; yet the anchyloses of the superoccipital, parietal, and frontal above the cranium, and of the basi-occipital, basi-sphenoid, and pre-sphenoid below the cranium, in *Lepidosiren*, and the constant confluence of the basi- and pre-sphenoids in all bony fishes, disprove the constancy of the supposed relationship, and lead us to look for other explanations of such coalescence of primitively or essentially distinct bones. We shall find a final cause for the rapid consolidation and union of the elongated bodies of the two middle cranial vertebræ of Fishes in the necessity for strength in the basis of that part of the skull, from the sides of which the large and heavy mandibular and hyoid arches and their appendages are to be suspended, and

<sup>1</sup> XXIII. t. i. p. 309.

to swing freely to and fro. The posterior and anterior sphenoids continue distinct bones in all Mammals during a period of life at which they form one continuous bone in Fishes.

The loose connections of most of the bones of the face may likewise remind the homologist of their condition in the imperfectly developed skull of the embryos of higher animals; but this condition is especially subservient to the peculiar and extensive movements of the jaws, and of the bones connected with the hyoid and branchial apparatus.

Not any of the limbs, properly so called, of Fishes, are prehensile; the mouth may be propelled and guided by them to the food, but the act of seizing must be performed by the jaws. Hence in many fishes both upper and lower maxillary bones enjoy movements of protraction and retraction, as well as of opening and shutting. The firm connections of the upper jaw, and wedged fixity of the bone suspending the under jaw, which characterise the higher Reptiles and Mammals, would be imperfections in the Fish; in which, therefore, such characters are not only absent, but special development in the opposite direction not unfrequently goes so far as to produce the most admirable mechanical adjustments of the maxillary apparatus, compensating for the absence of hands and arms, like those which have been exemplified in the instance of the *Epibulus insidiator*.<sup>1</sup> We must guard ourselves, however, from inferring absolute superiority of structure from apparent complexity. The lower jaw of fishes might at first view seem more complex than that of man, because it consists of a greater number of pieces, each ramus being composed of two or three, and sometimes more separate bones. But, by parity of reasoning, the dental system of that jaw might be regarded as more complex, because it supports often three times, or ten times, perhaps fifty times, the number of teeth which are found in the human jaw. We here perceive, however, only an illustration of the law of vegetative repetition as the character of inferior organisms; and we may view in the same light the multiplication of pieces of which the supporting pedicle of the jaw is composed in Fishes. But the great size and the double glenoid or trochlear articulation of that pedicle, are developements beyond, and in advance of the condition of the bones supporting the lower jaw in Mammals, and relate both to the increase of the capacity of the mouth in Fishes for the lodgment of the great hyoid and branchial apparatus, and to the support of the opercula or doors which open and close the branchial chambers. The division of the long

<sup>1</sup> p. 119, fig. 87.

tympanic pedicle of Osseous Fishes into several partly overlapping pieces adds to its strength, and by permitting a slight elastic bending of the whole diminishes the liability to fracture. The enormous size, moreover, of the tympano-mandibular arch, and of its diverging appendages, contributes to ensure that proportion of the head to the trunk which is best adapted for the progressive motion of the fish through the water. But without the admission and appreciation of these pre-ordained adaptations to special exigencies in the skeleton of Fishes, the superior strength and complex developement of the tympanic pedicle and its appendages would be inexplicable and unintelligible in this lowest and first created class of Vertebrate animals.

All writers on Animal Mechanics have shown how admirably the whole form of the fish is adapted to the element in which it lives and moves: the viscera are packed in a small compass, in a cavity brought forwards close to the head; and whilst the consequent abrogation of the neck gives the advantage of a more fixed and resisting connection of the head to the trunk, a greater proportion of the trunk behind is left free for the developement and allocation of the muscular masses which are to move the tail. In the caudal, which is usually the longest, portion of the trunk, transverse processes cease to be developed, whilst dermal and intercalary spines shoot out from the middle line above and below, and give the vertically extended, compressed form, most efficient for the lateral strokes, by the rapid alternation of which the fish is propelled forwards in the diagonal, between the direction of those forces. The advantage of the bi-concave form of vertebra with intervening elastic capsules of gelatinous fluid, in effecting a combination of the resilient with the muscular power, is still more obvious in the Bony Fishes than in the Shark.

The normal character of Ichthyic myology shows itself in the vast proportion of the vegetatively-repeated myocommas, corresponding with the vertebral segments, as compared with the superadded system of muscles subservient to the action of their diverging appendages: but this condition, which, inasmuch as it deviates so little from the fundamental type, throws so much light upon the essential nature and homologies of the muscles of the Vertebrata, is not less admirably and expressly adapted to the habits and medium of existence of the Fish. The interlocked myocommas of the trunk constitute, physiologically, two great lateral muscular masses, adapted by their attachments, and especially by those of the anterior and posterior ends, to bend vigorously from side to side, with the whole force of their alter-



nating antagonistic contractions, the caudal moiety of the trunk, producing that double lash of the tail by which the fish darts forwards with such velocity. When the lateral muscles are more violently contracted, so as to bend the whole trunk, the recoil may even raise and propel the fish some distance from its native element: thus the salmon overleaps the roaring cataract which opposes its migration to the shallow sources whither an irresistible instinct impels it to the business of spawning; and thus the flying-fish, in the extremity of danger, baffles its pursuer by springing aloft, and prolongs its oblique course through the air by the aid of its outspread pectorals. When the anterior portions of the great lateral masses act from the trunk as a fixed point upon the head, they move it rapidly and forcibly from side to side: in this way the Siluri deal severe blows with their outstretched serrated pectoral spines; thus the Percoid and Cottoid Fishes strike with their opercular spines; and so likewise may the Saw-fish (*Pristis*) and Sword-fish (*Xiphias*) wield their formidable weapons, although their deadly cut or thrust is commonly delivered with the whole impetus of the onward course, the head being rigidly fixed upon the trunk.

The supracarinales, combining with the dorsal portions of the myocommata, give tension to the region of the back, slightly raise the tail, and depress the dorsal fins. The infracarinales, in combination with the retractores pubis, tend to compress the abdomen, to constrict the anus, and to depress the tail.

The muscles of the pectoral fins, though, compared with those of the homologous members in higher Vertebrates, they are very small, few, and simple, yet suffice for all the requisite movements of the fins; elevating, depressing, advancing, and again laying them prone and flat, by an oblique stroke, upon the sides of the body. The rays or digits of both pectorals and ventrals, as well as those of the median fins, can be divaricated and approximated, the intervening webs spread out or folded up, and the extent of surface required to react upon the ambient medium in each change and degree of motion, can be duly regulated at pleasure.

In the ordinary forward movement the tail first bends from the vertebral axis, which is the axis of motion, fig. 159, *f*, *d*, to *a*. During this action the centre of gravity, *c*, slightly recedes. From *a* the tail is next forcibly bent by the muscles on the opposite side, in the direction of the line *a i*. The force of the action upon the water in *a i* is translated to the body in *i a*, causing the centre of gravity, *c*, to move obliquely forward, in the direction of *c h*, parallel to *i a*. The tail, continuing its

flexion in  $eo$ , acts backward, in the direction of  $oe$ ; having reached the point  $o$ , it is again forcibly bent in the line  $oe$ , causing an impulse on the centre of gravity in  $cb$ , parallel to  $oe$ ; if the two forces  $ch$  and  $cb$  acted simultaneously, we should obtain the resultant  $cf$ ; but, as they do not, the point  $c$  will not move exactly in the line  $cf$ , but in a curved line, evenly between  $dcf$  and a line drawn parallel to it through  $h$ . The fish being in motion, the tail describes the arc of an ellipse; whereas, if it were stationary, it would describe the arc of a circle. The power of varying the position and expanse of the tail-fin during the side-strokes complicates the problem; its plane may be perpendicular to the stroke's direction, and its expansion greatest at the beginning of the stroke, as in  $ai$ ; and it may be oblique to the direction of the rest of the stroke, as in  $eo$ , with contraction of the surface. It must, further, be considered that the water having been set in motion by flexion in one direction, produces, when meeting the tail moving in the opposite direction, a resistance proportional to the sum of the squares of the two velocities.

The shape of the caudal fin varies much in fishes, according to the kind and degree of motion required: in the imprisoned embryo, or newly-hatched fry, in the long and slender undulating eel, in the sluggish *Lepidosiren*, the vertebræ continue to the end of the body in a straight line, distinct, and decreasing to a point; and the tail is bordered above and below by a vertical fold of skin; terminating either in a point, as in fig. 100, or obtusely. Such fold or fin is symmetrical, but not 'homocercal.'<sup>1</sup> The vertical folds deepen; at first, in some *Plagiostomes*, e. g., equably, forming a terminal lobe; then excessively, in the lower or hæmal fold, with the development therein of rays, and with an upward or neural inclination of the supporting vertebræ. Shorter rays are developed in the shallower neural fold, which terminates at the pointed end of the vertebral series. The anterior rays of the hæmal fold, which are the longest, form a second point. The tail-fin is thus bifurcate, but unsymmetrical; and this stage of

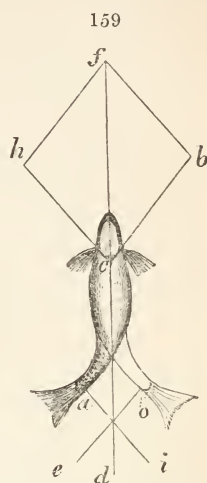


Diagram of locomotive act,  
Fish. CXXXI.

<sup>1</sup> By this latter term *M. Agassiz* signifies a subsequent grade of modification and development, and a grave fallacy lurks in its misapplication to the common embryonal condition of the tail-fin in Fishes, as by the Author of *cxcviii*.

development is termed the 'heterocercal' one. It is shown by the Sturgeon, fig. 29, and by the *Chimæras* and Sharks of the present day. It was the fashion of tail (fig. 127) which prevailed in Fishes throughout the palæozoic and triassic periods.

In some oolitic fishes first is observed such a lengthening of the dermoneurals of the tail, with such a shortening and running together of the terminal vertebræ, and such a proportion of the dermohæmals, as leads to an equal-lobed caudal fin, which has been termed 'homocercal;' but as it is only symmetrical in contour, and remains more or less unsymmetrical in its framework, I term it 'homocercoid.' The ganoid fishes of the mesozoic periods manifest several interesting gradations of this transitional state from the hetero- to the true homo-cercal form, each step being a permanent character of the extinct species presenting it. The embryos and young of *Salmonidæ*, of most *Malacopteri*, and of many *Acanthopteri*, go through closely analogous stages to those which were permanent in extinct fishes; and the slight upward twist of the coalesced terminal caudals, and the inequality of its upper and lower lobes, indicate the fact in the symmetrically-shaped 'homocercoid' tail-fin of the adults.<sup>1</sup> In the *Anacanthini*, fig. 34, and *Seomberoids*, fig. 33, the terminal tail-vertebræ shrink and coalesce in the line of the trunk's axis; the dermoneural and dermohæmal rays are equally developed, and a truly symmetrical or 'homocercal' caudal fin is the result; and this is the latest and greatest modification of the organ. The majority of existing species of bony fishes indicate, in the course of their acquisition of the symmetrical tail-fin, the heterocercal stages at which it is severally arrested in different older extinct species, doubtless in close relation with the power and kind of swimming required by each.

The heterocercal tail helps the fish to vary its onward course. The Shark wheels about in pursuit of prey, and rotates the trunk, to bring the inferiorly-opening mouth to bear upon the victim. The Sturgeon maintains its body in the oblique position while upturning the muddy bottom of the strongly-running stream, and avoids, by deftly bending to right or left, the drift bodies that are hurried down the river. The homocercal tail is a more effective form for a straight forward rush. When it is truncate and triangular, the apex being the centre of motion, the centre of force is three-fourths the distance of its base from the axis of oscillation, and the muscles of the tail act at a corresponding disadvantage. When the tail is forked, as in fig. 33, the area is in the inverse

<sup>1</sup> See the persistent "trace of the embryonal heterocercal form of the tail" in the Sea-perch (*Centropristis gigas*, Owen), No. 191, p. 51, XLIV.

ratio of the distance from the centre of gravity, and the centre of force is one-half the distance from the centre of motion; consequently the fishes so endowed have the greatest velocity. It is such in the Sword-fish as to enable it to drive its rostral weapon through a ship's timbers with the force of a cannon ball—for example, through fourteen inches of oak, after penetrating the copper sheathing, four inches of deal, and a layer of felt.<sup>1</sup>

As most fishes require to sustain themselves above the bed or bottom of their rivers, lakes, or seas, and as their specific gravity is greater than that of water, they are commonly provided with an air-bladder, situated immediately under the spine, and above the centre of gravity, and usually accompanied with powers of renewing, expelling, compressing, and dilating its gaseous contents. This hydrostatic apparatus thus becomes an important auxiliary organ of locomotion.

The Diodons and Tetrodons fill an immense expansion of the œsophagus by swallowing air; and as this lies below the centre of gravity, the body, so inflated, rolls over, and they are drifted, passively, back downward, by the winds and currents.

The air-bladder is absent in *Dermopteri*, *Plagiostomi*, *Pleuronectidæ*; and such fishes, unless endowed with compensating powers and proportions of body and fins, as in the Sharks, habitually grovel at the bottom, and exhibit flattened forms of body, as in the Rays and Flounders.

With the exception of the above-described modifications of a few terminal vertebræ, those of the trunk remain throughout life distinct from one another in Fishes, as they originally are in the embryos of all higher Vertebrates. The confluence of vertebræ at the base of the tail would have been a hindrance to the required movements of such part of the spine in creatures which progress by alternate vigorous inflections of a muscular tail. A sacrum is a consolidation of a greater or less proportion of the vertebral axis for the transference of more or less of the weight of the body upon limbs organised for its support on dry land; such a modification would have been useless to the fish, and not only useless, but a defect.

The pectoral fins—those curtailed prototypes of the fore-limbs of other Vertebrata, with the last segment, or hand, alone projecting freely from the trunk, and swathed in a common undivided tegumentary sheath—present a condition analogous to that of the embryo buds of the homologous members in the higher Ver-

<sup>1</sup> See the specimen in the Museum of the Royal College of Surgeons, London, described in *excv.* p. 5.



tebrata. But what would have been the effect if both arm and fore-arm had also extended freely from the side of the fish, and dangled as a long flexible many-jointed appendage in the water! This higher development, as it is termed, in relation to the prehensile limb of the denizen of dry land, would have been an imperfection in the structure of the creature which is to cleave the liquid element: in it, therefore, the fore limb is reduced to the smallest proportions consistent with its required functions: the brachial and antibrachial segments are abrogated, or hidden in the trunk: the hand alone projects and can be applied, when the fish darts forward, prone and flat, by flexion of the wrist, to the side of the trunk; or it may be extended at right angles, with its flat surfaces turned forward and backward, so as to check and arrest more or less suddenly, according to its degree of extension, the progress of the fish; its breadth may also be diminished or increased by approximating or divaricating the rays. In the act of flexion, the fin slightly rotates and gives an oblique stroke to the water. If one of the pectorals be extended, it will turn the fish in a curve towards that side: if the other only, it will turn it on the opposite side: they thus act as a rudder. For these functions, however, the hand requires as much extra development in breadth, as reduction in length and thickness; and this is gained by the addition of ten, twenty, or it may be even a hundred digital rays, beyond the number to which the fingers are restricted, in the hand of the higher classes of Vertebrata. We find, moreover, as numerous and striking modifications of the pectoral fins, in adjustment to the peculiar habits of the species in Fishes, as we do of the fore limbs in any of the higher classes. This fin may wield a formidable and special weapon of offence, as in many Siluroid fishes. But the modified hands have a more constant secondary office, that of touch, and are applied to ascertain the nature of surrounding objects, and particularly the character of the bottom of the water in which the fish may live. The tactile action of the pectoral fins may be witnessed when gold fish are transferred to a strange vessel; they compress their air-bladder, and allow themselves to sink near the bottom, which they sweep as it were, by rapid and delicate vibrations of the pectoral fins, apparently ascertaining that no sharp stone or stick projects upwards, which might injure them in their rapid movements round their prison. If the pectorals are to perform a special office of exploration, certain digits are liberated from the web, and are specially endowed with nervous power for a finer sense of touch, as we see in the Gurnards, fig. 82; in

which they also serve as limbs to creep along the bottom, when the fish is exploring the sand with its mailed mouth.

Some Gobioids (*Periophthalmus*) can use their muscular pectorals to shuffle along the shore, or hunt for insects in humid places.<sup>1</sup> Certain Lophioids living on sand-banks that are left dry at low water are enabled to hop after the retreating tide by a special prolongation of the carpal joint of the pectoral fin, fig. 102; which fin in these 'frog-fishes' projects like the limb of a terrestrial quadruped, and presents two distinct segments clear of the trunk.

The sharks, whose form of body and strength of tail enable them to swim near the surface of the ocean, are further adapted for this sphere of activity and compensated for the absence of an air-bladder by the large proportional size and strength of their pectoral fins, figs. 30, 104, which take a greater share in their active and varied evolutions than they can do in ordinary fishes.

The flat-bodied Rays, equally devoid of an air-bladder, and with a long and slender tail, deprived of its ordinary propelling powers, grovel at the bottom; but have a still greater development of the hands, fig. 64, 12, 12, which surpass in breadth the whole trunk, and react with greater force upon it in raising it from the bottom, by virtue of a special modification of the scapular arch, which is directly attached to the dorsal vertebræ.

Nor is the pectoral member restricted in length where its office, in subserviency to the special exigencies of the fish, demands a development in that direction; the fingers of the *Exocætus* and *Dactylopterus*, are as long, and the web which they sustain as broad, as in the expanded wing of the flying mammal. Everywhere, whatever resemblance or analogy we may perceive in the ichthyic modifications of the Vertebrate skeleton to the lower forms or the embryos of the higher classes, we shall find such analogies to be the result of special adaptations for the purpose or function for which that part of the fish is designed.

The ventral fins or homologues of the hind-legs are still more rudimental—still more embryonic, having in view the comparison with the stages of development in a land animal—than the pectoral fins; and their small proportional size reminds the homologist of the later appearance of the hind limbs, in the development of the land Vertebrate. But the hind limbs more immediately relate to the support and progression of an animal on dry land than the fore limbs: the legs are the sole terrestrial locomotive organs in Birds, whose fore limbs are exclusively modified, as wings, for motion in another element. The legs are the sole organ of sup-

<sup>1</sup> CLXXIV. vol. iii. p. 97.

port and progression in Man, whose pectoral members or arms are liberated from that office, and made entirely subservient to the varied purposes to which an inventive faculty and an intelligent will would apply them. To what purpose, then, encumber a creature, always floating in a medium of nearly the same specific gravity as itself, with hind limbs? They could be of no use: nay, to creatures that can only attain their prey, or escape their enemy, by vigorous alternate strokes of the hind part of the trunk, the attachment there of long flexible limbs would be a grievous hindrance, a very monstrosity. So, therefore, we find the developement and connections of the hind limbs of Fishes, figs. 29, 34, 38, 64, v, restricted to the dimensions and form which, whilst suited to the limited functions they are capable of in this class, would prevent their interfering with the action of more important parts of the locomotive machinery.

The plane of each ventral fin being horizontal, at right angles to that of the caudal fin, their action serves to balance the body, to incline it on either side when one fin only acts, and to elevate or depress the fish by their joint effort.

In most fishes the ventral fins merely combine with the pectoral fins in raising the body, and in preventing, as outriggers, the rolling movement: but some interesting modifications in relation to particular habits of certain species have previously been pointed out (p. 180). In the long-bodied and small-headed abdominal fishes, the ventrals are situated near the anus, where they best subserve the office of accessory balancers; in the large-headed thoracic and jugular fishes, the loose suspension of these fins, and the absence of any connection with a sacral part of the vertebral column, permits their transference forward, to aid the pectoral fins in raising the head.

The planes of the dorsal, figs. 24, 39, D, and anal, ib. A, fins are in that of the mesial longitudinal section, and their movements are usually restricted to elevation and depression. They accordingly increase or diminish the lateral surfaces of the fish, correcting any tendency to oscillate laterally, or to turn upside down, as the body would do without some muscular effort, since in the ordinary posture, back upward, the centre of gravity lies above the centre of figure. When the fins collapse and the muscular action ceases, as in death, the fish floats belly upward. However, in some singular exceptions, e. g. the Sun-fish, the dorsal and anal fins are unusually extended, and take a more direct share, by lateral undulating movements, in the locomotion of the fish.

In ordinary shaped Osseous Fishes, if the dorsal and anal fins be

cut off, the fish reels to the right and left. If the pectorals be cut off in a Perch or other big-headed fish, the head sinks; if one pectoral be cut off, the fish leans to that side; if the ventral of the same side be also removed, the fish loses its equilibrium; if the tail be cut off, the locomotive power is abrogated.

§ 49. *Locomotion of Serpents.* — The sole locomotive organs in serpents are the vertebral column, with its muscles, and the large stiff erectile epidermal scutes crossing the under surface of the body.

Although the vertebræ have synovial cup-and-ball terminal joints, their reciprocal movements are greatly restricted by the 'tenon-and-mortice' articulations of the double zygapophyses at each end, of which the inferior have flat horizontal surfaces, the superior slightly oblique planes. But as a single segment of the backbone may be but  $\frac{1}{30}$  part of the length of the body, the sum of the small movements between two vertebræ becomes considerable in a certain extent of the long trunk.

A serpent may, however, be seen to progress without any inflections, gliding slowly, with a ghost-like movement, in a straight line. If the observer have the nerve to lay his hand flat in the reptile's course, he will feel, as the body glides over the palm, the surface pressed, as it were, by the edges of a close-set series of paper-knives, successively falling flat after such application. The skin of the hand has been seized, so to speak, by the edges of the stiff, short, but broad, transverse, horny, ventral scutes, erected or made vertical for that purpose, and folding flat upon the body when the effect of the resistance has been gained. Each scute having secured a fulcrum in the plane of motion, the ribs connected with it rotate, and transmit the movement upon the trunk; it is, in fact, a step whose length depends on the arc through which the pair of ribs may oscillate and on the distances of the scutes from the axes of motion. As both these are small, and the motion has to be transmitted by the succession of short scutal steps through the whole length of the body, this first kind of progression is slow and gliding.

A second and swifter mode of locomotion on land is by successively bending and straightening portions of the body. Extension will carry the straightened part forward in the direction of least resistance. If most resistance be made by the point of the tail, fig. 160, *e*, or by the application to the ground of the edges of the erect scutes, between *d* and *e*, the extension of *ac* will carry the head to *h*, the smooth overlapping unerected scutes between *a* and *d* favouring the forward movement; and this being effected, and the ground grasped by the erection of the scutes



between *a* and *c*, flexion of the rest of the body will draw forward the tail, as from *b* to *e*. As the extent of the flexion of, say a fourth part of the body, exceeds the space through which a single scute is moved in erection, so does this mode of motion greatly exceed in swiftness the preceding. And this swiftness is accelerated when the serpent raises the body, in arched curves, from the ground, increasing their span, and progressing in a vertically, instead of a horizontally, undulating course; when, by augmented vigour of the muscular actions, the whole trunk may be raised into a single arc, and the movement acquire the character of a leap. Thus the body being bent, whilst the neck-scutes fix the head, as at *b*, the tail will advance from *a* to *e*, fig. 161; when, being fixed there by the subcaudal scutes, extension will carry the head forward to *d*, and the serpent will have advanced by the two actions of flexion and extension through a space equal to *a e* or *b h*. But, if the act of extension be vigorous and sudden, and an equivalent fulcrum be afforded by the tail, the whole body may be carried forward, as by a leap, farther than its own length. For the saltatory motion, however, the mechanism of a spiral spring is commonly simulated; the whole body is bent into a series of close-set coils, the sudden extension of which, reacting upon the point of earth against which the tail presses, throws the serpent obliquely forward into the air. In all these movements the curve is essentially lateral; the amount of rotation between the smaller vertebræ, at the two extremes of the body, permits the flexion of the intermediate joints to assume, as in fig. 161, the vertical position. There is no natural undulation of the body upward and downward — it can take place only from side to side. So closely and compactly do the ten pairs of joints between each of the two hundred or three hundred vertebræ fit together, that even in the relaxed and dead state the body cannot be twisted. If the attempt at rotation be made at the end of the tail on a dead snake outstretched, the part grasped may be half-twisted; but the rest of the trunk will turn over, rigid, like a stick.

Serpents derive the same advantage from their lungs in water as eels from their swim-bladder, the air-receptacles in both being much alike, and placed above the centre of gravity. They progress by a similar series of successive lateral undulations, generating a surplus force in the moving body equal to the difference between the force of the locomotive organs and the resistance of the medium. In water-snakes this resistance is made more effective by the lateral flattening or compression of the tail, which can be drawn forward edgewise, and flapped back breadthwise.

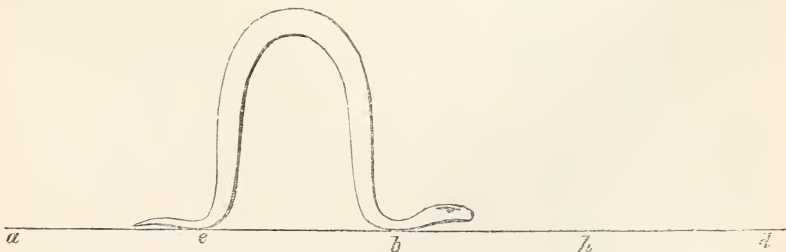
Serpents climb trees by the same mechanism and actions as in the first kind of locomotion; the edges of the erected scutes laying hold of the bark in succession, as the body glides spirally up the bough. The tail has a prehensile faculty, especially exercised by the great Constrictors while waiting for their prey. They instinctively select a tree at the part of the stream easiest of access to the thirsty mammals of the forest, and suspend themselves, like a parasitic creeper, from an overhanging branch, the head and fore-part of the body being floated by the bladder-like lungs upon the stream.

Serpents are too commonly looked down upon as animals degraded from a higher type; but their whole organisation, and especially their bony structure, demonstrate that their parts are as exquisitely adjusted to the form of their whole, and to their habits and sphere of life, as is the organisation of any animal which we call superior to them. It is true that the serpent has no limbs, yet it can outclimb the monkey, outswim the fish, outleap the jerboa, and, suddenly loosing the close coils of its crouching spiral, it can spring into the air and seize the bird upon the wing: all these creatures have been observed to fall its prey. The serpent has neither hands nor talons, yet it can outwrestle the athlete, and crush the tiger in the embrace of its ponderous overlapping folds. Instead of licking up its food as it glides along, the serpent uplifts its crushed prey, and presents it, grasped in the death-coil as in a hand, to its slimy gaping mouth.



Motion of serpent by undulations of trunk. ccv.

It is truly wonderful to see the work of hands, feet, and



Motion of serpent by arching the trunk . ccv.

fins, performed by a modification of the vertebral column — by

a multiplication of its segments with mobility of its ribs. But the vertebræ are specially modified, to compensate, by the strength of their numerous articulations, for the weakness of their manifold repetition, and the consequent elongation of the slender column. As serpents move chiefly on the surface of the earth, their danger is greatest from pressure and blows from above; all the joints are fashioned accordingly to resist yielding, and sustain pressure in a vertical direction.

§ 50. *Locomotion of limbed Reptiles.*—The fish-like Batrachia move in water by means of the lateral inflections of the hinder-half of the trunk, which is compressed and extended vertically by a marginal tegumentary fin. The parial limbs are small and feeble: they are limited, in the amphibious Siren, to the pectoral region, and to the function of raising the head and fore-part of the trunk upon the bank or shore. In the rest of the order both pairs are present: in the Amphiume they are too feeble to suggest any particular locomotive function; but they subserve, when somewhat more developed, a slow and awkward reptation, as in the Menopome and Newt. In the Land-Salamander, fig. 140, they acquire the due strength for terrestrial progression, and the tail is shortened and rounded. In the Toads and Frogs the tail is absorbed, and the legs lengthened and strengthened, especially the hinder pair; but with an outward direction from the body, and a position too horizontal to enable them to raise or support it above the ground.

The Frog, in repose, assumes a sitting posture, the thighs turned outward and forward, the legs bent backward, and the lengthened tarsi and feet directed forward. The fore-part of the trunk is propped up by the fore limbs, at an angle of  $45^{\circ}$ , with the base between the hind limbs, which, in their state of flexion, are ready on the least alarm to project the body forward by their sudden extension. The shoulder-joints of the limbs that receive the shock on alighting from the leap are strengthened by an interarticular ligament. The great Bull-Frog may clear six feet at a leap, and repeat them so rapidly as to escape a pursuer, unless chased at a great distance from the water. Both fore and hind feet are webbed for swimming, which is chiefly effected by strokes of the strong hind limbs. The large Indian frog (*Rana tigrina*) is said to be able to run along the surface of the water for a short distance.

The Tree-Frogs (*Hyla*) have a concave disc at the end of each toe, for climbing and adhering to the bark and leaves of trees.

Toads, with semipalmate feet, have an awkward, but not always slow, progression on land by alternate movements of the limbs. Some species are enabled, by peculiar tubercles or projections from the palm or sole, to clamber up old walls.

But the most remarkable climbers in the reptilian class are certain lizards, especially those called 'Geckos.' Each foot has five toes, which are spread wide apart, expanded at the ends, and terminated by a slender sharp claw. The flattened under surface of the toe-pad, fig. 162, is traversed by a series of transverse folds, with deep interspaces; the margins of the folds, when applied to a smooth surface, adhere thereto by atmospheric pressure, through the vacuum caused by muscular erection of the folds, with concomitant expansion of the interspaces; thus the animal, alternately applying and releasing its suckers, climbs a vertical wall or plate of glass, or proceeds along a ceiling with its back downward.

For climbing trees the adjustment of the toes in opposition to each other, in equal or sub-equal groups, as already described in the Chameleon, pp. 175, 193, figs. 119, 123, is an effective modification. In this reptile the limbs are short and strong, and a prehensile tail is added to the scansorial feet.

Ordinary lizards, by the great length of the trunk in proportion to its breadth, and by the outward extension of the humerus and femur, are under unfavourable mechanical conditions for rapid course upon land. Yet such is the energy of the muscular contractions in some species, under the stimulus of solar heat, that they are deservedly called 'agile,' and 'dart' out of view in the first rush from a pursuer. They have not, however, the power of maintaining the exertion, and are soon overtaken, if they happen to be far from their retreat. The swiftest runners, e. g. the *Tachydromi*, have the fore and hind limbs least differing in length, and consequently the vertebral column most parallel with the plane of motion.

In the Crocodiles the fore limbs are shorter than the hind ones, in which the foot is longer and more expanded, so as to present a larger surface for striking the water in swimming. But the chief natatory organ in these large amphibious reptiles is the long, compressed tail. In the act of swimming, the fore limbs are applied flat to the sides of the body, and the hind ones chiefly

162

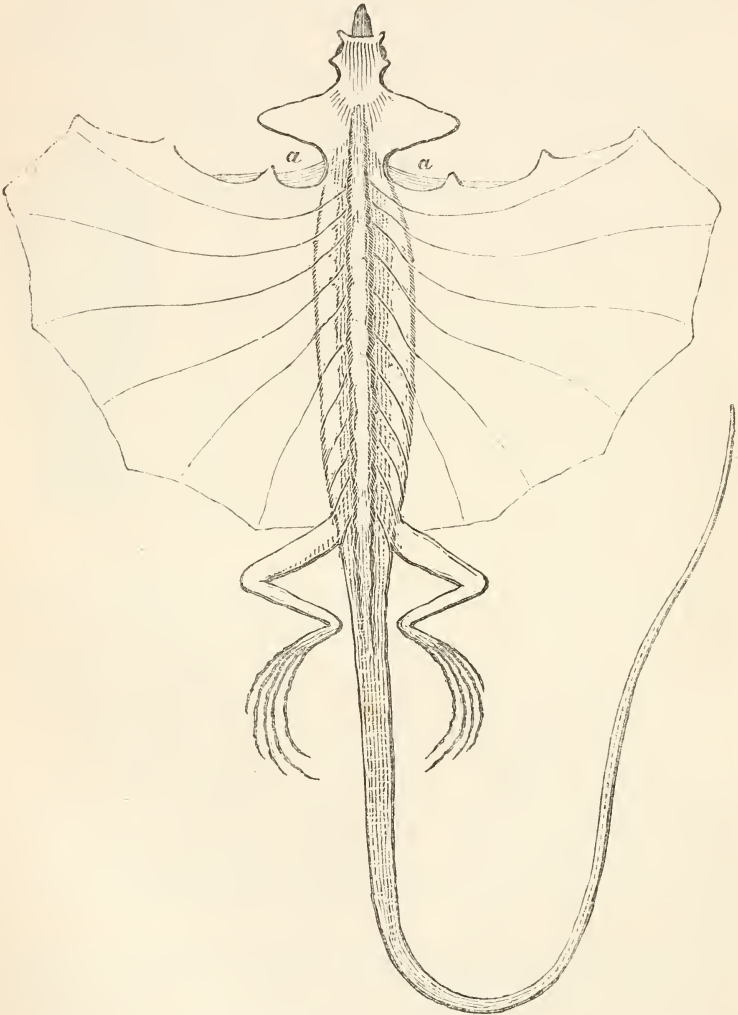


Toe of Gecko, magn.  
CCIII.



used in modifying the course through the water. The fore limbs were shorter, and the hind limbs longer in the extinct *Crocodylia* of marine habits. The stiffness of the neck, produced by the overlapping of the expanded cervical ribs, adds to the power of the head in overcoming the resistance of the water; but detracts,

163



Flying lizard (*Draco volans*), LINN. CCIV.

with the almost inflexible cuirassed trunk, from the capacity to capture prey on land, which is seldom overtaken, except by a

straight-forward rush: this, for a short extent, is dangerously rapid; but the Crocodiles are most formidable and agile in their habitual element the water.

The little *Draco volans* has a body which rarely exceeds 110 grains in weight; the delicate tegumentary parachute, sustained by the long slender ribs, fig. 163, like the nervures of the insect's wing, measures about five square inches — its area being as great in proportion to the weight of the animal as that of the wings in many birds. But the muscular apparatus, *a, a*, subserves only the expansion and folding up of the membrane, which would seem, therefore, to act, if the animal ever leaps into air or darts through that element, merely as a sustaining parachute to break the fall.

The Reptilia in which the fore limb was developed and modified, in order to work membranous expansions with sufficient force to raise and move the body in air, ceased to exist, apparently, during the deposition of the cretaceous beds, prior to the tertiary epoch in Geology. We learn from the fossilized remains of Pterodactyles, that the weight of the body, compared to the area of their outspread wings, must have been very small, fig. 111, A; that the bones were light, of a thin but compact osseous texture, permeated by air. The digit, so enormously developed for sustaining the main part of the wing, fig. 111, 5, was restricted, like the antibrachium in birds, to movements of abduction and adduction, lying along the ulnar side of the fore-arm, and reaching beyond the sacrum, when the wing was folded. The proportion of the area of the outstretched wings to the body was greater in Pterodactyles than in most birds, and equalled that in the bats; like which, the Pterodactyles would alter the alar area by alternate abduction and adduction of the sustaining digit, combined with flexion and extension of the arm and fore-arm.

The large head and strong neck of the Pterodactyle seem to have called for that extension and forward direction of the antibrachium, which would cause the centres of gravity and magnitude to be more in advance than in either bird or bat. Their pelvic limbs were little more developed than in Bats — must have been unequal to sustain the body — may have concurred with the short unguiculate digits of the fore limb, fig. 111, 1, 2, 3, 4, in a crawling progress along the ground — and, being terminated by toes of equal length, probably served, as in bats, to suspend the body, head downward, during sleep.

## CHAPTER IV.

## NERVOUS SYSTEM OF HÆMATOCRYA.

§ 51. *Nervous tissues.*—Nervous substance, like muscular, ranks with the most complex of animal tissues in chemical constitution, and possesses the greatest atomic weight: but the albuminous form of proteine here prevails. Nervous tissue presents two formal characters; one vesicular and grey in colour, the other fibrous and white: but the neurine inclosed by neurilemma being softer than myonine, and less definite in arrangement after death, the nerve-fibre usually appears as a tube with white contents.

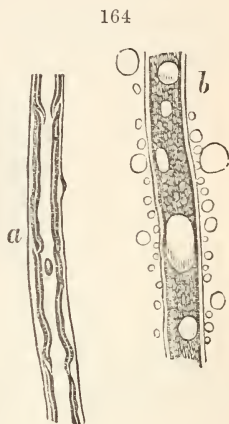
Nervous substance has two principal dispositions; one in masses, called ‘centres,’ the other in threads, called ‘nerves.’ The centres in Vertebrate animals constitute, according to their relative size or position, the spinal chord (myelon), the brain (encephalon), and ganglions. In these the vesicular, grey, or dynamic form of tissue is associated with the fibrous, white, or conductive form. Most nerves consist of the white fibres, and all are internuncial in office, establishing a communication between the centres and the various parts of the body.

The centres, and their grey or vesicular constituent more especially, appear to originate the nervous force: certain nerves conduct it to the tissues, principally muscular, on which it acts by producing contraction; other nerves carry the impressions received at their distal ends to the centres: the first are termed ‘motory,’ from the function they excite, and ‘efferent,’ from the direction of conduction: the second are termed ‘sensory’ and ‘afferent.’ Sensation, or the appreciation of the impression by the individual, seems to follow only when the ‘afferent’ nerve conveys its impressions to the brain; when it stops short in the myelon, or ends in a ganglion, it may excite a corresponding or connected ‘efferent’ nerve to produce motion, or a ‘reflex’ action, which may then take place without sensation or volition.

The myelon, the encephalon, and their nerves, constitute the ‘myelencephalous’ or ‘cerebro-spinal’ system, to which belong the ganglions on the sensory roots of the spinal and trigeminal nerves, and those in the glosso-pharyngeal and vagal nerves.

A chain of ganglions is situated on each side, near the vertebral foramina, through which the cerebro-spinal nerves issue. These ganglions radiate many nerves, connecting them one with another and with the cerebro-spinal nerves, and ramifying in a plexiform way upon the viscera and coats of the blood-vessels: they constitute the 'sympathetic' or 'ganglionic' system in Vertebrates.

In the cerebro-spinal nerves the primitive fibre consists of a transparent elastic homogeneous tubular membrane (neurilemma), fig. 164, *a*; its contents are pulpy, homogeneous in the living or recently dead state, and may be pressed out of the sheath; when treated with water, as in fig. 164, *a*, or with alcohol, they condense into a white layer, giving that colour to the tube: within the white substance Remak defines a 'flattened band,' and Purkinje an 'axis-cylinder.' When treated with ether, oil-globules coalesce in the interior, and accumulate around the exterior of the tube, fig. 164, *b*.



Nerve tubes altered by re-agents. ccv.

The delicacy of the neurilemma, and mobility of its contents, lead, in many cases, to partial dilatations of the tube, of a 'varicose' character, probably due to post-mortem influences: in the living or natural state, the primitive nerve-tube or fibre appears to be perfectly cylindrical.

The following are results of Todd's admeasurements of their diameter, in the different vertebrate classes:—

Fishes (Eel)  $\frac{1}{1043}$  of an inch.

Reptiles (Frog)  $\frac{1}{1280}$  to  $\frac{1}{2280}$  of an inch.

Birds  $\frac{1}{2000}$  to  $\frac{1}{3000}$  of an inch.

Mammals  $\frac{1}{1625}$  to  $\frac{1}{6500}$  of an inch.<sup>1</sup>

Primitive nerve-fibres do not divide or branch; they are associated together, in simple juxtaposition, supported by fine layers of areolar tissue, which condense at the periphery into a common sheath, to which the term 'neurilemma' is commonly, but not properly, given: it answers to the sheath which surrounds a muscle, similarly binding the constituent fibres of the nerve together, and supporting their nutrient capillaries. These are the smallest in the body; they run chiefly parallel with the nerve-fibres, forming oblong meshes, completed at intervals by cross-vessels. Sometimes the nerve-fibres have a wavy course within the general sheath, fig. 165. In a few instances they have been

<sup>1</sup> ccv. p. 593.



observed to decussate, as in fig. 166, changing their relative position within the sheath.

165



Wavy course of nerve fibres, within the common sheath. ccv.

The termination of efferent nerves on sentient surfaces of the skin appears to be plexiform: but they have been seen to enter the bases of the tactile papillæ in the form of loops. The looped termination has been distinctly seen by Henle upon the membrana nictitans of the frog, and by Valentin on parts of the formative matrix of teeth, fig. 167.

166

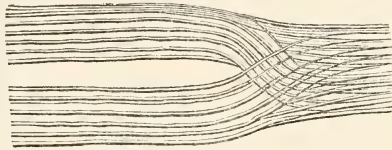
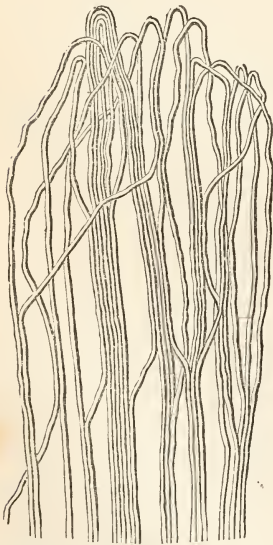


Diagram to show the decussation of the primitive fibres within the trunk of a nerve. ccv. ccvi.

Amongst the nerve-fibres of the sympathetic system are some of a grey colour, sometimes called 'soft fibres,' which are flattened, homogeneous, more minute than the primitive fibres of the cerebro-spinal system, and characterised by small multinucleate bodies upon their surface, fig. 168.

167



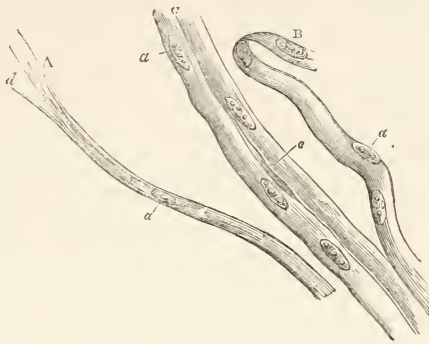
Terminal nerves on the sac of the second molar tooth of the lower jaw in the sheep, showing the arrangement in loops. ccvi.

§ 52. *Myelencephalon of Fishes.*—In the cold-blooded Vertebrates the proportion of the mass-form, or centres, to the thread-form, or conductors, of the nervous system is less than in the warm-blooded classes.

In the Lancelet (*Branchiostoma*), fig. 169, the neural axis, *md*, shows no distinction between brain and myelon; it is a slender tract of nucleated cells, inclosed in a delicate pia mater, constituting a continuous chord, of opaline sub-transparency, ductile and elastic. It is depressed or band-like along its middle third, which is slightly grooved along the medial line of the dorsal surface,

and tapering to both ends, but more gradually to the hinder one, the fore-end being less acute. A streak of pigment-cells marks the middle of the upper surface: darker cells mark the origins of the nerves. These number from fifty to sixty

168



Nervous fibres from a soft or grey nerve in the Calf. *ccvii*.  
 A, fibre resolving itself into fibrilla. B, a fibre doubled on itself, showing the flattened character. C, Two fibres lying in juxtaposition. *a, a, a, nuclei. e, a nuclear fibre (Kernfaser). d, a fibrilla.*

pairs, and appear to come off as simple chords, fig. 170. They perforate the membranous neural canal, and accompany the inter-muscular septa, dividing into two principal branches — one to the neural or dorsal, the other to the haemal or ventral, muscular

169

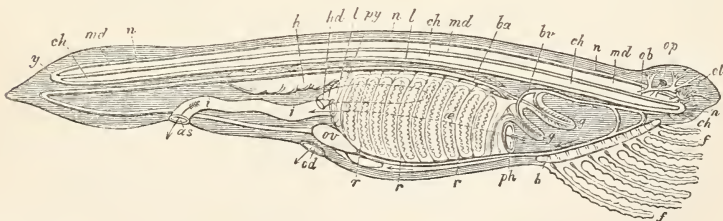
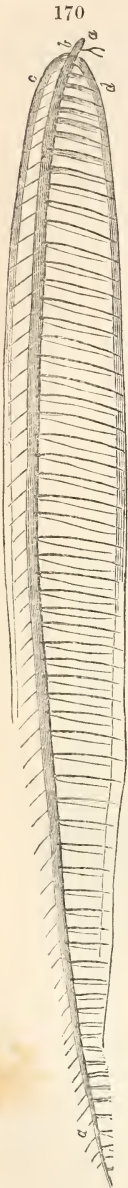


Diagram of Anatomy of the Lancelet, *Branchiostoma*

segments. The first pair of nerves, fig. 170, *b*, which Professor Goodsir<sup>1</sup> thinks might correspond to the 'trifacial,' passes to the membranous parts above the mouth: it may be the homologue of that, which, when a part of such membrane becomes specialised as an olfactory sac, becomes the olfactory nerve, as, e. g., in the

<sup>1</sup> xc.

Lamprey. The second pair is much larger; it passes out of the neural canal, anterior to the first myocomma, and sends a branch, *c*, fig. 170, upward and backward toward the front edge of that segment, which communicates with the dorsal branches of several successive nerves of its own side, like the branch from the combined trifacial and vagal nerves, marked 1 in fig. 204: the main trunk of the second nerve curves downward and backward, *d*, fig. 170, communicating with the corresponding parts of the succeeding nerves of its own side, to some way beyond the vent, fig. 169, *as*: this portion answers to the branches 3 and 4 of the 'nervus lateralis' in fig. 204. From the principal function of the second (conspicuous) pair of nerves in the Lancelet, as a 'nerve of association,' it probably answers to both the trigeminal and vagal, which in most higher fishes combine to form the 'lateral nerve,' with the same relations to the spinal nerves and median fins as the nerves *c* and *d*, fig. 170, show in the Lancelet.



Costa<sup>1</sup> describes and figures 'la macchia bruna degli occhi' (p. 14), 'l'opacità corrispondente sopra e dietro degli occhi' (ib.),<sup>2</sup> and 'talvota i gangli olfattori' (Tab. i., fig. 2, *gy*). Retzius<sup>3</sup> rediscovers the ocellus; and Kölliker<sup>4</sup> has more particularly described the sub-terminal ciliated depression, described as an 'olfactory sac,' and indicated in the diagram, fig. 169, *ol*. According to those observations, olfactory and optic nerve-filaments may be inferred; and the fore part of the neural axis, including the trigemino-vagal nerves, *c b*, fig. 169, will answer to the brain.

The succeeding nerves divide, soon after emerging, into dorsal and ventral branches, as in higher fishes, corresponding in number with the muscular segments. The nerves consist of the primitive cylindrical fibres.

This is the most simple persistent condition of the central organs of the nervous system known

The nervous system of *Branchiostoma lanceolatum*.  
xc.

<sup>1</sup> XXX.

<sup>2</sup> Query, can this opaque spot be an acoustic sac?

<sup>3</sup> CXXI.

<sup>4</sup> XXXII.

in the vertebrate subkingdom. In all other Fishes the fore part of the neural axis receives the vagal, trigeminal, and special sense nerves, and develops and supports ganglionic masses, principally disposed in a linear series parallel with the axis: this part is the 'brain' (encephalon); the rest of the axis retaining its columnar or chord-like character is the 'myelon,' and being lodged in the canal of the spinal column, it is usually defined as the *medulla spinalis* (spinal marrow, or spinal chord).

In the Lamprey the myelon is flattened, opaline, ductile, and elastic, as in the Lancelet and other *Dermopteri*: in typical Fishes it is inelastic and opaque, cylindrical or sub-depressed; of nearly uniform diameter, gradually tapering in the caudal region to a point in heterocercal Fishes, but swelling into a small terminal ganglion<sup>1</sup> in most homocercal Fishes.

The Hunterian preparation of the skate (*Raia Batis*)<sup>2</sup> shows a slight (brachial or pectoral) enlargement of the myelon, where the numerous large nerves are sent off to the great pectoral fins: a feebler brachial enlargement may be noticed in the Sharks. I have not recognised it in Osseous Fishes, not even in those with enormous pectorals adapted for flight, e. g. *Exocætus* and *Dactylopterus*: in the latter the small ganglionic risings upon the dorsal columns of the cervical region of the myelon receive nerves of sensation from the free soft rays of the pectorals, and the homologous ganglions are more marked in other Gurnards (*Trigla*), which have from three to five and sometimes six pairs<sup>3</sup>, e. g. in *Trigla Adriatica*. Similar myelonal cervical ganglions are present, also, in *Polynemus*. In the heterocercal Sturgeon there is a feeble expansion of the myelon at the beginning of the caudal region, whence it is continued, gradually diminishing to a point along the neural canal in the upper lobe of the tail. In some bony fishes (Trout, Blenny) the caudal ganglion is not quite terminal, and is less marked than in the Cod or Bream, in which it is of a hard texture, but receives the last pair of spinal nerves. The absence of this ganglion in the Shark shows that it relates not to the strength of the tail but to its form, as depending on the concentration and coalescence of the terminal vertebræ; except, indeed, where such metamorphosis is extreme, as, e. g. in *Orthogoriscus mola*, and where it affects the entire condition of the myelon, which has shrunk into a short, conical, and, according

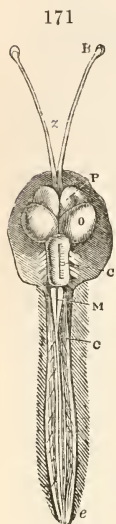
<sup>1</sup> LIII. p. 6; LIV. p. 26 (in the Cod).

<sup>2</sup> XX. vol. iii. p. 40, prep. No. 1347.

<sup>3</sup> LV. pl. 2, fig. 4, p. 106; and LIII. p. 6, pl. 2, fig. 24, 25.



to Arsaki (LIII. tab. iii. fig. 10), gangliated appendage to the encephalon. A like singular modification, but without the ganglionic structure, obtains in *Tetrodon* and *Diodon*, in a species of which latter genus I found the myelon, fig. 171, M, only four lines long, in a fish of seven inches in length and measuring three inches across the head. The neural canal in these Plectognathic fishes is chiefly occupied by a long 'cauda equina,' *ib. c c.* But, insignificant as the myelon here seems, it is something more than merely unresolved nerve-fibres: transverse white striæ are discernible in it, with grey matter, showing it to be a centre of nervous force, not a mere conductor. In the *Lophius* a long cauda equina partly conceals a short myelon, which terminates in a point at about the twelfth vertebra. In other fishes the myelon is very nearly or quite co-extensive with the neural canal, and there is no cauda equina, or bundle of nerve-roots, in the canal: a tendinous thread sometimes ties the terminal ganglion to the end of the canal.



Brain and myelon, *Diodon*, natural size

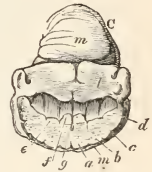
A shallow longitudinal fissure divides the ventral surface, and a deeper one the dorsal surface, of the myelon, into equal moieties: a feeble longitudinal lateral impression (Sturgeon) subdivides these into dorsal and ventral columns; in other fishes (Cod, Herring) these are separated by a lateral tract, and six columns or chords may be distinguished in the myelon—two dorsal or sensory, two ventral or motory, and two lateral or restiform tracts. A minute cylindrical canal extends from the fourth ventricle, beneath (ventrad of) the bottom of the dorsal fissure, along the entire myelon; this canal is not exposed in the recent fish by merely divaricating the dorsal columns. Both lateral halves of the myelon have grey matter in their interior, and white transverse striæ. Although many fishes (Bream, Dorsk) show a slight enlargement at each junction of the nerve-roots with the myelon, the anatomical student will look in vain in the recent Eel, or Lump-fish, for that ganglionic structure of the myelon which the descriptions of Cuvier<sup>1</sup> might lead him to expect.

As the myelon approaches the encephalon, it expands; and the following changes may be here observed in the Cod and Shark:—

<sup>1</sup> XXIII, i. p. 323; XIII. iii. p. 176.

in the ventral columns a short longitudinal groove divides a narrower median 'pre-pyramidal' tract, fig. 172, *a*, from a broader lateral 'olivary' tract, ib. *b*: in the dorsal columns a median 'funicular' tract, ib. *e*, is similarly marked off from a lateral 'post-pyramidal' tract, *d*: this is now, also, distinguished by a deeper fissure from the true lateral or 'restiform' tract, *c*, at the inferior part of which a distinct slender portion is also sometimes defined. The post-pyramidal tracts diverge, expand and blend anteriorly with the similarly bulging restiform tracts, forming the side-walls of a triangular or rhomboidal cavity, called the 'fourth ventricle,' fig. 173,  $\gamma$ : the pre-pyramidal and olivary tracts, forming the floor of the ventricle, are covered below by a thin superficial layer of transverse 'arciform fibres'<sup>1</sup> ib. *m*, concealing their boundary fissures. At the bottom of the ventricle the myelonal canal is exposed, and its sides swell and rise as rounded or 'teretial' tracts,<sup>2</sup> ib. *f*, from the floor of the ventricle, diverging slightly as they advance, and exposing an intermediate 'nodular' tract; this structure is well seen in the basking shark (*Selache*): two lateral prominent 'vagal' columns also project inwards into the ventricle, from the conjoined restiform and post-pyramidal tracts; these vagal columns present a series of nodules, fig. 173,  $\epsilon$ , corresponding with the fasciculi of the roots of the great vagal nerve in *Selache*.<sup>3</sup>

172



Section of medulla oblongata, *Carcharias*

In the Cyprinoid Fishes the median inferior tract rises into the ventricle, and is developed into a smooth hemispheric mass, the 'nodulus,' fig. 178, *k*: the conjoined post-pyramidal and restiform walls swell outwards, and form lateral 'vagal' lobes, large and nodulated in the Carp, fig. 178, *h*, which is so tenacious of life. The vagal lobes are enormously developed in the Torpedo; they join the trigeminal lobes, and present a yellowish colour in the recent fish: many non-nucleated cells are present in their substance; they give origin to the nerves of the electric organs, and have been called 'lobi electrici;' but the vagal lobes are scarcely less remarkable for their size in the Gymnotus, where they have no direct connection with any of the nerves of the electric organs. In the Cod the vagal ganglions are obsolete, and the nodulus slightly swells above, and obliterates the 'calamus scriptorius.' In the *Lucioperca* the vagal lobes are not very distinct, but they mark

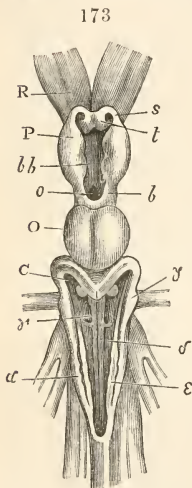
<sup>1</sup> Homologous with the 'filamenti arciformi' of Rolando, LVIII. p 170, t. i. fig. 2.

<sup>2</sup> These are called 'vordere pyramiden' by Dr. Stannius. LVI. p. 43.

<sup>3</sup> xx. vol. III. p. 22; Prep. no. 1311A.

the commencement, and form the broadest part, of the very long medulla oblongata, the restiform tracts diminishing in size as they advance. In no other Vertebrates save Fishes are the vagal lobes and the nodulus present.

The posterior pyramids, which are the anterior continuation of the posterior myelonal columns, diverging as they are pushed aside by the deeper-seated tracts that form the floor of the fourth ventricle, and combining with the lateral columns to form the corpus restiforme and the basis of the vagal lobes, again quit those columns, converge, ascend, and unite together above the anterior opening of the fourth ventricle: they there form either a simple bridge or commissure, fig. 173, c, or are developed upwards and backwards into a ganglionic mass, overarching the ventricle; this mass is the 'cerebellum,' figs. 174—179, c. It is



Brain; Sturgeon. CXCIX.

formed chiefly by the post-pyramidal columns, but doubtless derives some share of the proper lateral or restiform fibres, as the result of the previous confluence of these with the post-pyramids.

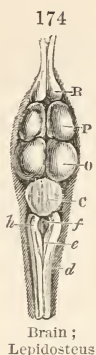
The cerebellum retains its earliest embryonic form of a simple commissural bridge or fold in the parasitic suctorial Cyclostomes, in the heavily-laden Sturgeon, fig. 173, c, and Polypterus,<sup>1</sup> and in the almost finless Lepidosiren,<sup>2</sup> fig. 186, c: it attains its highest development, in the present class, in the Sharks, where it not only covers the fourth ventricle, but advances over the optic lobes, and in the Saw-fish extends beyond them to rest upon the cerebrum; its surface is further extended in these active predaceous fishes by numerous transverse folds, fig. 187, c. In most Osseous Fishes the

cerebellum is a smooth convex body, hemispheroid, fig. 175, c, or transversely subelliptic (Eel, fig. 176, c), or longitudinally subelliptic (Lepidosteus), fig. 174, c; but it may be an oblong body (Diodon), fig. 171, c, or be depressed and tongue-shaped (Cod, fig. 183, f), or oval, or pyramidal (Perch, fig. 182, a); it is very rarely found extending forward, as in *Echeneis* and *Amblyopsis*, fig. 175, c, over any part of the optic lobes; but often backward over the whole fourth ventricle, as in the Cod, fig. 183, f, and the Diodon, fig. 171, c; or over the major part of the ventricle, as in the

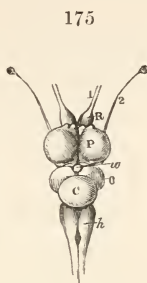
<sup>1</sup> xxv. p. 24, pl. ii. figs. 5, 7.

<sup>2</sup> xxxiii. p. 339, pl. 27.

Herring, fig. 184, c; but sometimes covering only a small portion, as in the Chub, fig. 177, c, the Lump-fish, and the Lepidosteus, fig. 174, c. The relative size of the cerebellum, accordingly, varies



Brain ;  
Lepidosteus



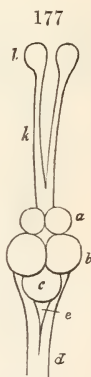
Brain; Amblyopsis  
magnified



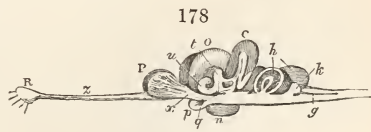
Brain; Eel. OÖL.

greatly in different bony fishes; it is very small in the lazy Lump-fish, and extremely large in the active and warm-blooded Tunny, where, also, its surface shows transverse groovings. The cerebellum is unsymmetrically placed in the Pike and some Flat-fish (*Pleuronectidæ*), and is unsymmetrically shaped in the Sharks: it presents a longitudinal groove in the Diodon, and a posterior notch in the Herring: a transverse notch divides it into an anterior and posterior lobe in the Lophius: it bears a crucial depression in the Skate. The cerebellum presents in many fishes a small cavity or fossa at its under part, continued from the fourth ventricle, fig. 178, c: it is solid in the Tench, the Garpike, and the common Eel: some grey matter is usually found in its interior, with feeble indications of white striæ; but there is no ‘arbor vitæ,’ except in the Tunny and Sharks.

The posterior ‘crura cerebelli’ are formed by the posterior pyramids, fig. 172, d, with part of the restiform tracts, ib. c; vertical fibres from the sides of the cerebellum continue to attach it to the sides of the restiform or trigeminal lobes, and some of these are continued as arciform filaments upon the under surface of the medulla oblongata: they answer to the ‘crura cerebelli ad pontem’ of Mammalia; but, as



Brain and portion of  
spinal marrow of  
Chub (*Luciscus*)

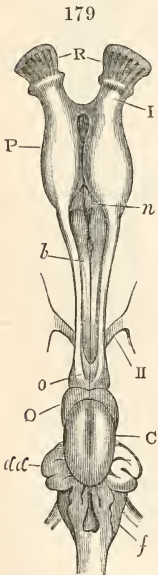


Section of Brain, Carp



there are no lateral lobes in the cerebellum in Fishes, these crura are rudimentary, and the 'pons' is absent. In the Shark they connect the sides of the base of the cerebellum with the 'restiform commissure,' figs. 172 & 187, *l*. In most Fishes two fasciculi of medullary fibres proceed, as 'anterior crura,' from the under and fore part of the cerebellum, or converge from the lateral and fore-part forward, to form the inner wall or septum, fig. 184, *r*, of the optic lobes: these answer to the 'processus à cerebello ad testes' of the human brain: they are connected below their origin at the under part of the cerebellum by one or two transverse fasciculi of white fibres, forming the 'commissura ansulata,' which crosses the pre-pyramids just behind the 'hypoaria,' fig. 185, *n*. The inferior white surface of the cerebellum, which forms the roof of the fourth ventricle, is called 'discus cerebelli,' and from this part small tubercles project in a few fishes (e. g. *Blennius* and *Sturio*, fig. 173, *c*).

The restiform columns, quitting the post-pyramidal crura of the cerebellum, and having effected by their previous confluence therewith some interchange of filaments, swell out at the anterior lateral parts of the medulla oblongata, and give origin to the great trigeminal nerve. They here form considerable 'trigeminal lobes' in the Loach and Herring, fig. 184, *i*, and are folded or 'fimbriate' in *Chimæra*, fig. 179, *dd*, and most Plagiostomes, where they are closely connected with a thick vascular mass of pia mater and arachnoid. The trigeminal lobes are convolute in the Skate; enormous and blended with the vagal lobes in the Torpedo; but in most Osseous Fishes (*Lepidosteus*, Cod) they are not developed so as to merit the name of lobes. In the Cod the inner surfaces of the restiform bodies project into the fourth ventricle, and obliterate the fore part of the calamus by meeting above it; this commissure, which is beneath the cerebellum, is the 'commissura restiformis,' fig. 182. It is remarkably developed in *Carcharias*, where it seems to form a small supplemental cerebellum beneath the large normal one: in fig. 172 the medulla oblongata is cut across, the fourth ventricle exposed from behind, and the restiform commissure, *l*, is raised: it has an anterior and posterior median notch.



Brain of *Chimæra monstrosa*. CXCIX.

The primary division of the brain, which consists of the medulla oblongata with the cerebellum and other less constant appendages

The primary division of the brain, which consists of the medulla oblongata with the cerebellum and other less constant appendages

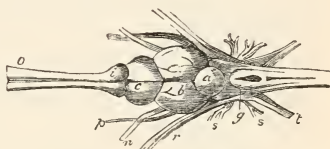
in Fishes, is called the ‘epencephalon,’ fig. 179, *f*, *c*, fig. 178, *g*, *c*; it is relatively larger, occupies a greater proportion of the cranium, and is more complex and diversified in this than in any of the higher classes of Vertebrata.

The next succeeding primary division of the brain is called the ‘mesencephalon,’ figs. 180 & 181, *b*, *e*, *f*: it is usually the largest division in Osseous Fishes, and consists of two upper spheroidal bodies, called ‘optic lobes,’<sup>1</sup> figs. 176, 177, 180, *b* (in most of the figures, *o*), of two lower subspherical bodies, called ‘hypoaria,’<sup>2</sup> figs. 178, 185, *n*, fig. 181, *e*, with intervening connecting walls enclosing a cavity, called the ‘third ventricle,’ which

is prolonged downward into the pedicle of the ‘hypophysis,’ or pituitary gland, fig. 185, *p*, and upward into that of the ‘conarium’ or pineal gland, fig. 175, *w*. The prepyramidal columns are continued forwards, along the floor of the fourth ventricle, where they are covered by a thin layer of medullary fibres, to the hypoaria and prosencephalon: some fibres blending with the wall of the third ventricle and the base of the optic lobes. The transverse ‘ansulate’ commissure,<sup>3</sup> which unites or crosses the prepyramids before they penetrate the hypoaria, may be regarded as the most anterior of the arciform filaments, which feebly represent the pons Varolii in Fishes. The restiform columns are expended chiefly in forming the walls of the third ventricle and the base and exterior walls of the optic lobes, a small part only being continued forwards to the cerebrum in most Osseous Fishes. The anterior cerebellar crura are chiefly lost in the inner walls or septum of the optic lobes.

These lobes are commonly of a subspherical figure, and larger than the cerebral lobes, as in figs. 177, 180, *b*, 171, 184, *o*; they are often larger than the cerebellum, *ib. ib.*; but of nearly equal size with the cerebellum in the Eel, fig. 176; they are smaller than the cerebral lobes, but larger than the cerebellum, in the Polypterus and Lepidosiren, fig. 186, *o*; they are smaller than either the cerebrum or cerebellum in the *Amblyopsis spelæus*, fig. 175, *o*, in

180



Brain of Perch, upper surface. XXIII.

181



Brain of Perch, under surface. XXIII.

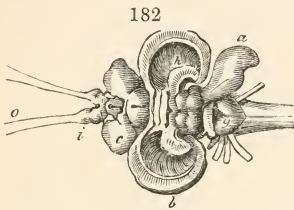
<sup>1</sup> ‘Lobes creux,’ Cuvier.

<sup>2</sup> ‘Lobes inférieurs,’ *Ib.*

<sup>3</sup> LVII. pl. iv., fig. 7, *l.*

the Chimæra, fig. 179, o, and in the Sharks, fig. 187, o. In the latter they bear the same proportion to the optic nerves and eyes as in other fishes, their small relative size depending on the advanced development of both cerebellum and cerebrum: in the blind Amblyops of the subterraneous waters, the diminution of the optic lobes relates to the almost total abrogation of the visual organ; but since both in the Amblyops and the equally blind Myxine these lobes are present, they cannot be exclusively the central ganglion of the optic nerve, nor their sole function that of receiving the impressions of the sense of sight, and making them perceptible as ideas by the animal.

The optic lobes are hollow in most Fishes, fig. 182, b. The exterior surface shows blended grey and white matter, the white



Brain of Perch, with the optic lobes laid open, and the cerebellum turned to the right side. XXIII.

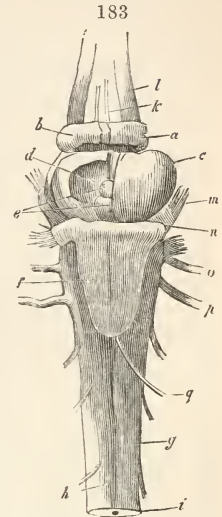
fibres usually converging to the optic nerves; some of the fibres unite with the anterior crura of the cerebellum to form the septum of the optic lobes, fig. 184, r, which consists of two or four medullary fasciculi, decreasing in the Tench, increasing in the Cod, as they pass forward. On divaricating the optic lobes from above, as in fig.

182, or by a horizontal section, as in fig. 183, their cavity, d, or ventricle, is exposed: it communicates with the expanded myelencephalous canal, called 'third' and 'fourth' ventricles, as shown by the bristle, q. Its floor is variously configured in different fishes. There are one or two small white tubercles, 'tuberculi optici,' figs. 182, 183, e, on each side of the back part of the septum; the Cod, Salmon, Pike, and Perch, show four of these bodies; the Carp and Herring, fig. 184, t, two: in the Carp they are oblong, juxtaposed, and were called 'tuberculum cordiforme' by Haller;<sup>1</sup> they are not present in the Polypterus, Lepidosiren, Sturgeon, or Plagiostome fishes. External to these tubercles the floor of the ventricle usually rises into a curved eminence, with its convexity outwards; this is the 'torus semicircularis' of Haller,<sup>2</sup> fig. 184, w. It is not homologous with either the 'thalamus opticus' or the 'corpus striatum' of the mammal's brain. In the Carp, where the great physiologist first described and named them, the 'tori' are large, and much curved; in general they describe only a

<sup>1</sup> In *Salmo Umbla* Haller calls them 'corpora quadrigemina,' as does Cuvier, in *Perca fluviatilis*: they are analogous in form to the parts so named, in Mammals; but are not homologous therewith.

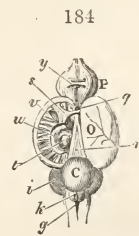
<sup>2</sup> LIX. t. iii. p. 201.

small portion of a circle, fig. 182, *h*; and in some bony fish, as the Garpike, Loach, and Lumpfish, they are scarcely raised above the level of the floor of the ventricle. They are not developed in the Polypterus, the Lepidosiren, or the higher Plagiostomes; and both tori and tuberculi are peculiar ichthyic developments in the ventricles of the optic lobes. The bottom of the optic ventricle, fig. 184, *v*, anterior and external to the 'tori,' is grey, and usually prominent, with white fibres radiating through it to rise and expand upon the walls of the lobes. The optic lobes have almost coalesced in the Sturgeon, fig. 274, *o*, Polypterus, Lepidosiren, Amblyopsis, and Loach (*Cobitis*). Where they are quite distinct externally, as in most Osseous Fishes, they are brought into mutual communication by one or two commissures; the anterior 'commissura transversa' is the most constant; it is shown in the Perch, fig. 182, and in the Herring, fig. 184, *s*; it passes in front of the entry to the third ventricle.

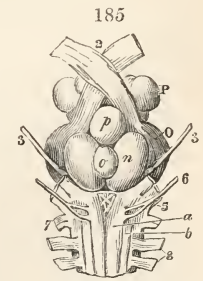


Brain and portion of myelon Cod. CCXVI.

In the Myxine and Lepidosiren the prepyramidal fibres curve suddenly forward and upward before expanding into the floor and sides of the third ventricle, and they thus form a small protuberance beneath the basis of the optic lobes, fig. 186, *n*. In the Shark the same columns swell out laterally, and form two small protuberances, fig. 187, *n*, separated below by the vascular (hypophysial) floor of the third ventricle. In most Osseous Fishes the corresponding fibres of the prepyramidal tracts swell out suddenly, beneath the optic lobes, into two protuberant well-defined oval ganglions ('hypoaria,' fig. 185, *n*, fig. 181, *e*): their bulk is increased by added grey matter, which variegates their outer surface; they are well developed in the common Cod, in which, as in some other fishes, they contain a cavity (hypoarian ventricle). In some *Salmonidæ* their surface is striated; in some *Cyprinidæ* (Tench) they are confluent; but commonly they are distinct, and have in



Optic ventricles; Herring



Base of brain; Cod



their inferior interspace a vascular medullary depressed sac (the 'hæmatosac,' fig. 185, *o*), usually oblong, as in the Cod, rarely bifid or cordiform, as in the Lumpfish. These prominences from the floor of the mesencephalon, posterior to the infundibulum and hypophysis, *ib. p.*, are peculiar to the brain of fishes, and, in their full developement, are restricted to the typical osseous member of the class; they are absent in the lowest, and disappear in the highest orders; they are mere rudiments, or are wanting, in the Pterygerus, as in the still more amphiboid *Lepidosiren*.

The true vasculo-membranous infundibular downward prolongation of the third ventricle exists in all Osseous Fishes, and extends from the anterior angle of the hypoaria, where these exist: the infundibulum is commonly short and thick, so that the hypophysis is almost sessile, as in the Cod; but in the *Lophius*, the infundibulum is longer than the entire brain, and the hypophysis lies at the fore-part of the cranial cavity, far in advance of the cerebral lobes.<sup>1</sup> In the Cod the hypophysis, fig. 185, *p.*, is a subspherical mass, with an irregular or slightly nodulated surface, almost half the size of the human, so called, 'pituitary gland,' and illustrating the vast proportional size of this constant appendage to the brain of Fishes. In the *Lepidosiren* the infundibulum is wide, and the hypophysis a white flattened discoid body, fig. 186, *o*.<sup>2</sup> In all Fishes it is richly supplied with vessels, and is closely attached to the floor of the cranium; but, although its early developement checks or modifies that of the cranial vertebræ, it is not provided with a special chamber or 'sella.' The prolongations of the fibres from the mesencephalon which expand into the prosencephalic or proper cerebral lobes rarely show any preliminary developement of 'thalami;' but the parts homologous with those recruiting ganglia are constantly indicated by the attachment of the conarium, or upper prolongation of the third ventricle.

The conarium, figs. 175, 186, 187, *w.*, is as constant an appendage of the encephalon in Fishes as the hypophysis; but it is commonly only a vasculo-membranous pyramidal sac continued from the third ventricle, the base expanding from between the anterior interspace of the optic lobes, and the apex directed forward and attached to the roof of the cranium. Some medullary matter mingles with the membranous walls of the conarium in the Clupeoid and Cyprinoid Fishes: in some Fishes there is grey matter in the conarium: in most it is membranous only, as in the

<sup>1</sup> LX. p. 56, t. ii. fig. 1.

<sup>2</sup> The hypophysis is marked *g* in xxxiii. pl. 27, fig. 4; and is called 'mammillary body' in *Lepidosiren annectens*, *ib.* p. 361.

Lepidosiren, Sturgeon, and Shark: in all it is highly vascular. In the Bream the conarium shows an analogous peculiarity to that of the hypophysis in the Angler, viz. in the length and tenuity of its attachment; but this consists of two distinct crura. The value of the constancy of the hypophysis and conarium consists chiefly in their marking the boundary line between the mes- and pros-encephala, although they belong to the mesencephalon, and are both essentially vertical prolongations of the third ventricle through an interspace produced by the divarication of the main lateral columns of the encephalon.

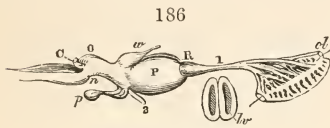
The fasciculi continued forward from the parietes of the third ventricle or mesencephalic basis, are principally those which may be traced back through the epencephalon to the anterior and lateral myelonal tracts, augmented by fibres from the grey centres or lobes through which they have passed, and retaining a small admixture of post-pyramidal fibres from the optic septum, fig. 184, *r*. In Osseous Fishes the two cerebral crura, so constituted, rarely undergo any enlargement, homologous with the 'thalami,' where they form the anterior boundary of the third ventricle; but after a very brief course, as 'crura cerebri,' fig. 178, *x*, radiate into two small subspherical 'prosencephalic' masses of grey matter, ib. *p*, situated anterior to the optic lobes, and there in great part terminate. A few of the medullary fibres extend along the base of the prosencephalon, receive a small tract of its grey matter, converge to the anterior interspace of its lobes, and either expand there into 'rhinencephala,' figs. 174, 175, 186, *r*, or are continued forward and outward, as 'rhinencephalic crura,' figs. 178, 187, *z*, to form the olfactory lobes or ganglia, ib. *r*, at some distance from the brain. Although the prosencephalic lobes are commonly in contact with the optic lobes, yet something analogous to the displacement of the rhinencephalon may be seen in the prosencephalon of the Chimæra, in which the cerebral crura, fig. 179, *b*, advance some way before they expand into the prosencephala, *p*: in the Plagiostomes, also, the prosencephalic crura, fig. 187, *x*, have a short independent tract in advance of the optic lobes.

The prosencephala, figs. 177, *a*, 180 and 182, *c*, 183, *a*, *b*, in other figs. *p*, are distinguished from the optic lobes by their grey pinkish exterior, and, generally, also by their fissured or nodulated surface. The first of these characters must be looked for in recent fish: the second is more permanent.<sup>1</sup> With

<sup>1</sup> xx. vol. iii. it may be seen in preparations of the brain of the Eel (*Anguilla acuti-rostris*, No. 1309, B); of the Lump-fish (*Cyclopterus*, No. 1309, C); of the Gurnard (*Trigla lyra*, No. 1309, D); and especially in this specimen of the brain of the Cod

regard to the 'cerebrum' of the Cod, a median tract or convolution is marked off by a longitudinal fissure, which extends along the back of each prosencephalon, defining a posterior and inferior convolution; the median convolution is vertically fissured on its inner side. In the *Amblyopsis*, fig. 175, p, it is cleft anteriorly; and here, as in most fishes, the median longitudinal tract is the most constant subdivision of the prosencephalic superficies.

The large elongated prosencephala are smooth in *Chimæra*, fig. 179, p, *Polypterus*, and *Lepidosiren*, fig. 186, p, and in the



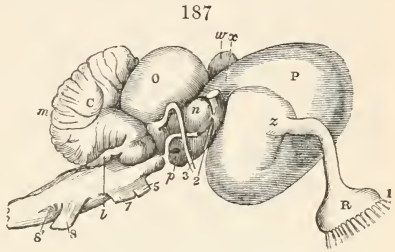
Brain of *Lepidosiren*

still more developed confluent mass in the Sharks, fig. 187, p; the prosencephala are, also, smooth in the *Myxines*, where they are relatively smallest. The comparative anatomists, who have failed to

recognise the true homology of the prosencephalon in Osseous Fishes, appear to have been misled chiefly by its small proportional size, which is commonly that exhibited in the brain of the Cod, the Carp, and the Globe-fish; in some species the prosencephalon is even smaller, as in the Gar-fish, the Herring, or the Lump-fish. The prosencephalon equals the cerebellum in size, but is less than the optic lobes in the Perch and Bream; it equals the optic lobes, but is less than the cerebellum, in the Eel; in the Stickleback and Gurnard the prosencephalon exceeds the cerebellum, still more so in the *Lepidosteus*, but is less than the optic lobes; in the *Lucioperca*, the *Amblyopsis*, the *Chimæra*, and the Skate, neither the cerebellum nor the optic lobes are so large as the prosencephalon; in the large Sharks their united size scarcely equals that of the prosencephalon; and in the Salamandroid *Polypterus* and the *Lepidosiren* the prosencephalic lobes surpass all the rest of the brain, and vindicate their true cerebral character and importance. In the *Amblyopsis* the relative magnitude of the prosencephalon is due to the diminution of the optic lobes in that blind fish; in the *Plagiostomes* it is due to absolute development; as it is, also, in the *Polypterus* and *Lepidosiren*, where the prosencephalon presents the closest similarity in form and structure to that division of the brain in the Batrachian Reptiles: each lobe, for

(No. 1309), which Hunter truly, though briefly, describes as follows:—"The *cerebrum* fissured; the *cerebellum* a long projecting body, also fissured in a less degree; the *notes* two projecting bodies: the optic nerves decussate one another." This is the earliest recognition of the homology of the optic lobes with the anterior of the bigeminal bodies of the human brain.

example, is elongated in the axis of the skull, and is of a sub-compressed oval form, and has a large 'lateral ventricle' in its interior in the *Lepidosiren*, fig. 186, *lv*. In the Skate, the prosencephala coalesce into a subdepressed transversely elongated mass, their essential distinction being indicated by a mere superficial median fissure; in *Carcharias*, fig. 187, the prosencephalon forms an almost globular mass, with scarcely a trace of a median fissure. Among bony fishes the prosencephalic lobes are more or less confluent in *Lucioperca sandra*, *Trachinus draco*, *Sargus*, *Mullus*, *Scomber trachinus*, *Belone*, *Clupea harengus*, and *Clupea sprattus*; they appear distinct symmetrical spheroids in most other fishes, their union being reduced to a small trans-



Brain of Shark, *Carcharias*

verse medullary band (prosencephalic commissure).<sup>1</sup> The symmetrical character of the prosencephala, as of the optic lobes, is wanting in most *Pleuronectidæ*.

The grey vascular neurine forms the greatest part of the prosencephalon in most Osseous Fishes; the white fibres radiate through this, and rarely appear on any part of the exterior surface; the white substance, however, predominates in the Plagiostomes and *Lepidosiren*. As a rule, the prosencephalic lobes are solid; but the brain of *Carcharias*<sup>2</sup> shows a deep ventricular fissure at the anterior and under part of the prosencephalon, with a vascular fold of membrane or 'choroid plexus' penetrating the fissure, which is continued forward into the crus of the olfactory lobe. The lateral ventricle is more extensive in the *Lepidosiren*, and is continued directly into the olfactory lobe.

The 'rhinencephalon' figs. 173—176, *r*, consists of two always distinct lobes of grey matter, which receive the prolongations of chiefly white fibres from the prosencephalon and its crura, and give off the nerves to the olfactory capsule, whence they are termed 'olfactory lobes,' 'tubera,' or 'ganglia.' The rhinencephala are solid bodies, always distinct, wide apart from each other when remote from, and in mutual contact when near to, the rest of the brain, but never united by a commissure. The rhinence-

<sup>1</sup> Carus well recognises the homology of this commissure with that of the corpus striatum, called 'anterior commissure' in the human brain, I. p. 24.

<sup>2</sup> (No. 1310, A), XX. vol. iii.



phalic crura, figs. 171, 175, 178, 187, z, vary exceedingly in length. In the *Lepidosiren*, fig. 186, they are feebly indicated by a continuous indentation circumscribing the base of the rhinencephalon, R, and defining it from the anterior end of each prosencephalic lobe, P; in *Polypterus* and *Lepidosteus* the indentation is deeper, and the attachment of the base of the now pyriform rhinencephalon, fig. 174, R, sinks to the prolonged crus or basis of the prosencephalon. From this substratum the rhinencephalic crura are prolonged in all Osseous Fishes: in some they are so short that the rhinencephala are partly overlapped by the prosencephala (*Trigla*), or rise into view immediately in front of them (*Amblyopsis*, *Anguilla*, fig. 176, R, *Cottus*, *Cyclopterus*); but in many fishes the rhinencephala are developed far in advance of the rest of the brain, and their crura are prolonged close to the olfactory capsules. This has led to a denial of the existence of olfactory lobes in such fishes; but the rhinencephala are truly present in both the Cod and Carp, fig. 178, R; they are merely removed to juxtaposition with the olfactory capsules, with a concomitant prolongation of their crura. These crura, so prolonged, *ib. z*, have been called 'olfactory nerves' by those who, failing to appreciate the true homology of the remote 'rhinencephala,' have described them as ganglionic swellings of the ends of the olfactory nerves.<sup>1</sup> These ganglions, wherever situated, consist of proper nervous matter over and above the mere radiation or expansion of the fibres of the so-called 'olfactory nerves.' The true olfactory nerve quits the rhinencephalon as a plexiform chord, or as a group of distinct fibres. If the thick olfactory nerve of the Gurnard be compared with the thick rhinencephalic crus of the Skate, or if the long olfactory nerve of the Eel be compared with the long rhinencephalic crus of the Chub, fig. 177, *h*, their respective difference of structure will be readily appreciated. The crus is a compact tract of medullary with a small proportion of grey matter; the nerve is a bundle of nerve filaments: the medullary tract of the crus is fibrous, but the fibres are as fine as in the crus cerebri, and much more numerous and less easily separable than in the true olfactory nerve. In this there is no grey tract: it consists wholly of comparatively large and readily separable white fibres, which radiate at once upon the olfactory capsule; the divergence and radiation of the true end of the olfactory nerve is well seen in the *Lepidosiren*, fig. 186, 1, *ol*. In Sharks a ventricle is continued to each rhinencephalon along its crus from the prosencephalon. The

<sup>1</sup> Camper, LXI. p. 95; Cuvier, XXIII. p. 321.

olfactory nerve never forms a ganglion before spreading upon the olfactory capsule; the rhinencephalic crus, when prolonged to the capsule, always expands into a 'tuberculum olfactorium,' or rhinencephalon, before it transmits the true olfactory nerves to the capsule. In other words, the olfactory nerve conveys impressions to a proper centre or lobe, which, in Fishes, may be situated close to the capsule, or close to the rest of the brain, and the length of its crus will be inversely as that of the nerve. The olfactory lobes or rhinencephala are serially homologous with the optic lobes. As to the prosencephalon, since this does not immediately receive or transmit any nerve, it resembles in this important character the cerebellum, and proceeds, even in the present class, to be developed to a degree beyond the ganglions of any special nerves or organs of sense.

The more special homology of the prosencephalic lobes, under their normal proportions and solid structure in Osseous Fishes, with the parts of the complex and fully developed prosencephalon in Mammals, will be made manifest as we trace the progress of that complication synthetically. Cuvier had already, by the opposite course of analysis, reduced the hemispheres in birds to the 'corpora striata,' with their commissures and a thin supraventricular covering. 'Le corps cannelé,' he says, 'forme à lui seul presque tout l'hémisphère.'<sup>1</sup> But he failed to recognise the homology of the prosencephala in Fishes. Since Arsaki's time<sup>2</sup> their homology with the cerebral lobes of Reptiles, Birds, and Mammals has been generally recognised. Girgensohn<sup>3</sup> says they may well be compared with the 'corpora striata;' but he notes the important difference, that, whereas these 'transmission ganglia' (*durchgangsknoten*) give passage to the radiating fibres of the cerebral crura in their course to other parts of the cerebrum in Mammals, those fibres terminate in the solid prosencephala of Fishes. The establishment of the lateral ventricles in the prosencephala of the Plagiostomes and Lepidosiren also show them to be something more than 'corpora striata.'

It now becomes important to note the mode of establishment of these cerebral ventricles: they are not formed by the super-addition of a layer or film of neurine overlapping parts answerable to the solid hemispheres in other Fishes, but are either central excavations, as in the elongated prosencephala of the Lepidosiren, fig. 186, *lv.* or they are deep fissures towards the under part, as in the coalesced hemispheres of the Shark; whence I

<sup>1</sup> cc. t. ii. 1799, p. 162.<sup>2</sup> LIII. 1813.<sup>3</sup> LXIII. p. 155.

conclude that the solid prosencephalon of Osseous Fishes is not a mere representative of a basal ganglion forming the floor of the ventricle of the hemispheres in the higher Vertebrates, where such ganglion is a medium of transmission or source of accession to the cerebral fibres; but that the fish's prosencephalon is the seat of the terminal expansion of the radiating medullary fibres of the cerebral crura. Dissection of the recent brain shows, as in fig. 178, P, that these fibres, besides being blended with grey matter, as in the corpora striata, are thickly covered with a layer of the same grey and highly vascular neurine, of which the hemispheric convolutions in Mammals are chiefly formed; and it is interesting to perceive on the superficies of the solid prosencephalon in many fishes the foreshadowing of the convolutions, which are not fully established until an advanced Mammalian grade is attained. The prosencephalon of the fish is far from being a miniature model, but it may be regarded as the potential representative, of the complex cerebral hemispheres of man.

The average proportional weight of the brain to the rest of the body in Fishes is as 1 to 3000. In a chub (*Leuciscus Cyprinus*) weighing 842 scruples, the brain, exclusive of the olfactory lobes, weighed one scruple; in a carp (*Cyprinus Carpio*), weighing 11,280 grains, the brain weighed 14 grains; in a lamprey weighing 750 grains, the brain weighed half a grain. A certain size seems to be essential to the performance of its functions, as a recipient of the impressions from the organs of sense; and it does not, therefore, vary in different species so as to accord precisely with the general bulk of the body. The size of the optic lobes, e.g. has a more constant and direct relation to that of the eyes, which soon acquire their full development. We find the entire brain proportionally greater in young than in old fishes: it acquires its full size long before the termination of the growth of the fish, if this has a fixed period. But as the head must grow with the growth of the fish, under the conditions of its progressive motion, provision for occupying the increasing capacity of the cranium is made by a concomitant development of the light cellular arachnoid, which has the further advantage of regulating the specific gravity of the head.

As the branchial respiration is a peculiarly active and important function in Fishes, and has an extraordinary apparatus of bony or gristly arches with their muscles, we may associate therewith the peculiar development and complexity of the medulla oblongata, as the centre of the vagal or respiratory nerves. The Carp and other Cyprinoid Fishes, which have not the mechanical

modifications for retaining water in contact with the gills, so characteristic of the Apodal, the Lophioid, and Labyrinthi-branch fishes, are remarkable, nevertheless, for their tenacity of life out of water; and the peculiarly developed vagal lobes may relate to this maintenance of the power of the respiratory organs during a suspension of their natural actions.

The extensive gradation of the cerebellum between the extremes of structure presented by the Myxine and the Shark, as might be expected, throws more direct light upon its function. With regard to this, two views have been taken. According to one it is the organ of amativeness; according to the other it is the seat of the muscular sense, or the regulator of voluntary motion. Many experiments in which the cerebellum has been mutilated or removed in warm-blooded animals support the idea of its intimate relation with the locomotive powers. But to the conclusions from these experiments has been objected the possibility of the convulsive muscular phenomena having arisen from the stimulus on the remaining centres, occasioned by the mutilation or destruction of the one in question; and it may well be doubted whether Nature ever answers so truly when put to the torture, as she does when speaking voluntarily through her own experiments, if we may so call the ablation and addition of parts which comparative anatomy offers to our contemplation.

If, in reference to the sexual hypothesis of the cerebellum, we contrast the Lamprey with the Shark, we shall be led, by the much larger proportional size of the generative organs in the lower cartilaginous Fish, and from the observed fact of the male and female Lampreys entwining or wreathing themselves entirely about each other, mutually aiding in the expulsion of their respective generative products, and so absorbed in the passion as to permit themselves to be taken out of the water and replaced there, without interruption of the act, to expect a larger cerebellum in the Lamprey than in the Shark. But the very reverse of this is the fact: the Lamprey has the smallest, and the Shark the largest, cerebellum in the class of Fishes. If, on the other hand, we compare the Cyclostome and Plagiostome Cartilaginous Fishes, in reference to their modes and powers of locomotion, we shall find a contrast which directly accords with that in their cerebellar development. The Myxine commonly passes its life as the internal parasite of some higher organised fish: the Lamprey adheres by its suckorial mouth to a stone, and seldom moves far from its place: neither fish possesses pectoral or ventral fins. The Shark, on the contrary,



unaided by an air-bladder, sustains itself at the surface of the sea, by vigorous muscular exertion of well-developed pectoral and caudal fins, soars, as it were, in the upper regions of its atmosphere, is proverbial for the rapidity of its course, and subsists, like the Eagle, by pursuing and devouring a living prey: it is the fish in which the instruments of voluntary motion are best developed, and in which the cerebellum presents its largest size and most complex structure. And this structure cannot be the mere concomitant of a general advance of the organisation to a higher type, for the sluggish Rays, that grovel at the bottom, though they copulate, and have in most other respects the same grade and type of structure as the more active Squaloid Plagiostomes, yet have a much smaller cerebellum, with a mere crucial indentation instead of transverse laminae. A more decisive instance of the relation of the cerebellum to the power of locomotion is given by the *Lepidosiren* in which, with a more marked general advance of organisation than in the Ray or Shark, the cerebellum has not risen above the simple commissural condition which it presents in the Lamprey; the generative system, however, of the *Lepidosiren* is as complex as in the Plagiostomes, and is more extensive: but the fins are reduced to mere filaments, and the fish is known to pass half the year in a state of torpid inactivity. The cerebellum is large in the Chimera, fig. 179, c. In the heavy laden ganoid fishes, the cerebellum is smaller than in the ordinary Osseous Fishes: the imbricated armour of dense enamelled bony scales must limit the lateral inflections of the tail; so we find in *Polypterus* the cerebellum hardly more developed than in *Lepidosiren*, whilst in the somewhat more active and predaceous *Lepidosteus* it is the smallest of all the segments of the brain. In the grovelling Sturgeons the cerebellum offers a grade of development above that in the *Lepidosiren*. Finally, amongst the normal Osseous Fishes, the largest and highest organised cerebellum has been found in the Tunny, whose muscular system approaches, in some of its physical characters, most nearly to that of the warm-blooded classes.

If we could enter the sensorium of the fish, and experience the kind of sensations and ideas derived from the inlet of their peculiarly developed and enormous eyes, we might be enabled to understand the office of the peculiar complexities of their large optic lobes: without such experience, we can at best only indulge in vague conjecture from the analogy of our own sensations. We find, when Nature reduces the organs of sight to such minute specks as can give but a feeble idea of

the presence of light, sufficient, perhaps, to warn the Amblyopsis to retreat to the darker recesses of its subterranean abode, that the optic lobes are not reduced in the same proportion, but retain a form and size, which, as compared with their homologues in other animals, are sufficiently remarkable to suggest a function over and above that of receiving the impressions of visual spectra, and forming the ideas consequent thereon.

The anatomical condition of the prosencephalon, and its homology with the hemispheres of the bird's brain, experimented on by Flourens,<sup>1</sup> would lead to the belief that it was in this division of the fish's brain that impressions become sensations, and that here was the seat of distinct and tenable ideas: of such, for example, as teach the fish its safest lurking-places, and give it that degree of caution and discernment which requires the skill of the practised angler to overmatch. If different parts of the prosencephalon were special seats or organs of different psychical phenomena, such phenomena are sufficiently diversified in the class of Fishes, and are so energetically and exclusively manifested, as to justify the expectation, on that physiological hypothesis, of corresponding modifications in the form and development of the homologues of the cerebral hemispheres. Some species, as, for example, the Shark and Pike, are predatory and ferocious: some, as the Angler and the Skate, are crafty: some, as the Sword-fish and Stickleback, are combative: some, as the Carp and Barbel, are peaceful, timid browsers: many fishes are social, especially at the season of oviposition: a few are monogamous and copulate; still fewer nidificate and incubate their ova.

Now, if we compare the prosencephala of the Shark and Pike, fishes equally sanguinary and insatiable, alike unsocial, the tyrants respectively of the sea and lake, we find that those parts of the brain differ more in shape, in relative size, and in structure, than in any two fishes. The prosencephalon of the Pike is less than the cerebellum, much less than the optic lobes; in the Shark it exceeds in size all the rest of the brain: in the Pike, the prosencephalon consists of two distinct lobes brought into communication only by a slender transverse commissure; in the Shark, the hemispheres are indistinguishably blended into one large subglobular mass. If we compare the prosencephala of the Pike with those of the Carp, we find them narrow in the devourer, broad in the prey.

The *Lophius* lurks at the bottom, hidden in the sand, waiting, like the Skate, for its prey to come within the reach of its jaws:

<sup>1</sup> LXIV.

the difference in the shape, size, and structure of their prosencephala is hardly less than that between the Shark and Pike. The combative Stickleback has longer and narrower prosencephala than the cowardly Gudgeon. The nidificative and philo-progenitive *Callichthys* has neither the antero-lateral nor the posterior regions of the cerebrum more developed than in bony fishes generally.

§ 53. *Myelencephalon of Reptiles*.—The perennibranchiate Batrachia lead sluggish lives in swamps and pools; their senses are as little developed as those of the Lepidosiren, and their muscular movements are perhaps even more restricted: hence, if the cerebral lobes seem to preponderate, in proportion to other parts of the brain, over the prosencephalon of Osseous Fishes, it is rather by contrast with the rudimentary condition of the mes- and ep-encephala than in the relative size of the prosencephalon to the entire body.

In a Newt, weighing 39 grains, the brain weighs one-seventh of a grain: and in the large Sirens, Amphiumes, and Menopomes, the proportion of the brain to the body is less than in the Newts.

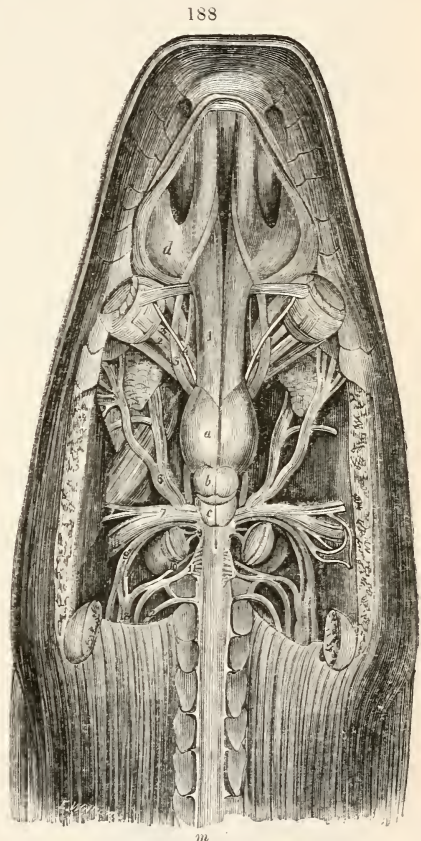
The medulla oblongata slightly expands; the post-pyramidal and restiform tracts diverge and expose a long and simple 'fourth ventricle,' with a median fissure: the convergence and confluence of the borders at the fore part of the 'calamus' offer a feeble rudiment of cerebellum. The optic lobe in the Axolotl is a long elliptical body, two-thirds the breadth of the epencephalon. A slight swelling below gives off the small optic nerves, and is produced anteriorly into a vascular 'hypophysis': a larger pineal body extends from before the optic lobe upon the posterior interspace of the cerebral lobes, completing the mesencephalon, which is the smallest of the primary divisions of the brain. The cerebral hemispheres, twice the length and breadth of the optic lobe, are smooth and hollow, like those of *Lepidosiren*. The olfactory lobes are pyriform, with the base sessile on the fore and outer part of the hemispheres; the nerve is shorter than in *Lepidosiren*. The cerebral ventricles are continued into the olfactory lobes.

The small and simple brain may be wholly removed from a torpid batrachian in the winter season, the medulla oblongata included, by section of the myelon in front of the roots of the second pair of cervical nerves; and, nevertheless the animal survives many weeks, preserving the reflex actions of the myelon and nerves, the contractility of the muscular fibre, and the



functions of organic life. In the active state of the summer season, such mutilation is followed by death in one or two hours, rarely more.<sup>1</sup>

In serpents, the cerebellum, fig. 188, *c*, expands into a depressed semicircular lobe directed backward from the confluence of the restiform crura and overlapping the major part of the fourth ventricle, which appears as a short median fissure. The optic lobes, *ib. b*, now expanded to the breadth of the cerebellum, show both a longitudinal and a transverse fissure, the latter crossing near the hinder border, and giving to this part of the brain a close resemblance to its homologue the 'bigenital bodies' in Mammals. The optic lobes are hollow: the cerebral crura show slight enlargements, like optic thalami, anterior to the optic lobes, before expanding into the hemispheres. These are pressed into close contact medially, and compose a prosencephalon nearly as broad as long, and double the breadth and length of the mesencephalon. The outer surface of the hemispheres is smooth, composed of a thin layer of vascular or grey neurine. Into their cavity or ventricle a 'corpus striatum' projects from the under and outer side; beneath or mesial of which is a minor prominence. The septum, formed by the thin mesial wall of each hemisphere, is perforated for the passage of a 'choroid plexus.' The ventricles are continued forward into the olfactory lobes, fig. 188, *1*; each is marked off by an oblique fissure from the fore part of the hemisphere, which it equals in breadth;



Brain and Nerves of the Boa Constrictor. LIV.

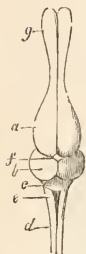
the under and outer side; beneath or mesial of which is a minor prominence. The septum, formed by the thin mesial wall of each hemisphere, is perforated for the passage of a 'choroid plexus.' The ventricles are continued forward into the olfactory lobes, fig. 188, *1*; each is marked off by an oblique fissure from the fore part of the hemisphere, which it equals in breadth;

<sup>1</sup> cci.



and after a short curve, resolves itself into a close fasciculus of olfactory nerves.

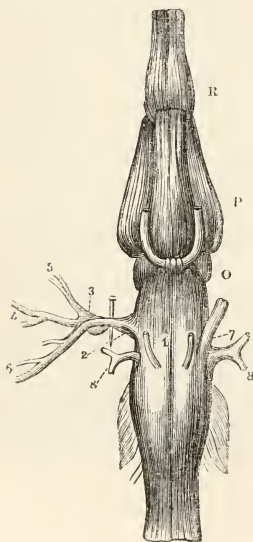
189



Brain of a Lizard (*Lacerta viridis*) upper view. CCXVI.

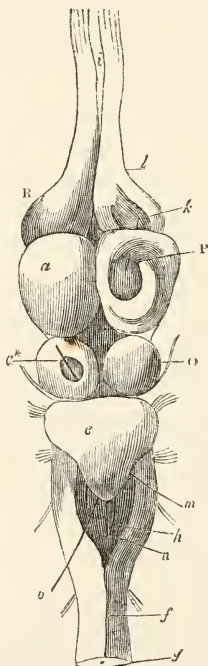
In the *Lacertilia*, the eyes being relatively larger and more active in function than in Serpents, the optic lobes, fig. 189, *b*, show corresponding increase of proportional size to other parts of the brain. The cerebellum, *ib. c*, is still smooth, depressed, semi-circular, and leaves more of the fourth ventricle, *e*, exposed than in *Python*. The optic lobes cease to show the transverse fissure, and form a pair of hemispherical hollow bodies. The cerebral hemispheres, *ib. a*, form an elongate oval body, more contracted anteriorly than in *Python*. The olfactory lobes, *ib. g*, are contracted at their junction with the hemispheres into the resemblance of 'crura rhinencephali.'

190



Brain of Tortoise, base view. CCVIII.

191



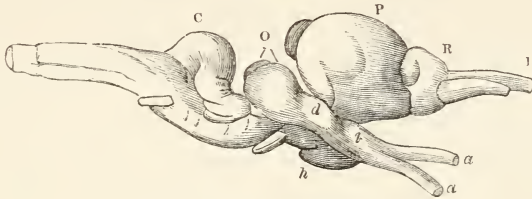
Brain of Turtle (*Chelone*), upper view. CCXVI.

In the base view of the brain of the Tortoise, given in fig. 190, the absence of 'pons Varolii' and of olivary or pyramidal bodies

is shown in the medulla oblongata, which is indicated by a slight tumefaction giving off the fifth, 3, 4, 5, 6, seventh, 7, eighth, 8, and ninth pairs of cerebral nerves: the tract is bounded anteriorly by the hypophysis covering the origin of the optic nerves. The continuation of the basal fibres of the hemispheres, P, into the rhinencephalon, R, is shown.

In a side view, the several primary divisions of the chelonian brain present the shapes and proportions shown in fig. 192, in which C is the epencephalon, O, the mesencephalon, P the prosencephalon; R, the rhinencephalon. The epencephalon includes the medulla oblongata, with the cerebellum.

192



Brain of a Turtle (*Chelone*), side view. CCH.

In the turtle (*Chelone*, fig. 191) the cerebellum, c, is slightly raised by the bristle, o, to expose the fourth ventricle, h, in which the sides of the calamus rise into 'teretial tracts.' The cerebellum is subelongate in its form, consisting of an arched layer of neurine, smooth externally, of equal thickness throughout, which spreads over a portion of the ventricle. The remainder of that cavity is covered by a vascular plexus, derived from the sides of the medulla oblongata, which forms a sort of valve, and by becoming united to the margin of the cerebellum, completes the roof of the fourth ventricle, which is large and prolonged very far back. The optic lobes, o, are smooth, spheroidal bodies, on a plane inferior to the cerebellum and cerebrum. Each lobe has its ventricle, c\*, which communicates, as shown by the bristle, m, with the fourth ventricle, and likewise with the third; the 'iter' to which may be seen by divaricating the optic lobes, covered by pia mater reflected down the interspace, and by a very thin layer of neurine. From the third ventricle a canal, or 'infundibulum,' is continued down to the hypophysis, and another upward to the 'pineal' body, which is pyriform, hollow, and highly vascular: it occupies the interspace between the optic, o, and cerebral lobes, P. These form the largest of the

primary divisions of the brain, but retain the form and character of simple smooth nodules. Each lobe has its ventricle, fig. 191, P, containing a 'corpus striatum,' fig. 193, 1, in which the 'crus cerebri,' fig. 194, 1, principally expands; also a smaller oblong eminence connected with the 'thalami optici,' fig. 193, 2; and a transverse body extending anteriorly to the mesencephalon from the base of one lateral ventricle to the other. The choroid plexus is shown in the left ventricle of fig. 193. The olfactory lobes, of a pyramidal form, have their base defined by a fissure from the hemispheres; each has its ventricle, fig. 191, k, which communicates with the 'lateral' one, P.

The myelonal canal, fig. 191, g, is continued along all the encephalic masses, in which it expands, and assumes the name of 'ventricles,' the narrower intercommunicating canal being the 'iter.' The 'fourth' or ependymal ventricle is single: the hypophyseal ventricles, in fishes, form a pair; as do, likewise, the mesencephalic, prosencephalic, and rhinencephalic ventricles. The 'iter' or common passage between the ep- mes- and prosencephalic ventricles, includes the cavity called 'third ventricle' in Anthropotomy: to which cavity the mesencephalic ventricles are reduced by the consolidation of the optic lobes in Mammals.<sup>1</sup>

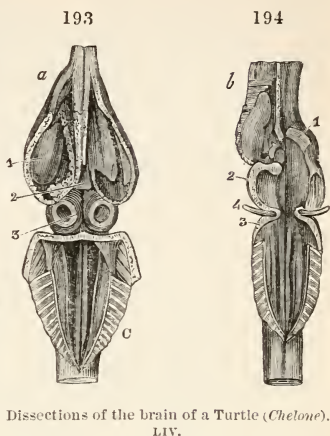
The ependymal or 'fourth' ventricle, exposed in figs. 193, and 194, c, shows the 'teretial' columns bounding the 'calamus' or median fissure: external to these are 'funicular' and 'pre-pyramidal tracts: the restiform columns, forming the sides and, anteriorly, the roof of the ventricle show grey and white striæ on their inner surface; the cerebellum is removed from their anterior union at 3, fig. 194. The mesencephalic base which

<sup>1</sup> The influence of the nomenclature of human anatomy, reflected downward upon the dawning structures of the lower animals which culminate in Man, is nowhere more obstructive to a plain and true indication of the nature of parts than in regard to those of the brain. The ventricles, for example, were indicated by numbers, or by position. But four of the primary ventricles, viz., the mesencephalic or optic pair, and the rhinencephalic or olfactory pair, which are present in the majority of vertebrates, are obliterated in Man; whilst the interspace of commissural lamellæ, exceptionally developed in the complex cerebrum of Man, and some higher Mammals, is made a 'fifth ventricle,' as if it were a structure of correlative significance and importance with the ventricles properly so called. Those cavities moreover in the human prosencephalon are specialized as 'lateral,' being the only ventricles retaining the parial state which is shown by the mes- and rhin-encephalic ventricles in all oviparous Vertebrates. Whoever will carry out the application of neat substantive names to the homologous parts and structures of the encephalon, as they may be ascensively determined, will perform a good work in true Anatomy.

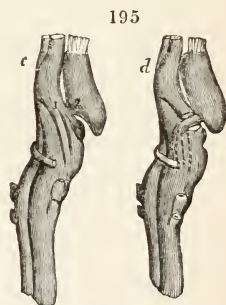
supports the optic lobes, is exposed from above, by their removal, in fig. 194, 2, showing the continuation of the ventricular cavity through that segment of the brain. The base of the excised 'corpus striatum' into which the 'crus cerebri' expands, is shown at 1, fig. 194. The prolongation of the optic lobe crosses the cerebral crus, externally, in its way to the optic tract, fig. 195, *d*; a portion has been removed in this figure to expose the crus cerebri in its ascent to the hemisphere. Three tracts of neurine may be traced from the prosencephalon to the rhinencephalon, of which the inferior one is the most distinct, fig. 190.<sup>1</sup>

In the brain of the Crocodile a marked advance is seen in the relative size of the cerebral lobes, especially in regard to their breadth and height posteriorly, giving a pyriform shape to the prosencephalon; the optic lobes, also, are not inferior in bulk to the cerebellum, and this body shows a transverse fissure on its exterior. The olfactory lobes, which are situated near the hemispheres in the newly hatched Crocodile, recede therefrom, and advance, with a proportional prolongation of the rhinencephalic crura. The optic lobe shows a convex body projecting into the ventricle from its posterior wall, which body is serially homologous with the 'corpus striatum' in the ventricle of the cerebral hemisphere. In other respects the brain of the Crocodile closely conforms with that of the Turtle.

With the exception of the anourus Batrachia, the myelon (spinal chord) is continued into the tail, gradually decreasing to a point, and is not resolved into a 'cauda equina.' Such, indeed, is its condition in the tadpole state of the frogs and toads; but, with the acquisition of the mature form, the myelon shrinks in length, and terminates midway between the fore and hind limbs, being resolved in the frog, into the three pairs of nerves which



Dissections of the brain of a Turtle (*Chelone*). LIV.



Dissections of the brain of a Turtle (*Chelone*). LIV.

<sup>1</sup> xx. vol. iii. p. 22, No. 1312.



form the sciatic, and into a few filaments passing on to the sacrum, fig. 208, *f*.

In all Reptiles there is an anterior and a posterior longitudinal fissure and a central canal dilating into the epencephalic ventricle. The myelonal canal is surrounded by a thin layer of grey neurine, and, in Lacertians and Crocodilians, it extends as far as the first caudal vertebra: in Ophidians, which have the longest spinal chord, the canal is continued to near the end, which goes as far as the penultimate caudal. The enlargements giving origin to the nerves of the limbs are best marked in *Chelonia*, owing to the relative slenderness of the myelon in the trunk. In the Lizards and Crocodiles with nearly equally developed limbs, the more muscular trunk and tail demand a myelonal mass which renders the brachial and iliac enlargements less conspicuous. There are no partial enlargements of the myelon in Serpents; the nerves, as numerous as the vertebræ, are given off at short and regular distances, as in fig. 188, *m*.

§ 54. *Membranes of the Myelencephalon in Hæmatocrya*.—Both brain and myelon are immediately invested by a thin but firm and vascular membrane, the outer surface of which, in most Fishes and many Reptiles, bears a stratum of pigment-cells belonging properly to the central layer of the arachnoid, which has here coalesced with the pia mater. This vascular membrane seems, therefore, to be coloured with dark points, and sometimes to be minutely speckled upon a silvery ground; and the pigmental stratum often accompanies the processes of the pia mater into the ventricles of the brain. There is commonly a remarkable developement of the vascular and pigmental membrane over the fourth, or epencephalic ventricle; it is largely developed in the Sturgeon, and conceals the rudimental cerebellum in the Lepidosiren. In the Axolotl calcareous particles are superadded to this covering of the epencephalon. In Osseous Fishes the commonly considerable space between the brain and cranial walls is occupied by a peculiar loose cellular structure, filled by gelatinous or albuminous fluid, and by oily matter: in the Perch and Bream it seems to consist of an aggregate of minute spherical cells filled with fine colourless oil, the mass being traversed by blood-vessels. Cuvier<sup>1</sup> found the cells, which he compares to a kind of arachnoid, filled by a compact adipose matter in the Tunny and Sturgeon. This modified arachnoid exists, but in less quantity, in the spinal canal, and

<sup>1</sup> XXIII, i. p. 309.

even accompanies the cerebral nerves in their exit from the skull in some fishes with large nerve-foramina. There is much cellular arachnoid above the cerebral lobes in the *Lepidosiren*. A large arachnoid is abundantly interposed between the dura mater and pia mater in the Turtle (*Chelone*), where two ligaments converge from the arachnoid at the sides of the epencephalon to be attached to a cartilaginous tubercle on the basioccipital. A number of filamentary processes pass from the space between the cerebral and optic lobes to the arachnoid above, like a rudimentary 'falx.'

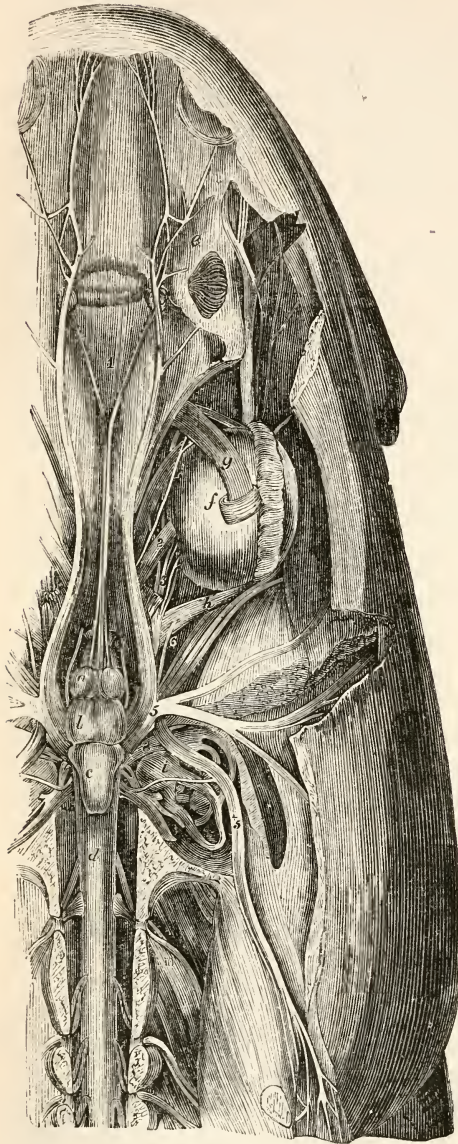
The primitive fibrous capsule of the neural axis, the unossified or unchondrified remains of which, or of its inner layer, form the so-called 'dura mater,' is most distinct in the low-organised *Dermopteri*; in the *Plagiostomi* it is reduced to a few thin shining aponeurotic bands closely adherent to the inner surface of the cartilaginous walls of the cranium and spinal canal; such traces of dura mater are more feeble and indistinct in Osseous Fishes, in which no proper continuous fibrous membrane can be distinguished from the inner periosteum of the walls of the cerebro-spinal cavity: no curtains of dura mater divide the cerebral from the acoustic compartments of the cranium in the Osseous Fishes. The dura mater, as a distinct fibrous membrane, lines the cavity of the skull and spinal column in Reptiles.

§ 55. *Nerves of Fishes.*—*First pair or Olfactory nerves.*—The head is short and obtuse in the embryo fish; the ganglionic centres of the olfactory nerves are always originally developed in close contiguity with the prosencephalon; they are protected, primarily, by the rhinencephalic arch; and, as this advances in the elongation of the skull, and recedes from the prosencephalic arch, two modes of growth take place in the contained nervous axis: either the brain is co-elongated, the rhinencephalon retaining its primitive relation with its vertebra, and the prolonged crura occupying the narrow interorbital tract of the cranial cavity, or the rhinencephalon retains its primitive juxtaposition with the prosencephalon, and the olfactory nerves, figs. 180—182, *o*, 203, *o*, are prolonged through the interorbital space, perforate or traverse a notch in the prefrontals, and expand, as a resolved plexus, upon the pituitary plicated sac.

The rhinencephalon accompanies its vertebra and recedes from the rest of the brain in *Salmo*, *Cyprinus* proper, *Brama*, *Tinca*, *Gadus*, *Lota*, *Hippoglossus*, *Clupea*, *Belone*, *Lucioperca*, *Cobitis*, *Plectognathi*, and *Plagiostomi*; it retains its primitive contiguity with the prosencephalon in *Perca*, *Scomber*, *Esox*, *Pleuronectes*,

*Blennius, Anguilla, Cyclopterus, Gasterosteus, Eperlanus, Cotus, Trigla, Amblyopsis, Echeuis, the Ganoidei, and Lepidosiren.*

196



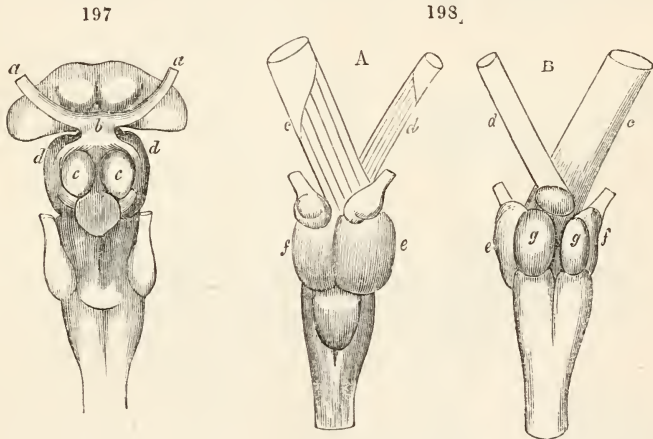
Brain and cerebral nerves of Cod-fish (*Gadus morrhua*). LIV.

As the crus of the rhinencephalon is formed not only of fibres continued from the prosencephalon, but also, and in some fishes chiefly, of distinct white and grey tracts, traceable along the base of the mesencephalon, in part as far back as the prepyramidal bodies, so the origin of the olfactory nerve has been described as characterised by this complexity and extent; and it is true that in some instances (e. g. in the Perch), where the rhinencephalon, figs. 180—182, *i*, is in contact with the prosencephalon, *ib. c*, a small portion of the true olfactory nerve may be distinctly traced backward as far as the mesencephalon: just as we find in some fishes (e. g. Sturgeon) a portion of the optic nerve traceable as far back as the cerebellum, and in the Eel to the hypochord, and not exclusively terminating in the optic lobe. Most of the characteristics of origin and course attributed in works of Comparative Anatomy to the olfactory nerves are to be understood of the ‘*crura rhinencephali*.’ In the



Lancelet the little ciliated olfactory sac is brought into close contact with the rhinencephalic extremity of the neural axis. When the olfactory lobe or ganglion, in other Fishes, is near the organ of smell, as in the Cod, fig. 196, o, it sends off the nerves by numerous very short fasciculi. This multiplicity of virtual origins of the proper nerve is less conspicuous where the rhinencephalon is near the rest of the brain; but a careful analysis of the long olfactory nerve in the Eel, fig. 176, will show that it is a fasciculus of filaments distinct from their origin.

The *optic nerves*, like the eyes, are of large relative size in most fishes; but where the organs of sight are small, the nerves are slender, as in the *Silurus*: they are still more slender in the *Myxinoids*, and they are scarcely discernible filaments in the



Brain of Skate (*Raia*), base view. CCL.

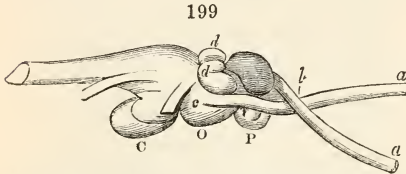
Brain of a Halibut (*Hippoglossus*), A upper, B under view. CCL.

*Amblyopsis*, fig. 175, 2. In the *Plagiostomes*, fig. 197, *Holocephali*, *Ganoidei*, and *Protopteri*, the optic nerves, *ib. a, a*, arise in part from the optic lobes, *ib. d*, in part from the hypoaria, *ib. e, e*, closely adhering to the fore part of the base of the mesencephalon, and are there connected together by a transverse commissure, *ib. b*, or close interblending of substance: they do not freely cross each other. In ordinary Osseous Fishes, figs. 181, 185, the exterior white fibres of the optic lobes converge to their under and anterior part, to form the chief part of the origin of the optic nerves; but a portion of the origin may be traced through the septum opticum to the cerebellum; and in the Eel, the Garpike, and the Lump-fish, a portion may be traced to the hypoaria: in the Cod, fig. 185, and



Take some fibres of the optic nerve, *ib. 2*, are derived from both the hypoaria, *ib. n* and *fig. 199, d*, and from the wall of the third ventricle. The relation of the hypoaria to the nerves of sight is illustrated in the fishes with unsymmetrical heads and eyes, e. g. *Pleuronectidæ*; in *fig. 198*, the optic lobe, *e*, and hypoarion, *g*, giving origin to the larger optic nerve, *e*, are larger than the optic lobe, *f*, and hypoarion, *g*, giving origin to the smaller optic nerve, *d*. The nerves cross one another without interchange of fibres; sometimes the right nerve in its passage to the left eye passes under, *fig. 199, b, a*, *fig. 201*, sometimes over, *figs. 185, 198*, the left nerve:<sup>1</sup> rarely does one nerve perforate the other, as, e. g. in the Herring. The nerves are flattened where they decussate. In most Osseous Fishes the structure of the optic nerve is peculiar; it consists of a folded plate of membrane and neurine, *fig. 200, a*, which usually prevails throughout the length of the nerve, from its cerebral

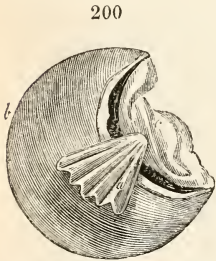
attachment to the eyeball: in some instances the inner surface of the optic lobe is also folded: and, in all, the plaits may be observed to be faintly continued upon the retina, which is formed by the unfolding of the



Brain of a Hake (*Merluccius*) with the base upward. CCL.

nerve. The optic nerve escapes, in Osseous Fishes, either through the anterior fibrous wall of the cranium beneath the orbito-sphenoid, or through a notch or a foramen in that bone. In the *Pleuronectidæ* one optic nerve is usually shorter, as well as smaller, than the other, *fig. 198*. In the Eel the nerves form, after decussation, a very acute angle in the axis of the body, *fig. 176, a*: in the Lump-fish they form an obtuse open angle.

Since there are no muscles of the eyeball in the Lancelet, the Myxinoids, the Amblyopsis, and the Lepidosiren, there are no motory nerves of the orbit. In the Lamprey a small third nerve and a fourth nerve, which are closely connected where they quit the cranium, again separate, the one to supply the rectus superior and rectus internus, the other the obliquus superior; the filaments supplying the other



Plaited optic nerve of a Mullet. *a*, optic nerve deprived of its sheath, exhibiting the plaited disposition; *b*, sclerotic coat of the eye through which the nerve is passing; *c*, retina, in which the nerve terminates. CCL.

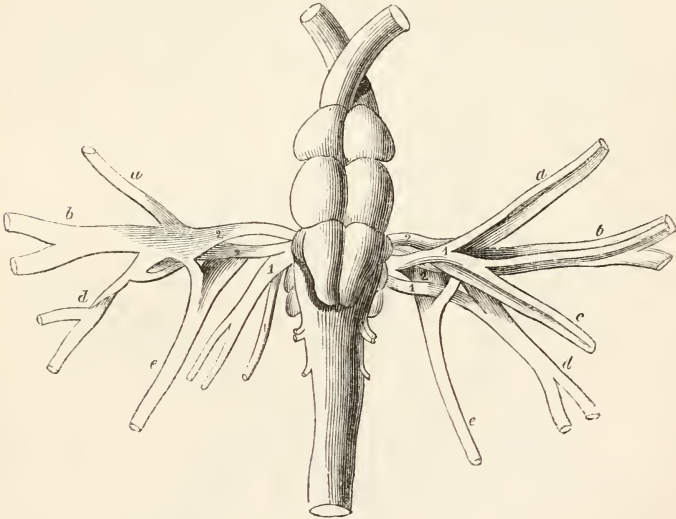
other the obliquus

<sup>1</sup> The writer has seen both varieties in different individuals of *Gadus morrhua*.

muscles of the eyeball cannot be separated from the fifth pair. In all other fishes the sixth or *abducent* nerve, fig. 185, 6, has its proper origin, as well as the fourth and third. The third, or *oculomotorius*, ib. 3, rises from the base of the mesencephalon, behind the hypoaria, ib. *n*, or from the commissura ansulata; it escapes through the orbito-sphenoid (Carp), or the unossified membrane beneath it (Cod, fig. 196, 3), and is distributed constantly to the recti superior, inferior, and internus, and to the obliquus inferior; it also sends filaments into the eyeball: the ciliary stem, or a branch of it, usually unites with a branch of the fifth nerve, and sometimes, as in the Mackerel, Gar-pike, and Lump-fish, develops a small ciliary ganglion at the point of communication.

The fourth nerve, or *trochlearis*, fig. 196, 4, rises from the back of the base of the optic lobes, between these and the cerebellum;

201



Brain and origins of the fifth nerves of the Cod. ccviii.

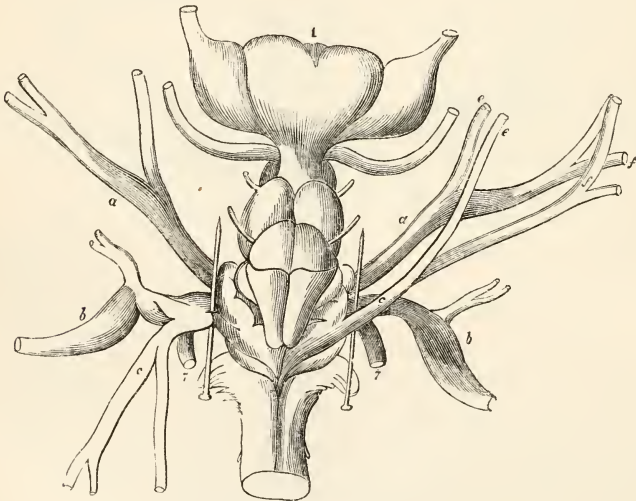
it escapes either through the orbito-sphenoid (Carp), or the contiguous membrane (Cod), and is constantly and exclusively distributed to the superior oblique eye-muscle, ib. *g*.

The sixth, or *abducent*, nerve, figs. 185, 196, 6, rises from the prepyramidal tracts of the medulla oblongata, fig. 185, *a*, beneath the fifth, and, in most Osseous Fishes, by two roots, as in the Cod, ib. 6. It usually closely adheres to the ganglionic origin of the fifth. In the Carp and Lump-fish it receives a filament from the sympathetic, before its final distribution to the rectus externus,

fig. 196, *b*: it escapes by the foramen or anterior notch of the alisphenoid, in advance of the fifth nerve.

This nerve, the *trigeminal*, enormous in all Fishes, from the Lancelet to the Lepidosiren, rises, often by two or more roots, from the restiform, or from the anterior angle between the olivary and restiform tracts; in some fishes from a special ganglion or enlargement of that part of the medulla oblongata, as in the Herring, fig. 184, *i*: in a few (Conger, Lump-fish) by a smaller origin resolved into several roots. The trigeminus shows well its spinal (myelonal) character in Fishes, only its double root is more deeply buried in the medulla oblongata. In the Cod, fig. 201, the non-ganglionic portion is shown at 1, the roots of the ganglionic portion at 2, 2. On the left side the non-ganglionic portion is separated and turned back: on the right side its divisions are seen accompanying the first, *a*, second, *b*, and third, *c*, branches of the trigeminal. The fourth branch, *d*, is also composed of both portions of the nerve: the fifth branch, *e*, is exclusively from the ganglionic portion. The trigeminal is in close contact with the acoustic nerve, at their

202



Brain and fifth nerves of the Ray. CCVIII.

origins. In *Cottus*, *Blennius*, *Cobitis*, and *Leuciscus*, the ganglionic or dorsal roots recede from the ventral ones, as they penetrate the medullary substance. The non-ganglionic roots in the Blenny join the facial and glossopharyngeal. Of the five roots of the trigeminal in the Sturgeon, the first, second, and fourth form a

ganglion (Gasserianum). In the Skate (*Raia*) the roots of the two ganglionic portions, fig. 202, *a, b*, of the trigeminal, arise from the restiform tract: the non-ganglionic part, *c*, from the folded or fimbriate part of the tract. A pin is passed between the second ganglionic and the non-ganglionic portion; the latter, *c*, being reflected back on the left side of the figure; on the right side the non-ganglionic branches, *e, f*, are left, accompanying the corresponding branches of the ganglionic portion, *a, e, f*. The acoustic nerve, 7, comes off as a branch of the second ganglionic part of the trigeminal.

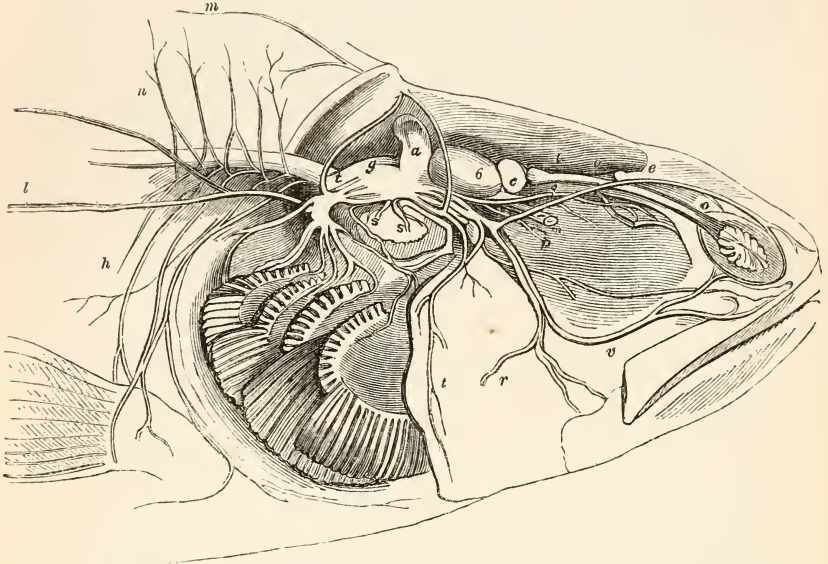
In Osseous Fishes the hindmost branch of the fifth nerve divides, one part descending to the 'opercular' nerve, fig. 203, *t*, the other ascending to the 'lateral' nerve, *ib. m*; but both receiving an accession from other sources to form those nerves respectively. A branch of the vagus, fig. 202, *t*, ascends forward to join the fifth in forming the dorsal division of the 'nervus lateralis,' *ib. m*, which escapes by a foramen in the parietal bone; the rest of the fifth emerges from the skull by a hole (Carp), or a notch (Cod), of the alisphenoid. The lateral nerve in the Cod is formed chiefly by the fifth, fig. 196,  $\frac{5}{2}$ , and receives only a slender filament of the vagus. In the Carp the vagus chiefly forms the lateral nerve. In the Cod, fig. 205, the lateral nerve first sends off a branch, *ib. 1*, which runs along the sides of the interneural spines, receiving branches from all the spinal nerves; it then curves down along the scapular arch, gives branches to the pectoral, *ib. p*, and ventral, *ib. v*, fins, supplies the great lateral muscular masses, *ib. 2*, and the mucous canal, *ib. 3*, and sends a nerve, *ib. 4*, to the interhæmal spines, which communicates with filaments from the corresponding spinal nerves: both interneural and interhæmal branches terminate in the plexus supplying the caudal fin: thus all the locomotive members are associated in action by means of the nervi laterales. The mandibular division of the fifth (*ramus mandibularis*, seu *maxillaris inferior*) consists chiefly of motory filaments which supply the muscles of the hyoid and mandibular arches, and the '*ramus opercularis* seu *facialis*,' fig. 202, *t*, to those of the gill-cover; the sensory filaments go to the teguments of the sides of the head, *ib. r*, and under jaw, enter the dental canal, supply the teeth, and, in the Cod, the symphysial tentacle.<sup>1</sup> The maxillary division (*r. maxillaris*) bifurcates behind the orbit, one branch passes outward to supply the suborbital mucous canals and integuments on the sides of the head; the other, after sending a branch obliquely outward, curves forward along the floor of the orbit,

<sup>1</sup> CCXXVI. p. 45, fig. 2.



ib. *v*, gives off a palatine nerve (*r. pterygo-palatinus*), and supplies the integuments, mucous tubes, and teeth of the upper jaw. The super-orbital division, ib. *e*, gives off the two ciliary nerves, one

203



Cerebral nerves, Perch. XXIII.

of which joins the ciliary branch of the third; it supplies the olfactory sacs, and the integuments of the upper and fore part of the head.

In the Skate the large sensory branches of the fifth, sent to the integuments, and to the singularly developed mucous canals, have ganglionic enlargements near their origins, fig. 202, *a*, *b*, where they leave the main trunk. The first electric nerve is given off by the fifth in the Torpedo, fig. 139, *5*, and many of the terminal filaments of the tegumentary branches of the fifth are connected with the peculiar muco-ganglionic corpuscles, described at p. 324, fig. 215.<sup>1</sup> In the Sturgeon the snout and its tentacula are supplied by branches of the infra-orbital, not from the supra-orbital, division of the fifth; the opercular or facial branch supplies, in addition to the gill-cover, the integuments and lips of the protractile mouth, and the pseudobranchia: it communicates with the glosso-pharyngeal.

In the Lancelet the fifth nerve, fig. 169, *ob*, distributes many filaments to the expanded sensitive integument which represents

<sup>1</sup> LXXVII.

the head, and forms the sides of the wide oval opening; it also supplies the oral tentacula. In the Myxinoids the same nerve supplies both the muscles and the integuments of the head, the tentacula, the nasal tube, the mucous membrane of the mouth and tongue, the hyoid and palatal teeth, and the pharynx. The trigeminus supplies the same parts in the Lamprey, but in a more compact manner, i. e. by fewer primary branches: that which sends filaments to the rectus externus and rectus inferior of the eyeball is continued forward beneath the skin and resolves itself into a rich plexus, which supplies the thick cirrate border of the suctorial lip: the nerves to the muscular parts of the jaws and tongue arise distinct from the fifth, and their trunk may be regarded as a 'facial' nerve; one of the filaments of this joins a branch of the vagus to form a short 'nervus lateralis.'

Thus in reference to the motor filaments of the trigeminus or great spinal nerve of the head, those that form the portio dura or facial nerve in higher Vertebrata are not distinct from the rest of the trigeminus at its apparent origin, except in the Lamprey; in which, on the other hand, the motory filaments of the rectus externus, forming the sixth nerve of higher Fishes and Vertebrates, retain an associated origin with the trigeminal. The 'facial' part of the operculo-lateral division of the fifth, in the Perch,<sup>1</sup> is that which supplies the mandibular, opercular, and branchiostegal muscles. In the extended medulla oblongata of the Sander (*Lucioperca*) the facial nerve has a distinct origin between the trigeminal and acoustic.

The *acoustic* nerve appears to be a primary branch of the fifth, in the Skate, fig. 201, 7: its distribution on the labyrinth is beautifully shown by Swan in LIV. pl. x. fig. 2. It communicates on the great otolithic sac with a motor branch from the vagus, which, after giving filaments to the posterior semicircular canal, passes out to supply the first and the adjacent surface of the second gill, and the faucial membrane. Swan calls this branch the 'glossopharyngeal,' and says, 'this nerve, on being touched near its origin in a recently-dead animal, immediately produces a contraction of the muscular appendages of the gills' (ib. p. 41). In the Cod the acoustic nerve, fig. 185, 7, which here as in all fishes above the *Dermopteri* is of large size, rises close behind, but distinct from, the fifth pair, ib. 5, between it and the vagus, ib. 8: the acoustic nerve receives a filament from the vagus, extends in a crescentic form, fig. 196, s, upon the labyrinth, expands upon

<sup>1</sup> XXIII. tom. i. p. 325, pl. vi. fig. v.  $\mu$ .

the large sac of the otolite, *ib. i*, and sends filaments to the ampulliform ends of the semicircular canals. In other Osseous Fishes (Pike, Blenny) the acoustic blends at its origin with the back part of that of the fifth: it sometimes communicates with the opercular branch of the fifth, as well as with the glossopharyngeal of the vagus. Its division on the acoustic sac is shown, in the Perch, at *s, s*, *fig. 203*.

The *nervus vagus*, *ib. t*, has a development proportional to the extent and complexity of the branchial apparatus in Fishes, and is usually larger than the trigeminal: it rises, *fig. 185, s*, from the restiform tract forming the side of the medulla oblongata, and commonly from a specially developed lobe; and is distributed to the branchial apparatus, the pharynx and pharyngeal arches, the œsophagus and stomach; it sends filaments to the heart, and to the air-bladder when this exists; and it forms, or helps to form, the ‘*nervus lateralis*.’ In the Lamprey a portion of the vagus combines with branches of the facial and hypoglossal nerves to form a short side-nerve extending to the middle third part of the body. In *Salmo*, *Clupea*, *Acipenser*, the ‘*nervus lateralis*’ is formed exclusively by the vagus: in the latter, as in *Chimæra*, *Balistes*, *Diodon*, *Cyclopterus*, this nerve is a single longitudinal one: in most bony fishes there are two which run parallel or nearly so. In all these fishes it is continued very far back along the lateral or latero-dorsal region of the body; sometimes lodged deeply in the lateral mass of muscles, *e. g.* *Belone*, *Clupea*, and *Scomber*,<sup>1</sup> but more commonly the nerve or a main branch lies just under the skin, and in the course of the lateral mucous line, as in the Salmon and Sturgeon; in the Flat-fish and Bull-heads it has both a deep-seated and a superficial branch. In *Upeneus* the superficial branch is sent off, dorsad, at an open angle from the main trunk, to the lateral line, above which it runs in the *Belone*, the superficial branch descends to gain the lateral line. In the Carp and Herring the vagal ‘*ramus lateralis*’ sends off a strong branch to the dorsal fin; in the Garpike it sends, as in the Cod, branches to the pectoral and ventral fins; it distributes other branches to the skin and mucous ducts; and some of these, in most fishes, anastomose with branches of the spinal nerves, *fig. 205*. In the Perch there are two ‘*nervi laterales*’ on each side; the dorsal one, *fig. 203, m*, above described, and the proper lateral nerve, *ib. l*: this is formed exclusively by the vagus, and divides into a superficial branch, supplying the lateral line, and a deep-

<sup>1</sup> xx. vol. iii. p. 49, prep. no. 1384 (mackerel).

seated branch, communicating with the spinal nerves, and supplying the myocommatal aponeuroses and the skin.<sup>1</sup> Whether the vagus forms the whole or a part of the 'nervus lateralis,' this does not arise like the 'nervus accessorius' of higher Vertebrates, from a motory tract of the myelon, but from a ganglionic part of the vagus. The 'nervus lateralis' chiefly supplies the skin, mucous line, intermuscular septa, and vertical fins, most of them peculiarly ichthyic parts, either by their preponderating development, or their very existence.

The vagus sends supra-temporal branches to the head, and opercular branches to the gill-covers. The usually double roots of the nervus vagus pass out, in most Fishes, by a single foramen in the exoccipital bone. The fore part of the root is the largest, and is ganglionic: it is the true pneumo-gastric, supplying the gills, pharynx, heart, and stomach, and sending filaments to the septum dividing the branchial from the abdominal cavity. In the Tunny the branchial nerves are remarkable for their size and their radical ganglions. The hinder second origin is the source of the glosso-pharyngeal and lateral nerves. The former, which has a distinct ganglion in the Herring and some other fishes, supplies the first gill and contiguous parts, and thence passes forward to the tongue. Some filaments rising behind the vagus have been traced to the parts surrounding the brain within the cranial cavity.<sup>2</sup> Each vagal nerve of the Sturgeon equals the spinal chord in size, and rises by numerous roots. The nerve has a like extensive tract of origin in the Sharks; in which a posterior fasciculus, fig. 187, 8, representing the 'nervus accessorius,' can be best demonstrated.

There is no 'nervus lateralis' in the Myxinoids, but the gastric branches of the vagus are continued, united as a single nerve, along the intestine to the anus. The vagus is represented in the Branchiostoma by a branch sent from the fifth to the pharynx. In the Myxine its origin is close to that of the fifth. The erectile palatal organ of the Cyprinoids is wholly, and the electric organs of the Torpedo are, in great part, supplied by this remarkable vagal nerve. The proportion of grey to white filaments in the vagus of Fishes is greater than in that nerve in higher Vertebrates, which illustrates the progressive differentiation of the great sympathetic.<sup>3</sup>

The *first spinal*, or myelonal, nerve rises usually by two roots, the dorsal one having a ganglion, rarely by non-ganglionic roots exclusively from the prepyramidal tracts: it usually emerges

<sup>1</sup> XXIII. tom. i. pp. 325-27.

<sup>2</sup> CCXXVII.

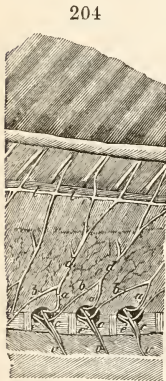
<sup>3</sup> CCXII.



between the ex-occipital and the atlas, and divides into a small dorsal and a larger ventral branch: this communicates with the ventral branch of the next spinal nerve, and supplies the pectoral fin-muscles, the subcoradoideus, 1, the retractor hyoidei, *c*, and geniohyoidei, 27, fig. 135. It is called 'hypoglossal nerve' by some Ichthyotomists; but this name more properly applies to a nerve which, in some fishes, arises from the medulla oblongata behind the vagus, is distributed to the muscles between the scapular and hyoid arches, and unites with the first spinal nerve.

Each of the spinal nerves has a dorsal or sensory, and a ventral or motory origin; sometimes each rises singly; sometimes, as in the Cod, by two or more filaments, fig. 196. Both sensory and motory roots are long in most fishes: the sensory root is the largest, arises by more filaments, and further back than the motory roots, in the Sturgeon.

In most Osseous Fishes one dorsal root goes to form the dorsal branch of the spinal nerve, and the other dorsal root joins the ventral branch of the same nerve: sometimes the ganglion is formed on the dorsal root of the dorsal branch, as in the Cod; more commonly upon the whole sensory origin of the nerve, where it emerges from the neural canal. In some fishes (Bream and Garpike) the ganglions on the dorsal root are situated in the spinal canal: more commonly (as in the Cod, the Ling, the Sander) the ganglions are external to the spinal canal. In both cases the nerve is increased in size beyond the ganglion and the union of the ventral root. This is well seen in the Skate, in which the ganglions are situated beyond the holes of emergence, and the junction of the two roots takes place quite exterior to the neural canal.



204  
Connections of spinal and lateral nerves, Cod. LIV.

The connection of the roots with the myelon is weaker in Fishes than in air-breathing animals: it is so easily broken in the *Dermopteri* as to have led to a denial of its existence.<sup>1</sup> The peculiar combination of the dorsal and ventral roots of the spinal nerves in Osseous Fishes is well seen in the Cod.<sup>2</sup> The dorsal root sends a filament, fig. 204, *a*, upward, which joins a ventral filament, *b*, from the preceding nerve, and forms the ramus dorsalis, *d*; the dorsal root sends two filaments, *c*, downward, which unite together, and with a ventral filament, *e*, of the same nerve

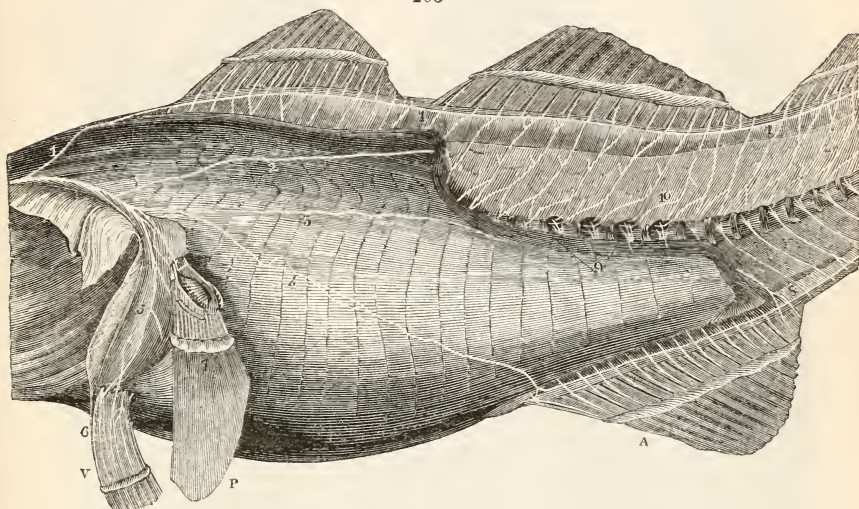
<sup>1</sup> LXXIX. ii. p. 479.

<sup>2</sup> LIV. pl. x.

to form the 'ramus ventralis,' *v*. The filament of the ventral root sent to the ramus dorsalis of the succeeding nerve perforates the lower division of the dorsal root of its own nerve.

Thus each spinal nerve forms a 'ramus dorsalis,' fig. 205, 10, and a 'ramus ventralis,' *ib.* 8; the ramus dorsalis includes a sensory filament of its own nerve, and a motory filament of the antecedent nerve: the 'ramus ventralis' is formed by a motory

205



Lateral nerve and branches, Cod. LIV.

and a sensory filament of its own nerve; both rami 'ventrales' and 'dorsales' are associated together, and with the vagal and trigeminal nerves through the medium of the great 'nervus lateralis,' fig. 205, 1, 8.

The dorsal roots of the nerves distributed to the free, exploratory, pectoral rays of the Gurnards, rise from special ganglionic swellings of the cervical portion of the dorsal myelonal columns.

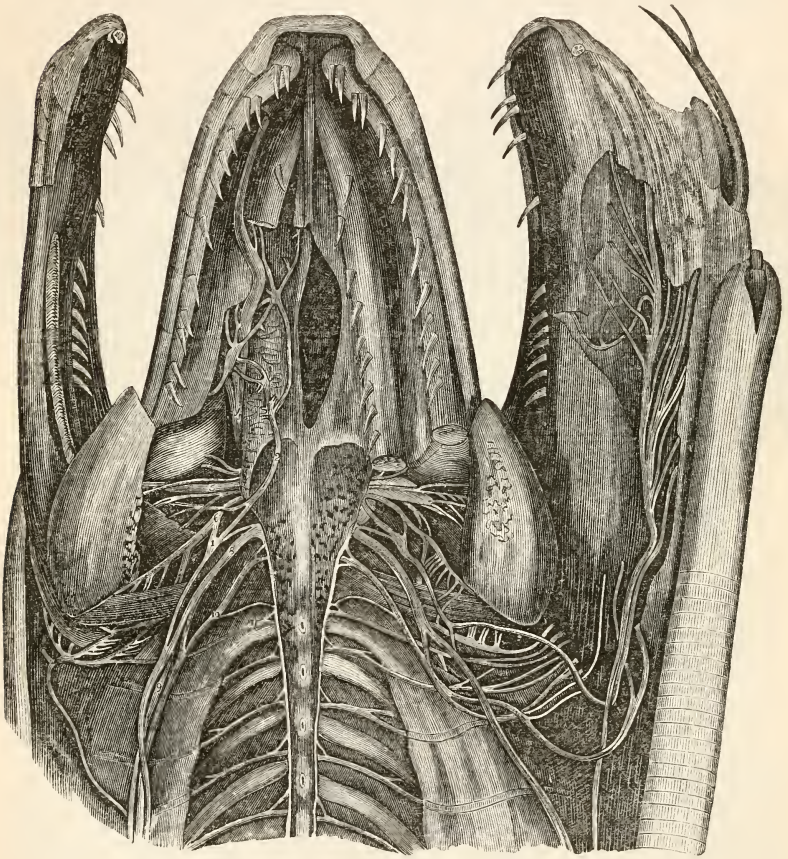
§ 56. *Nerves of Reptiles.*—The olfactory nerves are continued in Reptiles, for a greater or less extent, from the rhinencephalon, figs. 188, 191, to the olfactory sacs; the white and grey tracts beneath the prosencephalon, fig. 190, P, described as roots of this nerve, belong to the rhinencephalic crura: the true olfactory nerves are less distinct from their centres than in other Vertebrates. In the Python, fig. 188, the nerves, 1, of equal diameter with their centres, gradually expand, by resolution of their fibres, as they approach the olfactory sacs, *ib.* *d*, and are joined by part of the first division of the 'fifth.' The olfactory



nerves progressively increase in length in the Turtle, Iguana, and Crocodile. The distribution of their fibres upon the vascular pituitary membrane, supported by the turbinal cartilage, is well displayed in a Hunterian preparation of the Turtle.<sup>1</sup>

The optic nerves, corresponding in size with that of the eyes,

206



Cerebral, anterior spinal, and sympathetic nerves, Python. LIV.

are smallest in the fish-like Batrachians. They arise from the optic lobes, fig. 192, *o*, thalami, and optic tracts, *ib. d*, and blend, by a few decussating laminae, into a chiasma, *ib. b*, before diverging to the visual organ: their course is shown, in the Python, at 2, fig. 188. The position of the 'third' or oculo-motor nerve is

<sup>1</sup> xx. vol. iii. p. 89, nos. 1532, 1533.

shown at 3, fig. 188. The course of the 'fourth' to the upper oblique muscle is shown at 4, fig. 188. This nerve does not exist, separately, in the fish-like Batrachians.

The fifth or trigeminal nerve shows its double (ganglionic and non-ganglionic) origins in all Reptiles, and its threefold primary division very distinctly, in all above the Perennibranchiates. In the Serpent the first division is shown at 5, fig. 188, extending forward beneath the 'fourth' nerve and upper oblique muscle, and above the olfactory nerve and capsule. The second division, fig. 188, 6, fig. 206, 4, after communicating with the sympathetic nerve, divides: one branch supplies the membrane of the mouth and palate; the other passes out by canals in the upper jaw, and terminates on the follicles and substance of the upper lip. The third division, fig. 188, 7, fig. 206, 5, sends branches of its non-ganglionic part to the muscles of the jaws; a large branch enters the dental canal of the mandible, supplies the tooth-capsules, and emerges by three or more divisions: two of these, emerging at the lower part of the mandible, communicate with branches of the 'eighth' and 'ninth' nerves, to be distributed to the muscles and parts beneath the mandibular arch: another gives filaments to the membrane of the mouth as far as the sheath of the tongue; the main continuation, emerging at a foramen near the symphysis, supplies the lower lip.

In the Turtle the first or ophthalmic division of the fifth advances some way in the substance of the dura mater before entering the orbit; it sends a filament to combine with one of the third, to supply the ciliary nerves, without forming a ganglion: it supplies the lacrymal and harderian glands, and is continued to the olfactory fossa. The second or maxillary division quits the third on entering the floor of the orbit, along which it curves, sending from its concavity filaments to the lacrymal glands, and dividing into two chief branches; the internal branch, answering to the spheno-palatine and suborbital, supplies the palate and floor of the nasal cavity, and emerging at the fore-part of the orbit, it spreads upon the maxillary tegument: the external branch passes along the floor of the orbit, and emerges upon the face. The third or 'mandibular' division descends at the back-part of the orbit, in front of the tympanic bone, supplies the temporal and pterygoid muscles, enters the mandibular canal, and distributes branches inwardly to the tongue and floor of the mouth, outwardly to the mandibular follicles and tegument.

In the Frog the maxillary and mandibular divisions of the trigeminal, arising distinctly from the ganglion, diverge to their



respective destinations at the middle of the floor of the orbit: the hindmost branch, continuous with a filament from the acoustic nerve, unites with a branch of the vagus, and is distributed like the 'portio dura' of the 'seventh' nerve. The distinct origin of this nerve, between the 'fifth' and acoustic, is shown in the Python, fig. 188, 8; it communicates, fig. 206, 6, with the ganglion, ib. 1, of the sympathetic, then passes through the 'apertor oris,' to which it gives a branch; communicates with the first spinal nerve, and terminates on the 'costo-mandibularis' muscle. The acoustic nerve, fig. 188, 9, soon divides, and enters the labyrinth by two or more foramina. The glosso-pharyngeal, fig. 188, 10, is distinct at its origin in Serpents and higher Reptiles. In Batrachia it issues from the ganglion of the vagus. In the Python the glosso-pharyngeal passes chiefly to the ganglion, fig. 206, 1, of the sympathetic. The 'nervus vagus,' fig. 188, 11, arises by several filaments, and in the Chelonian and Crocodilian reptiles is recruited by an 'accessorius,' arising from the tract of the first and second spinal nerves. In the Python, fig. 206, 8, the vagus communicates with the sympathetic, and then receives the continuation of the glosso-pharyngeal from the ganglion, 1. It sends a branch to communicate with the 'ninth,' and to be distributed to the muscles and membrane of the fauces. The trunk is then continued down or back, close to the trachea and jugular vein: on the left side it also accompanies the carotid artery: it sends filaments along the large vessels to the heart, and others behind each aorta, similar to the recurrent nerves, to be distributed upon the trachea and œsophagus: each trunk for a short space accompanies the corresponding pulmonary artery to the lung. Before reaching the liver it passes ventrad of the lung for a short distance, and joins its fellow to form a single nerve. This is continued under the capsule of the liver supplying that organ, the lungs, and œsophagus. Near the end of the liver the vagus sends a large branch, which communicates freely with the sympathetic, to the left surface of the stomach, and this also gives filaments to the contiguous part of the lung. The trunk, on the right of the stomach, communicating with the sympathetic, and with the division on the left, is continued a short way on the membrane connecting the viscera, gives branches to the right side of the stomach, and terminates on the beginning of the intestine, at the pancreas.

In the *Chelonia* and *Crocodylia* the vagus quits the skull by two or three of its roots, which unite outside to form the trunk of the nerve; its communication with the glosso-pharyngeal, the ninth,

and the sympathetic, together with its ultimate distribution, are in the main like those in *Ophidia*; it exclusively supplies the heart. In the *Amphisbæna* the accessorius is partially blended with the vagus, and separates from it to be distributed to the cervical muscles, joining branches of the first two spinal nerves. In *Chelonia* and *Crocodylia* the accessorius blends with the ganglion of the vagus: its continuation may be recognised in the posterior branch sent by the vagus to the nuchal muscles.

The 'ninth' or hypoglossal nerve, fig. 188, 12, arises from the motory tract, behind the vagus, from the trunk of which it receives a branch; it receives a smaller branch from the facial nerve; communicates with the anterior cervical nerves; and is distributed to the muscles of the pharynx and tongue, to the forked end of which the lingual branch may be traced. It sends a communicating branch to those of the mandibular nerve, which are distributed to the muscular floor of the mouth. In the Tortoise the hypoglossal escapes by two precondyloid foramina; after the union of these origins the trunk communicates, as in *Ophidia*, with the vagal and glosso-pharyngeal nerves: it sends a branch to the hyoid muscles, a branch forward to the tongue, and a third downward to the omohyoideus: the latter accompanies the vagus as far as the fifth cervical.

The vagus enters in a larger proportion into the formation of the nerve, or rather plexus, distributing branches to the parts to which the source of nervous supply is ascribed to the hypoglossal; but this nerve has a distinct origin by two roots in the Turtle.

The first and second spinal nerves arise, in *Chelone*, like the hypoglossal, by motory roots only; the sensory or dorsal roots in the other cervicals are smaller than the motory ones. The skin of the neck is not very sensitive: the muscles are large and numerous. In the back, where muscles are few and small, the sensory roots of the spinal nerves exceed the motory ones in size.

The nerve which emerges between the first and second trunk-vertebræ in *Batrachia* supplies the muscles and integuments of the subjacent part of the throat, and sends a few filaments to those of the scapula. Four of the succeeding spinal nerves combine in the Salamander to form the brachial plexus: two only form that plexus in the Frog, that emerging between the second and third vertebræ being the largest. In the Crocodile the sixth and seventh cervical nerves, with the two following, combine to form the brachial plexus. In the Turtle the sixth, seventh, eighth, and ninth spinal nerves constitute the brachial plexus.

This distributes a 'circumflex' or axillary, an ulnar, a radial or 'musculo-spiral,' and a median nerve. The circumflex supplies the latissimus dorsi, claviculo-brachialis, supercoracoideus and teres minor, and terminates on the integument at the back of the arm. The ulnar nerve divides at the upper third of the humerus into a branch supplying the extensor communis digitorum, extensor proprius pollicis, and ulnaris externus, a branch for the triceps brachii, and a superficial cutaneous nerve distributed to the integument on the back of the fore-arm and hand. The radial nerve passes to the outer side of the humerus, distributing muscular branches in its course, winds to the inner side, descends in front of the elbow-joint, and terminates in muscular and cutaneous branches. The median nerve passes along the back-part of the scapula, giving branches to the pectoralis major, to the shoulder-joint and surrounding skin: passes between the humeral tuberosities, supplying the triceps brachii and brachialis internus: then divides into an external branch, passing between the pronator teres and radialis internus, and supplying the flexors of the digits, and into an internal branch, gliding between the radius and ulna, and ultimately forming the volar arch.

In the Frog the axillary nerve sends a branch to the muscles and skin above the scapula: it is continued into the brachial, which bifurcates. One branch winds round the humerus, like the 'musculo-spiral,' sends a branch to the extensor cubiti, and passing in front of the elbow-joint penetrates the mass of flexor muscles, and reappears at the outer side of the fore-arm: it sends one branch to the skin, and another to the back of the hand, which divides to supply the same aspect of the digits. The other division of the brachial nerve represents the 'median;' it divides into a larger branch, running along the interosseous furrow of the ulno-radial bone, which supplies the palm and palmar surface of the digits, and into a smaller branch, which supplies the flexor muscles of the digits.

The spinal nerves of the Serpent differ from those of the Eel in the more distinct ganglion on the posterior root, and this rises closer to the anterior root, which is rather larger. Each spinal nerve communicates with the sympathetic, and accompanies the rib, to be distributed to the vertebral muscles and integument, fig. 206.

In the Tortoise, nerves, analogous to the phrenic, are sent from the first three dorsal pairs to the sheets of the diaphragmaticus, fig. 150, 42. Succeeding dorsal nerves communicate with the sympathetic, and send filaments into the substance of the carapace,

most of which pass through, and terminate in the vascular beds of the horny scutes.

The seventh and eighth dorsal nerves, and the three consecutive pairs, contribute to the formation of the crural plexus. The sciatic nerve is formed by the last dorsal and the first two sacral nerves. In the Crocodiles and Lizards the sciatic is formed by but two spinal nerves: in the Frogs and Toads by three, figs. 207, 208.

The crural plexus in the Tortoise sends filaments to the transversalis, fig. 150, 41, and obliquus abdominis, fig. 151, 40; to some of the pelvic muscles and the glutæi; it is then continued into the limb as the 'crural nerve.' The obturator nerve is a direct branch of the last dorsal. The sciatic nerve gives a filament to the second glutæus and to the obturatorius, and continues, as a large trunk, to behind the knee-joint, where it divides into the tibial and peroneal nerves. The tibial subdivides into a popliteal branch, supplying the muscles at the back of the leg and the sole or plantar side of the foot, and into an external branch to the external muscles and integument. In the Turtle (*Chelone*),<sup>1</sup> one division of the sciatic gives branches to the muscles of the thigh, and is continued to the plantar surface of the foot, dividing into digital nerves, terminating on the skin; the other division, after giving off some muscular branches, passes to the skin on the dorsal surface of the fin.

In Lizards the crural nerve is formed by the two lumbar nerves, and is distributed to the muscles on the fore-part of the thigh; the sciatic nerve is formed by the last lumbar, the two sacral nerves, is continued along the inner side of the thigh, supplying the muscles as far as the digits, and branching to accompany them.

In the Frog a pearly vesicle, with calcareous molecules, covers each spinal nerve where it comes out of the spinal canal. Of the four pairs of nerves which proceed from the termination of the short myelon, three constitute on each side the 'sciatic plexus,' which unites into a single large nerve opposite the acetabulum. The sciatic nerve enters the muscles at the back-part of the thigh, supplies them, and divides near the knee-joint into an external and internal branch, distributed to the muscles, digits, and skin of the hind-leg and foot.

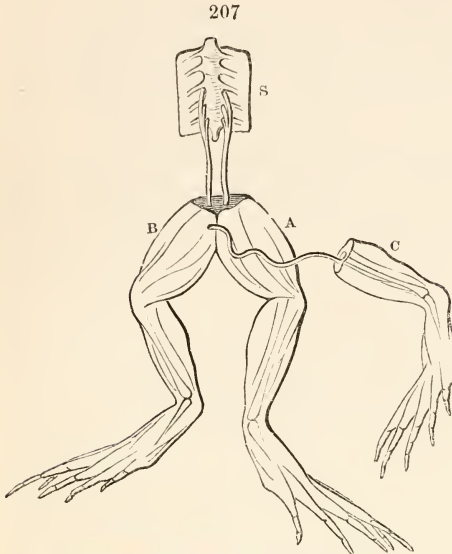
The tenacity of vital force in *Hæmatoerya*, and the seemingly peculiar susceptibility to the voltaic current in the Frog, have made that animal the usual subject of the experiments exemplifying

<sup>1</sup> LIV. pl. xvi.



relations between the electrical, nervous, and muscular forces. It may be convenient, therefore, to some readers to find here, in connection with the nervous system of the *Batrachia*,

an account of the chief modes of preparing it for the purpose of such experiments. Galvani removed the skin from the hinder part and limbs of the frog, exposed the lumbar plexus, leaving it in connection with the part of the spine from which the nerves issued, and cut away all the parts save the trunks of the sciatic nerves, between the spine, s, and the hind limbs, A & B, fig. 207. So prepared, it is usually called 'Galvani's frog.'



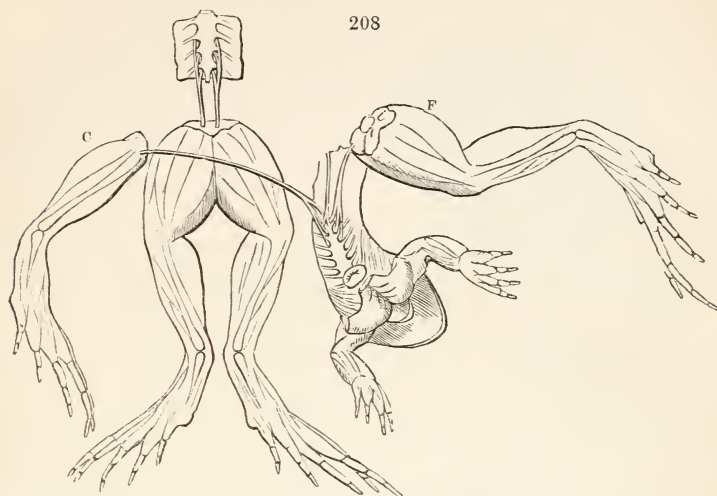
Galvani's frog, and the galvanoscopic leg. ccv.

The 'galvanoscopic leg,' fig. 207, C, is prepared by skinning it, dissecting out the sciatic nerve from among the muscles at the posterior part of the thigh, then amputating the leg just above the knee-joint, leaving the nerve connected with the leg, C.

If the nerve of C be laid upon the muscles of either leg of Galvani's frog, A or B, and if these muscles are excited to contraction, by pricking the myelon in s, the muscles of the galvanoscopic leg, C, will be simultaneously contracted. If a second galvanoscopic leg be prepared, and the nerve be laid upon the muscles of the first, and a third be placed in the same relation with the second, contractions will take place in all three legs, when the thigh-muscles of the Galvani's frog, A & B, are excited to contract. This 'induced contraction' cannot be extended to a fourth galvanoscopic leg.

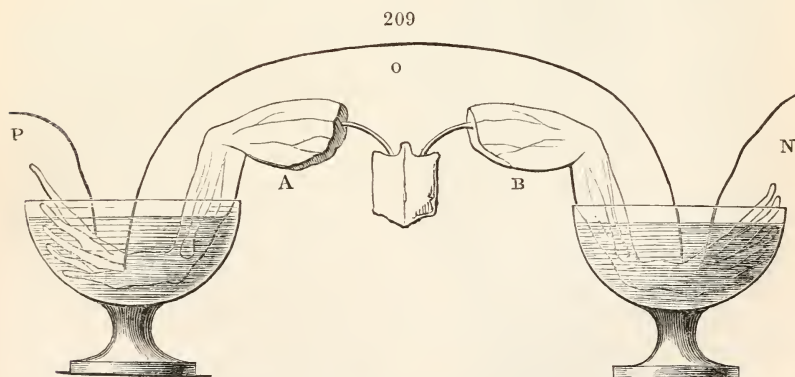
If the nerve of the galvanoscopic leg be left in connection with the rest of the frog's body, and the nerve be laid across the thighs of a 'Galvani's frog,' as in fig. 208; these being excited to contract, not only the galvanoscopic leg, C, but the opposite leg, F, contract; the one by direct stimulus of the sciatic nerve, the other by stimulus of the myelon from the inferent or 'sensitive'

fibres of the nerve, C, reflected upon the limb, F. In short, that muscle will contract when the stimulating current has its origin in a source external to that body.



Galvanoscopic leg, C, in connection with the rest of the frog, F, laid across a 'Galvani's frog.' ccv.

Immerse each leg of a 'Galvani's frog' in a cup of water, the positive wire, P, of a voltaic battery being placed in one cup, the negative wire, N, in the other, as in fig. 209. In



Frog, as prepared by Galvani. P, positive wire: N, negative wire: of the battery; O, connecting wire of the two vessels.

the limb A the current runs in the reverse direction of that of the volitional nervous force: in the limb B it runs in the same direction. After the voltaic current has passed a short time through the nerves, contractions occur in the limb B, not in

the limb A, in 'making' the current, or completing the circuit; whilst contractions occur in the limb A in 'breaking' the current, as by removing one of the wires: the limb in which the current is direct contracts on making the current; the limb in which the current is inverse contracts on breaking the current. It needs only to leave one wire in the water, and to remove or introduce the other, in order to 'break' or 'make' the current. If the two vessels be further connected by a conductor of copper wire, as at O, fig. 209, contractions of both limbs take place on both making and breaking the connection.

Neuricity<sup>1</sup> is not electricity, any more than is myonicity; both are peculiar modes of polar force. Any point of the surface of a nerve is positive in relation to any point of the transverse section of the same nerve, just as any point of the surface of a muscle is positive in relation to any point of the transverse section of the same muscle.<sup>2</sup> Ligature of a nerve arrests the nervous current, not the electric current; a divided nerve connected by an electric conductor transmits the electric current; but the nervous current excited by stimulus above the section is arrested by the electric conductor. Neuricity is convertible into myonicity and into other forms of polar force, just as myonicity or the muscular force may be disposed of by conversion into heat,<sup>3</sup> electricity,<sup>4</sup> and chemicity, the latter shown by the evolution of carbonic acid.<sup>5</sup> Molecular change, in nervous and in muscular fibre, attends the exercise of their respective forces.

§ 57. *Sympathetic system.*—This consists of one or more ganglia, usually a series of such arranged on each side of the vertebral centres from near the occiput to the opposite end of the abdominal cavity, or to the anterior caudal vertebræ. Where the ganglia are numerous they are connected in each lateral series by a band of nervous fibres, and resemble a pair of gangliated cords. These communicate with the contiguous spinal nerves, and with the cranial nerves, usually through small ganglia in different parts of the head, fig. 206. At the caudal end the two sympathetic cords usually unite with a single ganglion in the under or fore part of the body of the anterior caudal vertebra.

A sympathetic ganglion is a body connected with bundles of nerve-fibres, the chief proceeding to or from it in the direction of its axis, the smaller nerves diverging more or less transversely.

<sup>1</sup> 'Vis nervosa,' 'Nervous force,' 'Nervous fluid;' it is in relation to the latter name, expressive of an exploded idea, that the term 'current' is still used in reference to the course of the polar force, whether nervous, magnetic, or electric.

<sup>2</sup> CCXI.

<sup>3</sup> CCIX.

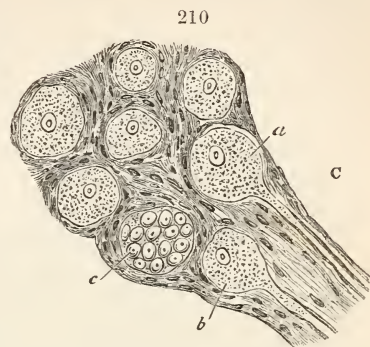
<sup>4</sup> Ib.

<sup>5</sup> Ib.

It consists of 'ganglionic corpuscles,' or ganglion-vesicles, fig. 210, *a, b, c*, and nerve-fibres, imbedded in a nucleated fibrous tissue.

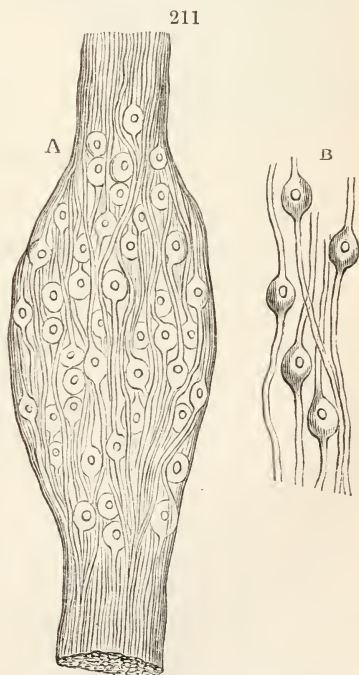
The ganglion vesicle may be circumscribed, or be continued into a nerve-fibre, or into two nerve-fibres from opposite poles of the vesicle; it is termed accordingly 'apolar,' 'unipolar,' and 'bi-polar:' the last is the most common form, the first probably a genetic stage. When a ganglion-cell is connected by more than two processes with nerves, it is a 'multipolar cell:' these are most common in the ganglia of the main cord of the sympathetic; the bipolar cells prevail in the ganglia of the posterior roots of the spinal nerves, fig. 201. The nerve-fibres in ganglions consist of the 'white' or broader kind, and of the 'grey' or finer kind; there are also still more minute but solid or homogeneous fibres, surrounding and connecting the true nervous constituents of the ganglion. A nerve on entering a ganglion breaks up into its component fibres, which interlace about the ganglion-cells, sometimes winding round them, with plexiform interchanges of fibres from other entering nerves and from the cells.

Bidder and Volkman<sup>1</sup> give the subjoined magnified view, fig. 212, of the 'intercommunicating' nerve-fibres between a sympathetic ganglion and a spinal nerve in the Frog. *HP* is the sympathetic, *H* showing the part next the head; *CP* is the spinal nerve, *C* showing the part next the myelon; *a* is a



From the sympathetic (gastric) ganglion of the Ray. CCXXII.

in the ganglia of the posterior



A. Spinal ganglion of the Ray, 40 diameters. B. Portion of the same, dissected. CCXXII.

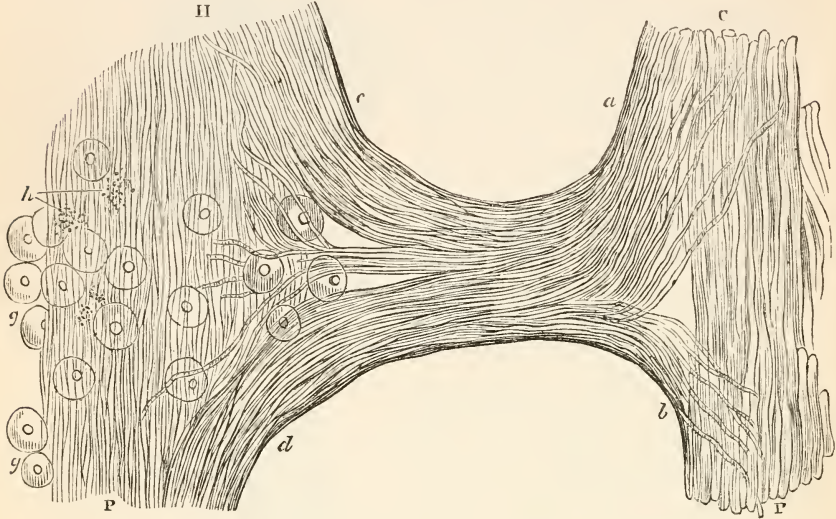
portion of the communicating

<sup>1</sup> CCXII.



branch passing to the myelon; *b*, a portion passing to the periphery; *c*, fibres of the communicating nerve passing in the sympathetic towards the head; *d*, similar fibres passing towards

212



Communication between the sympathetic and third spinal nerve in the Frog. CCXII.

the pelvis; *g, g*, are ganglion-cells; *h*, specks of pigment, which mark the ganglions in the Frog.

§ 58. *Sympathetic of Fishes*.—This system, as being an offshoot or subordinate element of the general myelencephalous series of nerve-organs, is differentiated by progressive steps. In the Myxinoid Fishes it is represented by the intestinal branch continued from the confluence of the two nervi vagi. In Osseous Fishes the visceral plexuses are continued into or connected with slender nerves, accompanying the aorta along the hæmal canal, and representing the trunks of the sympathetic in higher Vertebrates. The first or anterior communication of this nerve, in the Cod, is with a branch of the fifth, and a filament is sent forward to the ciliary ganglion: in the Carp a filament joins the abducent nerve, to which Cuvier thought he had also traced a filament of the sympathetic in the Cod; the sympathetic next communicates with that anterior portion of the vagus (the glosso-pharyngeal) which joins part of the acoustic nerve, and supplies the first partition of the gills; the sympathetic trunks also receive accessions from the trunks of the vagus, and, converging, intercommunicate

by a cross branch: they then send nerves which join the gastric branches of the vagi, in order to form or join a splanchnic ganglion and plexus on the mesenteric artery, from which plexus branches are sent to the intestines, pancreas, and spleen. The sympathetic trunks are continued on each side of the aorta, along the back of the abdomen, into the hæmal canal; communicate, in their course, with the ventral branches of each of the spinal nerves; supply by filaments, usually accompanying the arteries, the kidneys, the generative glands, and the urinary bladder, where this exists; and often, finally, blend together into a common trunk beneath the tail. Ganglions are sometimes found at the junction of the sympathetic with the fifth, as well as at that with the glosso-pharyngeal and with the vagus, before the great splanchnic is formed: small ganglions are more rarely discernible at the junction of the sympathetic with the spinal nerves.

The splanchnic ganglion of the Skate is a large fusiform body, of an ash-red colour; the succeeding ganglia on the trunks of the sympathetic are larger and more constant than in Osseous Fishes; but the intervening chords are semi-transparent.

§ 59. *Sympathetic of Reptiles.*—The trunks of the sympathetic appear, in the Frog, to be formed in a great proportion by contributions from or communications with the spinal nerves; there are, however, slight enlargements at the points of connection, often marked by pigment-cells, in which true ganglion-cells occur, as shown in fig. 212, *h*.

In *Ophidia* the trunks of the sympathetic, conspicuous at the anterior part of the trunk-cavity, on each side the vertebra. bodies, show as little any enlargements where they receive the communicating branches of the spinal nerves as in *Batrachia*. They slightly diverge as they approach the basis cranii, and are reflected outwards to the vagus, forming a conspicuous ganglion at the junction. From this ganglion the sympathetic is continued forward in a canal of the basisphenoid, and forms a small ganglion with a branch of the second division of the fifth; it sends filaments to the membrane covering the posterior part of the mouth and palate, one of which communicates again with the maxillary nerve. From the last ganglion there proceeds ‘another branch forward to form another ganglionic union’ (spheno-palatine) ‘with a branch of the second trunk of the fifth, and from this a branch is sent to the posterior part of the nose, to ramify on the schneiderian membrane; other branches are given to the membrane covering the mouth and palate, and one passes forward and communicates again with a branch of the second trunk of the fifth,

and is distributed on the membrane covering the anterior part of the mouth and palate. It is worthy of remark that the nerves distributed on the membrane of the mouth and nose communicate so many times with branches of the second trunk of the fifth, and their connection is so much greater than in the Turtle; but in this creature the palate is horny, and not so extensive in proportion to the size of the head. 3, prolongation of the sympathetic connected with the trunk of the par vagum, but not directly with the ganglion of the sympathetic; it communicates with the ninth nerve, then passes down the spine, and communicates with the eleven superior spinal nerves; it emerges on each side at the place the superior branches of the vertebral artery enter to distribute branches in the intercostal spaces; it is continued downwards in a very fine plexiform prolongation with the vertebral artery, as far as the origin from the right aorta; it then branches to each side beneath the membrane connecting the viscera with the ribs and spine, and communicates with filaments of the par vagum; it is afterwards continued downwards, receiving a filament from each spinal nerve; in its course it is a very fine nerve, and has not any more ganglia than the first, and those communicating with the second trunk of the fifth; but at different points from which the nerves pass to the viscera, there is an appearance of a delicate plexus: this plexiform structure varies in different parts, and becomes much greater about the beginning of the intestine, where it resembles that corresponding with the semilunar ganglion in the Turtle: near the kidney it assumes the form of a nervous membrane or retina, before it is distributed on the urinary and generative organs. Branches pass from the plexuses with the arteries to the different viscera.<sup>1</sup>

Bojanus describes the sympathetic nerve of the *Emys Europæa* as accompanying the carotid artery into the cranium, and uniting with the vidian and the facial nerves. On issuing from the cranium it is closely connected with the vagus and with the glosso-pharyngeal nerves, so that it is difficult to say whether a superior cervical ganglion exists or not; and as the cervical vertebræ are ribless, there is no 'vertebral canal,' and the nerve is closely connected with the vagus throughout the whole length of the neck. Below the sixth cervical vertebra the sympathetic nerve separates itself from the sheath of the vagus, and becomes connected with a middle cervical ganglion, whence issue filaments that are distributed to the aorta, the cardiac plexus, and the cœliac plexus. Between the seventh and eighth cervical vertebræ is situated the inferior cervical ganglion, like an elongated swelling

<sup>1</sup> XLIV. p. 66.

of the nerve; subsequently two dorsal ganglia occur, and further down, towards the middle of the back, there occurs a third and last ganglion, which furnishes the splanchnic nerve: the remainder of the sympathetic is made up of one or two cords, which, in the sacral region, give off a great number of branches, the divisions of which form the renal, hypogastric, and sacral plexuses.

In the Turtle (*Chelone*) the cervical portion of the sympathetic has the same exposed position, and communications, with the vagus above and the axillary plexus below, sending off filaments also to the arteries. The branch accompanying a division of the carotid in a canal at the base of the skull gives a filament to the portio dura, and communicates with the maxillary part of the fifth, to terminate on the back part of the palate. Another branch enters with another division of the carotid into the reticular sinus close to the auditory meatus, and communicates with the portio dura, glossopharyngeal, and ninth nerves. In the trunk-cavity, the sympathetic passes from ganglion to ganglion as two cords, a thick and a fine one, neither of which passes behind the neck of the rib; the intercommunicating branches with the spinal nerves are perforated by an anterior branch of the intercostal artery. The chief nerves given off from the sympathetic form two plexuses, in the place of the 'semilunar ganglia' of mammals: the smaller plexus sends filaments along the cœliac artery to the stomach, the larger plexus along the mesenteric artery to the intestines. Other branches pass to the kidneys, and the communications with the spinal nerves mark out the delicate prolongation of the sympathetic to behind the rectum.

In the Crocodile the cervical part of the sympathetic lies in the 'vertebral canal,' or between the neck and tubercle of the rib, and the ganglions are more distinct where the communications with the spinal nerves occur, from the cervical to the lumbar region. The interganglionic longitudinal trunks are two, one passing behind the neck of the rib where it exists, at the fore-part of the chest. The longitudinal trunks converge, and unite upon the beginning of the caudal artery. There is much pigmental matter upon the sheaths of the ganglions and nerves.

§ 60. *Appendages of the Nervous System.*—Certain nerves, as those of the palm and sole in Man, and those of the mesentery in other mammals, have peculiar corpuscles appended to them, called 'pacinian,' after their discoverer. Fig. 213 shows one of the nerves of the palm with the corpuscles appended, of the natural size. Those in the mesentery of the cat are numerous, conspicuous, and favourable subjects for microscopical investigation. They show

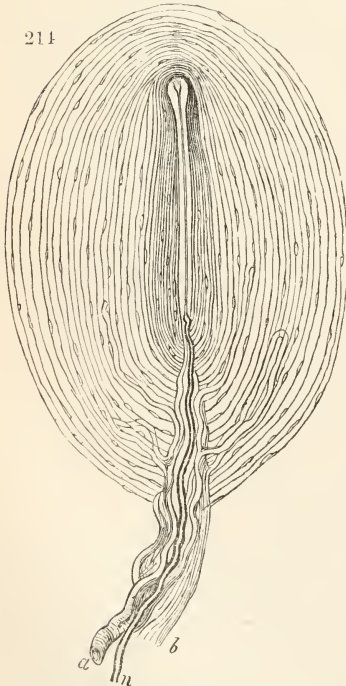


a pedicle and capsule, with a canal and central cavity. A single nervous fibre, fig. 214, *n*, leaves its fasciculus with a portion of the nerve-sheath, *ib. b*, and proceeds to the centre of a series of concentric capsules, of a nucleated fibrous tissue. The nerve, *n*, on entering the central cavity, loses its white substance, and, at the opposite end of the axial cavity, terminates by a tubercular enlargement. An arterial twig, *a*, accompanies the nerve-fibre along the pedicle, and divides into capillaries, which form loops in some of the intercapsular spaces. The central cavity contains a clear fluid: it varies much in shape.



Nerve of the palm,  
with Pacinian cor-  
puscles, Human.  
CCXXVIII.

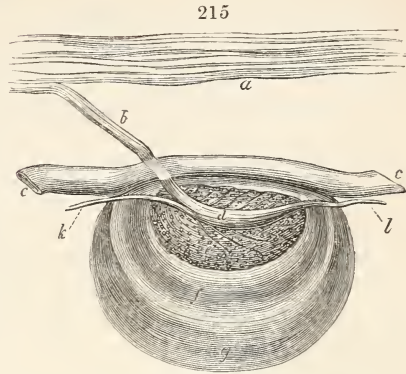
Analogous bodies were discovered by Savi, arranged in linear series, bordering the anterior part of the mouth and nostrils, and extending over the surface of the fore-part of the electrical organs in the Torpedo; they are appended to and appear to be terminal developments of the filaments of the fifth pair of nerves. Each follicle, fig. 215, is formed of two larger capsules, *f* and *g*, which adhere together near the fibrous band, *c, c*, supporting and fixing the organ; it contains a granular substance, *e*, on which lies the nerve-twig, *b, d*, transmitted from the nerve, *a*. This twig commonly receives a smaller anastomosing filament, *k*, from a contiguous follicle. Sometimes two nerve-twigs pass from the main branch to the same follicle, in which case it contains two distinct granular masses. These follicles are developed from ganglionic or sensory branches of the fifth nerve. No proper pacinian corpuscles have been observed in connection with this nerve, nor with the glosso-pharyngeal, the portio dura, or any purely motor nerve.



Pacinian corpuscle, on mesenteric nerve of cat.  
Magn. CCXXIX.

Besides the savian corpuscles

the Torpedo has a system of mucous organs in intimate connection with nerves of sensation: but this is common to it with other Plagiostomes. The system commences, in the Torpedo, by groups of globular vesicles, fig. 139, M, arranged symmetrically, outside the electrical organs, from which tubes are continued in parallel bundles until they separate themselves to perforate the skin, and terminate by orifices, some at the dorsal, some at the ventral surface of the head. A branch of the ganglionic part of the fifth expands upon the ampulliform commencement of each of the muciferous tubes. Similar organs exist in Sharks. Hunter placed first in the series of specimens of organs of touch in Fishes the snout of the Spotted Dog-fish (*Scyllium*), 'to show the manner of the nerves ramifying, as also their apparent termination in this part, each ultimate nerve appearing to terminate in the bottom of a tube or duct, the sides of which secrete and convey a thick mucus to the skin.'<sup>1</sup> Jacobson compares them to the whiskers in the Cat. Besides the rostrum, these nervo-mucous organs are situated upon the sides and under part of the head, and on the fore part of the trunk; they are crowded between the masseter, fig. 132, *l*, and the branchial openings, *ib. q*, where they separate into two groups, one diverging downward, forward, and backward, to beneath the pectoral fin; the other directed upward, forward, and backward, to the occiput.



One of the follicular nervous organs of the Torpedo.  
Magn. LXXVII.

§ 61. *Organ of Touch in Hematocrya.*—In the *Dermopteri*, the *Anguillidæ*, Siluroids, and a few other Fishes, with the integument wholly or in part scaleless, or with very minute and delicate scales, lubricated with mucus, the whole or major part of the external surface may be susceptible of impressions from the surface of extraneous bodies coming in contact therewith. But in the majority of the class the exercise of any faculty of touch must be limited to the lips, to parts of certain fins, or to the specially developed organs called 'barbules.'

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<sup>1</sup> xx. vol. iii. p. 55, prep. no. 1395.

Such an organisation of a fold of skin bordering the mouth as implies the tactile faculty is rare in Fishes; the Cyprinoids exemplify it, and more especially many of the Indian species: also the marine family of Labroids. In the Sturgeon the lip has numerous papillæ, and more minute papillæ occur on the lips of many fresh-water fishes. In the Eels the upper lip is richly supplied by the fifth nerve, and the upper lip of the Lepidosiren is papillose. The soft skin of the sucking-lip of the Lamprey is well supplied with a reticulate arrangement of sensitive filaments from the fifth; its margin is papillose, fig. 277. The associated pectoral and ventral fins, forming the sucker in the Lump-fishes, have a texture of the applied surface, which seems adapted to receive impressions from the part it touches, whereby the fish may ascertain its fitness or otherwise for the application of the anchoring organ.

The pectoral fins seem to be applied occasionally to explore the nature of the bed of the water inhabited by the fish; and in the Gurnards (*Triglidæ*) three soft flexible rays are detached from the fin, like fingers, fig. 82, and the large nerves supplying them have ganglionic enlargements at their origins. The filiform radial appendages of the *Polynemidæ*, and the prolonged ventral fins of *Ospromenus*, *Trichogaster*, and other Labyrinthibranchs, and of the Ophidiidæ, enter into the present class of organs. The barbules are long, slender, pointed processes of the skin, either median or in pairs: the former are limited to the under jaw, as in the Cod; the latter may be developed from both jaws, and are called, according to their position, 'premaxillary,' 'angular,' 'nasal,' &c. They are commonly found in the grovelling fishes, such as the Sheat-fishes, Loaches, Barbels, Sturgeons, fig. 123, *b*, or in the parasitic Myxines, fig. 248. The nerves supplying the barbules are large and derived from ganglionic divisions of the fifth pair. A Cod, blind by absence or destruction of both eyeballs, has been captured in good condition; and it may be supposed to have found its food by exploring with the symphyseal barbule, as well as by the sense of smell.<sup>1</sup> The sublingual filament of many *Uranoscopinæ*, and the rostral tentacle of *Malthe* and *Haliutea*,<sup>2</sup> may also exercise a tactile faculty. The limbs of Lepidosiren, fig. 100, have the general form rather of organs of exploration than of locomotion.

The scaleless condition of the skin in *Batrachia* makes it more

<sup>1</sup> xcviii. p. 72.

<sup>2</sup> clxxiv. iii. p. 204. The homologous organs in *Lophius* seem to act as bait, to attract small fishes.

susceptible of impressions than in higher *Reptilia*; the discoid expansions of the toe-ends in *Hyla*, and the filamentary appendages of the toes in *Pipa*, may have more sense of feeling than other parts, but seem not to be applied in active touch. The labial papillæ of larval Frogs are so placed and supplied by nerves as to suggest a tactile function. Certain Ophidians, e.g. *Herpeton tentaculatum*, have a pair of tentacular appendages upon the snout: but the long, extensile, forked, filiform tongue seems to be used rather as an organ of exploration than of taste in most Serpents, and in the slender-tongued Lizards. The expanded toes of Geckos, fig. 162, the short, thick, scansorially-opposed digits in Chameleons, and the concave surface of their prehensile tail, although mainly modifications for locomotive purposes, may well be supposed to have a surface more sensitive than other parts of the body. The snout-like production of the upper lip in *Trionychidæ* and *Chelys*, with the subsidiary tegumentary productions of the head in the latter, are probably more direct and active instruments of tactile exploration in these soft-skinned, mud-haunting, and chiefly nocturnal *Chelonia*. Some nocturnal Tree-Snakes (*Dryophys*, *Passerita*) have a prolonged snout.

§ 62. *Organ of Taste in Reptiles.*—The glosso-hyal, fig. 85, 42, does not support, in Fishes, an organisation of soft parts for a special sense of taste: and the description of the tongue and other projections and structures in the interior of the mouth will be given in connection with the preparatory digestive organs. A tongue, as a gustatory organ, is as little developed in the perenni-branchial Reptiles, and is absent in the marsupial Toads (*Pipa*). There is as little trace of tongue during most of the larval period in other *Anura*; but, about the time when the fore limbs are in bud, the membrane covering the basihyal begins to develop vascular fungiform papillæ, with looped capillaries and muscular fibre: the whole mass growing and extending from before backward, and constituting the retroflexed tongue, by the time the tail is atrophied. The free part is usually bifid or bilobed. It is mainly an organ of prehension, and will be described as such, together with the tongue of the Chameleon, in connection with the organs of nutrition. In the thick-tongued Lizards, e.g. *Iguana tuberculata*, the dorsum and sides of the tongue are minutely papillose; in *Tiliqua scincoides* they are coarsely papillose: both the food and the teeth of these *Sauria* indicate a certain amount of mastication, with which the sense of taste is correlated. In most *Reptilia* the food is bolted entire. In the Tortoise (*Testudo indica*) the tongue is beset with numerous elongated and pointed papillæ: in the Turtle (*Chelone*



*mydas*) the tongue is wrinkled and devoid of papillæ. In the Crocodiles the tongue has no projecting extremity, and is but slightly raised above the level of the membrane which attaches its circumference to the mandible: but its dorsum is marked by a group of follicles and increased vascularity of that part of its surface.

§ 63. *Organ of Smell in Hæmatocrya*.—The essential character of the organ of smell, in Fishes, is the pituitary membrane lining a sac with one or more apertures upon the external surface; and that, in the few exceptions in which it is extended into a canal communicating with the mouth or fauces, such naso-palatine canal is never traversed by the respiratory medium in its course to the respiratory organs.

The extremities of the olfactory nerves, fig. 203, *o*, expand upon the pituitary membrane, which is highly vascular, and is covered by ciliated epithelium: its extensive surface is packed into the small compass of the olfactory capsule by numerous folds. The capsule is formed by a fibrous membrane, which is sometimes supported by a cartilaginous, and more frequently by an osseous, basis, called the ‘turbinal bone,’ fig. 81, 19.<sup>1</sup>

In the *Dermopteri* the olfactory organ is single: Kölliker<sup>2</sup> regards as such a small, blind, tegumentary depression, fig. 169, *ol*, beset with vibratile cilia, and connected with the anterior end of the quasi-brain of the *Branchiostoma*. The more obvious and satisfactorily determined olfactory organ of the *Ammocete* is in the median line, opening above the mouth in front of the brain-sac, fig. 59, 19, whence a narrow canal is produced backward from the bottom of the sac to the base of the skull. In the Myxine the parietes of the olfactory canal are similarly situated, lined by a longitudinally-plicated pituitary membrane, and are strengthened by cartilaginous rings, like a trachea. The naso-palatine tube opens backward upon the roof of the mouth, and this opening is provided with a valve. In the Lamprey the flask-shaped nasal sac, fig. 61, *k*, opens upon the top of the head: a simple membranous tube is continued from the expanded bottom of the sac, which dilates as it descends, but terminates in a blind end at the hypophysial vacuity, fig. 60, *hy*, of the base of the skull, where the mucous membrane of the palate passes over it entire and imperforate.<sup>3</sup>

In all Fishes, save the *Dermopteri*, the olfactory organs are double, and they have no communication with the mouth. In

<sup>1</sup> LIV.

<sup>2</sup> XXXII. p. 32, pl. ii. fig. 5, A.

<sup>3</sup> XXI. pl. 43, figs. ii. & iv.

Osseous Fishes they are situated on the sides of the snout, in a cavity formed by the nasal, fig. 75, 15, the prefrontal, 14, the lacrymal, 73, the premaxillary, 22, and the vomer. The capsules are covered externally by the skin, which is usually pierced by two openings for each sac: the Chromides, and all the Wrasses with ctenoid scales, have a single opening for each nose-sac; where there are two nostrils the posterior is usually open, the anterior closed, as by a sphincter or a valve: the anterior aperture is often produced into a tubular process, as in the Loach, which acts, either by muscular power or by some modification of form, as a valve. Both apertures in some Lophioid Fishes are bell-shaped and pedunculate. In some Siluri a tentacle is continued from the external nasal tube. When the nasal sac is round, the pituitary plicæ radiate from its centre: when the sac is elongated, it is usually traversed by an axial partition with a row of folds on each side; and there are transitional arrangements, as in the Perch, figs. 131, *ol*, & 134. In a few Fishes these folds are further complicated by secondary processes. The Sturgeon presents the radiated type of the olfactory organ with secondary folds, fig. 125, 19, but, like the Polypterus and Lepidosteus, each nasal sac has a double aperture: the Lepidosiren has an elongated nasal sac, with the biserial arrangement of pituitary folds, and with two apertures, fig. 186, *ol*, upon the under part of the thick upper lip, but neither of these communicate with the mouth. In some Osseous Fishes the olfactory sac is divided into a plicated and a smooth part: the former exercising the sense-function, the latter that of a reservoir. In the Mackerel this extends down to the palate: in the Wolf-fish the reservoir passes backward, expanding, as far as the back part of the palate, where it ends blindly. The prolongation of the single nasal cavity in the Lamprey is analogous to this.

In the Plagiostomes the nasal cavities are situated beneath the snout, in the Sharks, figs. 30 & 63, *b*: beneath the fore part of the head, behind the base of the rostrum, in the Saw-fish (*Pristis*), fig. 65: or near the angles of the mouth, as in the Chimæra and the Rays, where a groove extends to the mouth. Each olfactory cavity has a single and commonly wide opening, defended by valvular processes, supported by peculiar cartilages more or less intimately connected with the proper olfactory cartilaginous sacs, and representing the superadded cartilages of the 'alæ nasi' in higher Vertebrata.<sup>1</sup> They have their proper muscles: whence we must conclude that these Fishes scent as well as smell, i. e. actively

<sup>1</sup> See the description of these 'nasenflügelknorpel' in *xxi*. p. 171.

search for odoriferous impressions by rapidly changing the current of water through the olfactory sac.<sup>1</sup>

The *Protopteri* show no outward signs of olfactory organs: the thick upper lip must be raised to bring the plicated sac, with its two remote orifices, into view. In *Amphiuma* the external nostrils are minute, approximate, and near the end of the snout. In the Siren and Axolotl the external nostril is conspicuous on each side the snout: the internal one opens outside the series of pterygo-vomerine teeth. In the Siren the maxillary does not extend back so as to divide the internal nostril from the inner or under part of the lip: in the Axolotl it is so extended, and the opening is situated between the maxillary and palatine series of teeth. In these, as in the *Proteus*, the olfactory membrane is plicated at right angles to a longitudinal seam. In the Newts and Salamanders the olfactory membrane is smooth, and lines an oval cavity with an external nostril and a palatal one, the former defended by a little fold of skin.

In tailless Batrachia the external nostril has an inferior flap, endowed with a slight movement: the palatal is widely open, between the palatine and maxillary bones, near the fore part of the mouth. The olfactory membrane is not augmented by any folds or prominences. In the *Pipa* it presents a cylindrical form, and its outer opening is much nearer that of the opposite side than in other Anoura. In *Ophidia* the external nostrils are double; the internal nostril is single and median: the bone and gristle supporting the olfactory sac make some prominences in it; the pituitary membrane is almost black in some Colubers. In *Anguis*, and other snake-like Lacertians, the palatal nostrils open separately.

In the Iguana a single broad turbinal cartilage extends into the olfactory cavity from the outer side, terminating below in two tuberosities. The meatus extends at first longitudinally backward, then bends downward to open upon the palate between the anterior maxillary and the pterygoid teeth. The turbinal projects, with slight modifications of proportion and form in the nasal cavity of other Lacertians. The external nostrils offer varieties of relative size, shape, and position, seldom receding far from the muzzle in existing species. In the extinct Saurians of marine habits, *Ichthyosaurus* and *Plesiosaurus*, the external nostrils opened near the orbits, at a distance from the muzzle. In *Chelonia*

<sup>1</sup> 'Is the mode of smelling in Fishes similar to tasting in other animals? Or is the air contained in water impregnated with the odoriferous parts, and is it this air which the fish smells?'—*John Hunter*, in xx. vol. iii. p. 88.

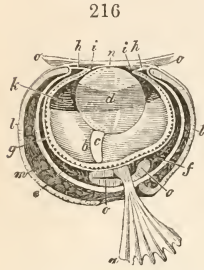
and *Crocodylia*, the external opening to the nasal organ in the skull is single and median, situated at or near the end of the muzzle. But in the *Chelonia* the nostrils are distinct, although approximate, on the integument: in *Trionyx* and *Chelys* they are tubular, continued along a short proboscidiform production of the integument. The septum narium is gristly. In the Turtle (*Chelone*) the nasal cavity suddenly expands to contain the turbinal cartilage. The periosteum of the cavity and the pituitary membrane are both coloured by dark pigment, and the latter is thick and vascular. The palatal orifice is median and single, towards the fore part of the roof of the mouth. In the *Crocodylia* the tegumentary nostril, like the osseous one, is single, crescentic, with the concavity backward, and closed by the fleshy posterior valvular lobe: in the *Gavial* the tegument surrounding the nostril is thick, abundant, and can be raised from the bone, or erected, to bring the orifice to the surface of the water without exposure of other parts of the head. The nasal cavity is of great length, commencing at the fore part of the muzzle, and terminating beneath the occiput, also by a single aperture, close to which the nasal septum terminates. The anterior third part of the meatus is most expanded: the pituitary membrane is extended upon a bilobed turbinal, partly bony and partly gristly: the meatus also communicates with large cells or sinuses.

§ 64. *Organ of Sight in Fishes.*—The organ of sight makes its appearance in the lowest of Fishes, e. g. the Lancelet and Myxine, under as simple a form as in the Leech: a minute tegumentary follicle is coated by dark pigment, which receives the end of a special cerebral nerve. This simple eyespeck, the first mechanism for the appreciation of light, is repeated in the *Amblyopsis spelæus*, fig. 175, o. Rudimental eyeballs covered by the skin exist in the *Apterichthys cæcus*: the small, but more complex, eyes of the *Lepidosiren*, with crystalline and vitreous humours, choroid and sclerotic tunics, are also covered by the skin, but this becomes transparent where it passes over them, and, adhering to the sclerotic, forms a ‘cornea.’ The eyes of the Eel tribe and the Siluroid Fishes are small: they are of moderate size in the Plagiostomes and Ganoids; but in most Osseous Fishes the eyes are remarkable for their large size, which becomes enormous in some, e. g. *Orthogoriscus*, *Myripristis*, *Priacanthus*. The eyes are usually placed in orbital cavities, one on each side of the head; only in the unsymmetrical Flat-fish are they both placed on the same side: in the Stargazer (*Uranoscopus*) the eyes are approximated on the upper surface of a nearly cubical head, and



are directed towards the heavens: in the Hammer-headed Sharks they are supported on long outward-projecting pedicles.

The optic nerve, fig. 216, *a*, usually perforates the eyeball obliquely out of its axis, but sometimes directly in its axis. In Osseous Fishes it is compressed where it passes through the sclerotic and choroid, and then forms the retina by unfolding itself, like a fan spread out and bent into the form of a cone, leaving a fissure, *b*, where the free lateral borders meet after lining about two-thirds of the hollow globe. This fissure extends from the entry of the nerve to the anterior margin of the retina, and through it a fold of the innermost layer of the choroid passes into the vitreous humour, sometimes accompanied by the dark pig-



Eye of Sword-fish; one-third natural size.

mental Ruyschian layer.<sup>1</sup> The fold of the vascular choroid, whether accompanied by the pigmental layer or not, is called the 'falciform process,' *c*; it carries before it a fold of the proper tunic of the vitreous humour ('membrana hyaloidea'), and usually extends to the capsule of the lens, *d*, to which it is attached by means of a clear but firm substance, called the 'campanula Halleri.'

The posterior or outer layer of the retina consists of the cellular basis, supporting the stratum of cylindricules, standing vertically upon its concave surface, with the interblended twin-fusiform corpuscles, both of which microscopic structures are more easily demonstrated in the present than in the higher classes of Vertebrata. Each twin-corpusele is surrounded by a circle of cylindricules. The primitive nerve-fibres radiate over the cylindricules, without anastomosing, and terminate in free ends, not by loops, at the basis of the ciliary zone. A delicate but well-defined raised rim or 'bead' runs along both the anterior margins of the retina, and along those which form the falciform slit.

The crystalline lens (*d*) is spherical, or nearly so, large, firm, with a dense nucleus: it is almost buried in the vitreous humour, where it is steadied by the attachment of the falciform ligament to its thin capsule: the fore part projects through the pupil against the flat cornea, and so nearly fills the anterior chamber, that but a very small space is left for 'aqueous humour.' In the cod and other *Gadidæ* the fibres of the lens converge, like the

<sup>1</sup> xx. vol. iii. p. 144; eye of the Bonito, prep. no. 1651.

meridians of a globe, to two opposite points or poles of the spheroid: in the *Salmonidæ* and Shark, they converge to a linear tract or septum at each pole, as in fig 218. In the fibres of the lens of a cod Brewster discovered the marginal teeth, like those of rack-work, by which the fibres are interlocked together, as in fig. 217.

This acute observer computes five millions of fibres and sixty-two thousand five hundred millions of teeth in the lens of a cod: yet in the living and fresh state this organ is transparent.

The radiating fibres and elongated cells of the hyaloid tissue,<sup>1</sup> with the interstitial 'vitreous humour,' present a firmer consistency than in the human eye, and show their intimate structure and arrangement more clearly under the microscope than in Mammalia.

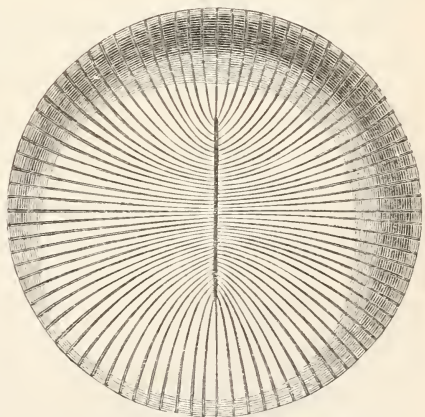
The membranes situated between the retina and sclerotica, called collectively 'choroid tunic,' are three in number: the external layer in Osseous Fishes, called '*membrana argentea*,' fig. 216, *e*, is composed chiefly of microscopical acicular crystals reflecting a silvery, or sometimes a golden lustre, with a delicate cellular basis, which assumes more firmness where it is continued upon the iris. The second or middle layer is the '*membrana vasculosa*,' seu '*Halleri*,' *ib. f*, and, as its name implies, is the chief seat of the ramifications of the choroid vessels: it also supports the ciliary nerves. The

217



Fibres of lens, highly magnified, showing interlocking of their toothed margins. CCXIII

218



Arrangement of fibres of lens, Salmon. CCXIII.

<sup>1</sup> LXV.

innermost layer is the '*membrana picta*,' seu '*Ruyschiana*,' *g*, also called '*uvea*,' which is composed of hexagonal pigment-cells, usually of a deep brown or black colour. In the Grey Shark (*Galeus*), the silvery layer is laid upon the central surface, not the periphery of the choroid.<sup>1</sup>

The formation of the iris, *h*, by the production of all these membranes is well shown in the eye of the Sword-fish *Xiphias*, fig. 216, where its thick base or '*ciliary ligament*' *h* overlaps the convex border of the bony sclerotic.<sup>2</sup> The *membrana argentea* upon the front of the iris gives great brilliancy to the eye, in many fishes. The pupil, *i*, is large and usually round: in many Plagiostomes it is elliptic; in *Galeus* it is quadrangular; in the flat-bodied Skates and Pleuronectidæ, that grovel at the bottom and receive the rays of light from above, a fringed process descends from the upper margin of the pupil, and regulates the quantities of admitted light by being let down or drawn up like a blind.

The muscular structure of the iris is very feebly developed in most fishes: it is best seen in the pupillary curtain of the Skate, the plicated anterior border of the uvea forms the so-called '*ciliary zone, or processes*,' *k*: they are the most complicated in the great Shark (*Selache*) where each process '*consists of two or three minute folds, which, as they run forward, unite into one, and terminate in a point at the circumference of the iris:*'<sup>3</sup> but they do not, as yet, project freely inward and forward from the surface of the uvea.

The subordinate and accessory character of the sclerotic capsule, fig. 216, *l, l*, fig. 219, *f, f*, is illustrated in most Osseous Fishes by its deviation from the sub-spherical form of the true eyeball which it protects, and by the great quantity of cellular, and often also of adipose tissue, fig. 216, which fills the wide interspace between the sclerotic and the choroid. In the fibrous tissue of the sclerotic are usually developed the two cartilaginous or osseous hemispheroid cups already described (p. 115, fig. 81, 17); but in place of these, in the *Orthogoriscus*, as in the Plagiostomes, the capsule is strengthened by a single hollow, cartilaginous, perforated spheroid. This varies in thickness at different parts, being usually thickest behind, and particularly so in the Sturgeon. The anterior aperture is closed by the cornea *n*, which is essentially a modified portion of the corium *o*, adhering to, as it passes over, the usually thickened borders of that aperture. In the eye of the *Xiphias*<sup>4</sup> may be traced an accession to the cornea from the outer

<sup>1</sup> xx. vol. iii. p. 147, prep. no. 1669.

<sup>2</sup> *Ib.* prep. no. 1661.

<sup>3</sup> *Ib.* prep. no. 1670, A.

<sup>4</sup> *Ib.* prep. no. 1661.

fibrous layer of the sclerotic, which undergoes the same change of tissue, and forms the posterior layer of the cornea. This transparent window of the eye-capsule is quite flat: its laminated structure is well displayed in the cornea of the *Orthogoriscus*,<sup>1</sup> and a dark-brown pigment here stains the soft integument or 'conjunctive membrane' (*o*), continued from the periphery of the cornea. In the eye of the same fish,<sup>2</sup> a very delicate layer or lining membrane is reflected from the posterior surface of the cornea, answering to the 'membrane of the aqueous humour' of land animals: this humour exists in very small quantity, just enough to lubricate the iris in the eyes of Fishes: the medium through which the rays of light reach the eye needs no refractive aid from an aqueous fluid interposed before the lens in the globe itself.

Amongst the most characteristic peculiarities of the eye in the typical or Osseous Fishes is the so-called 'choroid gland' fig. 216, *o*, fig. 219, *h*; this is of the class of bodies called 'vaso-ganglions: ' it usually presents a dark red colour, and lies between the 'silvery' and 'vascular' layers of the choroid, more or less encompassing, in the shape of a horse-shoe or bent magnet, the entry of the optic nerve. Dr. Albers<sup>3</sup> discovered the rich marginal plexuses of vessels, 'the roots of which have their origin in this body,' and the body itself he believed to consist also of a convolution of blood-vessels. Ordinary dissection, however, shows its compact substance to be arranged in parallel straight lines running between the convex and concave borders, and it has been called a 'muscle; ' but the supposed 'fibres consisted, in reality, of minute, parallel, and closely-disposed vessels, both arteries and veins.<sup>4</sup> Professor Müller has detected a relation of coexistence between the choroid vaso-ganglion and the pseudo-branchia, to which the Sturgeon, Lepidosiren, and the Plagiostomes are amongst the exceptions, having the pseudo-branchiæ but not the vaso-ganglia; *Silurus*, *Pimelodus*, *Synodon*, *Cobitis*, and all the Eel-tribe, have neither pseudo-branchiæ nor choroid vaso-ganglia.

The most remarkable exception in the structure of the eye in the present class is presented by the Anableps, the cornea of which is bisected by an opaque horizontal line, and the iris perforated by two pupils.

The general form of the eyeball, or rather its capsule, in Fishes, is a spheroid, flattened anteriorly, around which part the integuments commonly form a circular fold, yielding to the movements

<sup>1</sup> xx. vol. iii. p. 147, prep. no. 1665.

<sup>2</sup> *Ib.* prep. no. 1649.

<sup>3</sup> LXXVI.

<sup>4</sup> xx. vol. iii. (1836); p. 145, prep. 1656; and LXVII.



of the globe. In *Orthogoriscus* the circular palpebral fold is deeper, and is provided with a sphincter: in most Scomberoid and Clupeoid Fishes there is an anterior and a posterior vertical transparent fold or eyelid. In the eye of the tope and blue Shark, there is a nictitating membrane superadded to a well-developed circular palpebral fold of the skin. A conjunctive membrane is



Coats of the eye of the Perch  
XXIII.

reflected from the circular eyelid over the third eyelid, which is placed at the nasal side of the orbit, and then passes over the anterior half of the eyeball. A strong 'nictitator' muscle rises from the temporal side of the orbit, and passing through a muscular and ligamentous loop, descends obliquely to be inserted into the lower margin of the third lid. The trochlear muscle has an insertion into the upper part of the circular lid, and depresses that part simultaneously with the raising of the third lid.<sup>1</sup> The proper muscles of the eyeball exist in all fishes except the Myxinoids and Lepidosiren, and consist of the four *recti*, fig. 219, 1, 2, 3, 4, and two *obliqui*, ib. *a*, *b*: the latter rise from the nasal side of the orbit, and are inserted most favourably for effecting the rotatory movements of the eyeball: but the superior oblique, *a*, has not its direction changed by a trochlea in the present class. In the *Galeus* there is a special protuberance of the upper part of the cartilaginous sclerotic for the common insertion of the *rectus superior* and *obliquus superior*; and a second protuberance below for the common insertion of the *obliquus inferior* and *rectus inferior*. The *recti* muscles rise in many Osseous Fishes from the sub-cranial canal;<sup>2</sup> the origin of the *rectus externus* being prolonged furthest back. But the *recti* muscles are most remarkable for their length in the Hammer-headed Sharks, since they rise from the basis cranii, and extend along the lateral processes or peduncles, at the

<sup>1</sup> The family of Sharks, including *Galeus*, *Carcharias*, with this grade of palpebral structure, are called 'nictitantes;' they are amongst the most active and formidable of these great predatory Fishes.

<sup>2</sup> If, therefore, we regard this canal as part of the orbits, we must add the alisphenoid, basisphenoid, and even the basioccipital, to the bones enumerated at p. 116, as forming the chambers for the eyeballs and their appendages in Fishes; and this multiplicity of orbital bones interestingly repeats or parallels the characteristic formation of the otocranes or ear-chambers in the present class.

free extremities of which the eyeballs are situated. In all Plagiostomes the eyeball is supported on a cartilaginous peduncle: this is short and broad in the Rays; longer and cylindrical in the Sharks; in Selache it is articulated by a ball and socket synovial joint to a tubercle above, and external to the entry of the optic nerve.<sup>1</sup> A fibrous ligament attaches the sclerotic to the wall of the orbit in the Sturgeon and the Salmon.

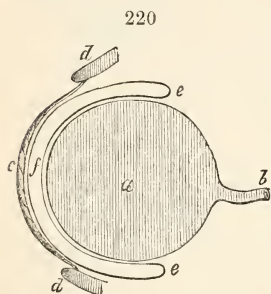
The space between the eyeball and the orbit contains a soft bed of gelatinous and adipose substance: but there is no lacrymal gland in Fishes. An apparatus to moisten the cornea was, of course, unnecessary in animals perpetually moving in a liquid medium. The cornea, which in most fishes is always exposed to that medium, is flat; it is, therefore, less liable to injury in the rapid movements of the fish, and being level with the side of the head, offers no impediment to those movements. This form of cornea diminishes the capacity of the aqueous chamber; but the aqueous humour is needed only to float the free border of the iris; and to make up for the small quantity of that humour, the refractive power of the lens is maximised by its spherical form. To compensate for the deviation from the spherical form of the eyeball, produced by the flattening of its fore-part, and the consequent loss of power to resist external pressure, the sclerotic capsule is cartilaginous or bony.

§ 65. *Organs of Sight in Reptiles.*—The eyes are very small, of simple structure, and concealed by the skin, which passes smoothly over them with little other change than subtransparency of texture, in both the ichthyo- and ophio-morphous Batrachia. The sclerotic, in *Proteus*, is lined by some dark pigment, and contains a minute spherical lens. It may serve to warn the animal, wandering into light, to retreat to the safe darkness of its native subterranean waters. The Axolotl has the eyeball better developed, and provided with muscles; but devoid of lids. In the Newts there is a horizontal fold of integument over each eyeball: the retina is thick, although the optic nerve is small: the choroid shows pigment: the pupil is transverse; the lens is spherical. The cornea is convex in the Land Salamander. In Newts the eyeballs are retracted in water, and are less prominent than in air; for this purpose there is a kind of choanoid muscle, besides the ordinary recti and obliqui. The eyeball is very small in *Pipa*, and has no eyelid. In the Frog, the eyeball is proportionally large, and is prominent; the globe is spherical; the sclerotic of subcartilaginous hardness anteriorly; elsewhere it

<sup>1</sup> xx. vol. iii. p. 175, prep. no. 1762.

allows the colour of the choroid to be seen through it: the cornea is very convex. The choroid has an argentine or nacreous layer externally, and a dark pigment internally; the former gives the bright colour to the iris in both Frogs and Toads. The pupil is subrhomboidal. A slightly plicated ciliary circle adheres to the capsule of the lens. The retina is thick, and is continued to the capsule of the crystalline, which forms a small spheroid lens. Besides the usual muscles of the eyeball, there is a choanoid muscle; the eyes are strongly retracted when the Frog dives. The chief nictitating lid is the lower one; the upper eyelid merely follows the movements of the eyeball when it is turned down. A small muscle arising from the lower and back part of the eyeball sends two tendons through the choanoid, which wind over the sides of the ball to a pulley at each angle of the orbit, through which they pass to be attached to the angles of the lower lid: this is transparent.

The eyes are small in Serpents: the sclerotic is fibro-cartilaginous, but thin: the choroid resembles that in the Frog, but with less brilliancy of the argentine layer: the ciliary plicæ are small and feeble: there is a delicate falciform process, without pigment: the lens is more spheroid than in Lizards: the pupil is round in most Serpents; but is a vertical slit in venomous Snakes, in *Boidea*, and in the nocturnal species of *Dipsosidae*; and is horizontal in most species of *Dryophis*, especially those which have the muzzle pointed and prolonged. But the chief peculiarity in the ophidian



Diagrammatic section of the eye of a Viper, magn. CCXIV.

organ of vision is in its defensive part, fig. 220. The integument, *c*, is continued from the surrounding circles of scales, *d*, directly over the eye: it consists of a layer of transparent epiderm, and a thin layer of chorium, which adheres to the outer part of the conjunctive sac, *f*. At the exuviating period, the epiderm, *c*, becomes opaque, and is shed in connection with that of the head and body. The conjunctiva covers a great proportion of the eyeball, *a*, before it is reflected, as at *e, e*, forward to line the antocular tegument, *c*. The cavity, *f*, is large, and receives the lacrymal secretion. In the Pythons and Colubers, a pore at the lower and forepart of the cavity, very minute in many species, but admitting a bristle in *Python*, leads to a slender membranous duct, which dilates into a pouch communicating with the mouth behind the premaxillary. In the Viper and other venomous Serpents, the lacrymal canal opens into the nasal meatus. The

lacrymal gland is large, especially in the Constrictors, and contributes its secretion to that of other sources of lubrication of the mouth during the long and difficult act of deglutition.

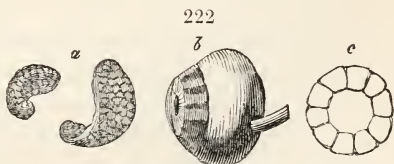
It is interesting to note the correspondence of condition between the eye and ear, in regard to the fore court of each organ, which Serpents exclusively exemplify, among air-breathing Vertebrates. The tympanic chamber parallels the conjunctive chamber; both are closed externally,—the one by the ear-drum, the other by the antocular membrane: the lacrymal canal is the homotype of the eustachian.

In Lizards, fig. 221, the eyeball is less globular, more flattened anteriorly than in Serpents, and the sclerotic is strengthened near the cornea by a circle of small sub-imbriate osseous plates, *d*. The lens, *ib. i*, is more convex behind than in front; a 'falciform process,' *ib. p*, is connected with its capsule; and in the Iguanas and Monitors it has a delicate layer of pigment-cells. The ciliary folds are more marked than in Serpents. In the Geckos the pupil is vertically oval: the retina shows a spot in the axis of vision. In the Chameleon the cornea is small; an antocular fold of skin is continued in front of the globe, but it is opaque and perforated in the middle: it moves with the eyeball; the conjunctiva attaching it to the fore-part of the ball, and the integument at its junction with the skin of the head, being very thin, yielding, and wrinkled. The sclerotic is so thin that the dark colour of the choroid appears through it: it becomes thicker anteriorly, especially at the insertion of the cornea. The retina shows the 'macula centralis,' or 'foramen Sœmmeringi,' on the nasal side and a little above the termination of the optic nerve, fig. 221, *o*.<sup>1</sup> The pupil is round; the lens is very small and almost spherical. The muscles have the usual disposition and number; but each eye enjoys an independent motion. The great extinct marine Lizards (*Ichthyosaurus*) had very large eyes, fig. 105, with the sclerotic plates developed even in greater proportion than in modern Lizards.

In the fresh-water Tortoise (*Emys*, fig. 222, *b*), the chief part of the eyeball is oblatly spheroid, with the segment of a smaller sphere at the fore-part; a circle of sclerotic plates, *c*, being imbedded at the junction, and sustaining the cornea.



Section of eye, Monitor (*Varanus*). CXXX.

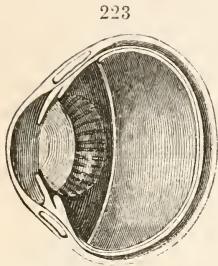


*a*, Lacrymal and Harderian glands: *b*, eye-ball  
*c*, Sclerotic plates. *Emys Europæa*. XXXVIII.

<sup>1</sup> ccxv. pp. 1. 104; xx. tom. iii. p. 156.



In the Turtle the sclerotic is cartilaginous, thickest behind, and thicker at the temporal than at the nasal side of the globe. The cornea is flatter than in the Emys or Land-Tortoise. The optic nerve penetrates the sclerotic, as in other reptiles, externally to the axis of vision, fig. 222, *b*, and makes a conical projection

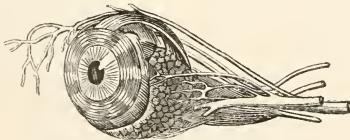


Section of the eye-ball of the *Emys Europæa*. XXXVIII.

in the interior of the eyeball, from which the thick retina expands and extends to the ciliary circle, fig. 223: there is no falciform ligament. The choroid is thick, and coloured by a deep-brown pigment. The ciliary plicæ are neatly defined, but do not project freely from the surface. The pupil is round; the crystalline is more convex in the Turtle than in the fresh-water or land-Tortoises. The short ciliary arteries form a plexus round the optic nerve in *Chelone*. The cornea is more convex in the Tortoise,

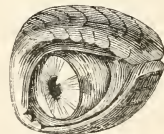
fig. 222, than in the Turtle. The lacrymal glands are two, fig. 222, *a*; the smaller (harderian) one is internal and inferior in position; the larger is external, applied to the eyeball, fig. 224, and sending its ducts to a deep fossa in the outer angle of the eyelids. These, fig. 225, are thick, opake, covered by polygonal epidermic scales; the lower lid is largest, most moveable, and has fewest scales

224



Eye-ball of *Emys Europæa*: shewing the external lacrymal gland. XXXVIII.

225



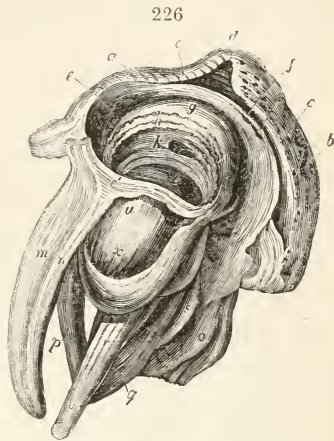
Eye-lids of *Emys Europæa*. XXXVIII.

upon it in *Chelone*: there is also a nictitant membrane situated vertically at the inner canthus, and having a horizontal motion. The duct of the harderian gland opens on its internal surface near the line of reflection of the conjunctive membrane upon it; and the secretion subserves the movements of the third lid. Besides the four recti and two obliqui muscles of the eyeball, there is a choanoid or retractor muscle divided into four fasciculi.

In the Crocodile, the sclerotic plates are not developed: the membrane, fig. 226, *x, u*, is of a firm fibro-cartilaginous tissue, allowing the dark hue of the choroid to appear through it: the cornea, *t*, is large and convex. The choroid is thinner and with

a blacker pigment than in other Reptiles, and the ciliary plicæ are longer and more distinct, extending beyond the origin of the iris. This is anteriorly of a pale yellow colour; the pupil is vertical.

The eye of the Crocodile is chiefly peculiar for the massive and complex character of its appendages, fig. 226, to which the eyeball itself, *x*, *u*, *t*, bears but a small proportion. No other or higher animal offers such a structure: it was one of the discoveries of Hunter, who left a drawing of it, which was engraved, and, with his preparation, no. 1770, described in xx. vol. iii. In the copy of this drawing, fig. 226, the upper, *e*, and lower, *b*, eyelids are severed at the outer canthus, and drawn apart to show the third or nictitant eyelid, *h*, and the extent of the conjunctiva. Of this membrane *e* is the free surface of the part which lines the ordinary eyelids, whence it is reflected over the nictitant lid at *g*, *h*, *k*; and then upon the cornea at the line marked *e'*, upon the part of the circumference next the outer canthus. The free margins of the upper and lower lids are marked *c*; they are devoid of cilia, as in all *Hæmatoecrya*: *h* is the free margin of the third lid. The glands sending their secretion to the conjunctival space are the proper lacrymal and the harderian; the duct of the latter terminates on the inner surface of the base of the nictitant lid, at *k*. From the conjunctival chamber the secretion of both glands is conveyed by the two puncta lacrymalia, *f*, to the duct terminating in the nasal cavity. The muscles are divisible into those of the eyelids and those of the eyeball. The nictitator, fig. 226, *z*, arises from the inner and upper part of the ball, proceeds outward and downward, winding round the optic nerve and choanoid muscle (which protects the nerve from the pressure of the nictitator in action), and is inserted into the inferior angle of the third lid. Whilst the muscle draws this outward over the eyeball, it at the same time rotates the ball inward beneath the third lid, being attached to movable points at both extremities. The upper eyelid has a levator muscle, *m*, chiefly inserted into the palpebral ossicle, but also sending a few fibres, *n*, to be attached to the palpebral conjunctiva near its angle of reflection. The under lid has a



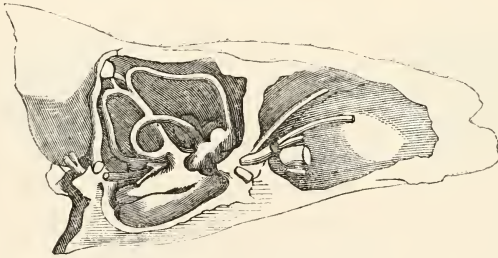
An external view of the eye, eyelids, muscles, &c. of a Crocodile. XX.

depressor muscle, *o*. Of the muscles of the eyeball, *p* marks the rectus superior; *q* the rectus inferior; *r* the rectus externus; *s* the obliquus inferior: the rectus internus and obliquus superior are likewise present. The letter *x* marks the insertion of the choanoid muscle or retractor of the eyeball, which consists of four portions surrounding the optic nerve, *v*. Counting these with the other muscles of the eyeball and lids, there are not fewer than thirteen; and the eye of the Crocodile has its special skeleton as well as muscles, represented by the super-palpebral ossicle.

In both Reptiles and Fishes the range of gradations of dioptric structures is very great; and the number of species in which the eye is a mere passive recipient of the stimulus of light, and unfit for sight, or the discernment of outward objects, is greater in the air-breathing than in the water-breathing *Hæmatocrya*.

§ 66. *Organ of Hearing in Fishes.*—The cartilaginous capsules of the acoustic organs are precociously developed in all Fishes: in the Myxinoids and Ammocetes they retain their primitive exterior position at the sides of the base of the proper cranium, fig. 58, 16; they are less conspicuous in the Lamprey, fig. 60, 16; they become involved in the thick cartilaginous walls of the cranium in the Plagiostomes; and, in Osseous Fishes, are walled up externally either by the surrounding cranial bones, or by a special

227



Otoerane and labyrinth of Perch. XXIII.

ossification of the exterior part of the capsule itself, forming an ‘os petrosum,’ as e. g. in the Carp, fig. 83, 16, and Perch, figs. 85, 84, 16. In the dry skull the ear-chamber appears as a large lateral compartment of the cranial cavity, fig. 227, *o*; and is formed as described in p. 115.

In the Myxinoids the membranous labyrinth is a simple annular tube, lined by vibratile cilia, filled with fluid, and supporting the ramifications of the acoustic nerve. In the Ammocete and Lamprey the labyrinth is specially attached to its cartilaginous capsule, and consists of a ‘vestibule’ and two ‘semicircular canals,’

each of which dilates, at its origin, into an 'ampulla,' which has some processes from its inner surface. The two canals again communicate with the vestibule, where they cross each other: the two divisions of the acoustic nerve first surround the ampullæ before they spread over the rest of the labyrinth. The acoustic communicates with the cranial cavity by two openings: the inferior and larger is oval and closed by membrane: the superior gives passage to the acoustic nerve.

In all other Fishes the membranous labyrinth, fig. 229, *a, o*, consists of a vestibule, *ib. a*, and three semicircular canals, *o*; the vestibule dilating into one or more 'sacculi,' separated by a constriction, or by a narrow canal, from the 'alveus communis,' and containing, besides the fluid called 'endolymph,' two or more masses of carbonate of lime, called 'otolites.'<sup>1</sup> These are compact and crystalline in Osseous Fishes. The largest, fig. 81, 16'', is an oval or round flattened body, striated and indented at the margins; convex, and sometimes grooved (*Ephippus*), on one side, more or less excavated on the other. The smaller otolite is less regular in its shape: there are often two of these. Each semicircular canal rises by an ampulliform end, fig. 229, *e, f, g*, from the 'alveus communis,' *a*, and communicates, by the opposite end, either with another canal, or with the vestibule separately, without previous dilatation: two of the canals are subvertical in their course, and are anterior, *e*, and posterior, *g*, in relative position: the third canal, *f*, is external and horizontal. A septum is continued across the ampulla from the line where the division of the acoustic nerve enters: a large proportion of the nerve expands upon the sac of the otolites. In some fishes this communicates with the vestibule by a narrow canal. All the parts of the labyrinth are of large size; yet the compartments of the otocrane which the semicircular canals, fig. 229, *e, f, g*, traverse, 'are much too wide for them, and they are supported in these passages by a very fine cellular membrane.'<sup>2</sup> In the Pike (*Esox lucius*) a pyriform membranous sac, lodged in the commencement of the spinal canal, opens into the vestibule near the entrance of the posterior semicircular canal.

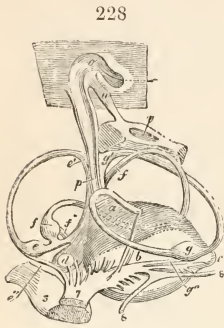
The Plectognaths, Lophobranchs, Holocephali, and Sturgeons resemble the bony fishes in the form and position of the labyrinth; but the otolites are represented by cretaceous particles; and in the Chimæra the communication between the cranium and otocrane begins to contract. The otolites are a hard chalky substance in

<sup>1</sup> Figures of these bodies will be found in xx. vol. iii. pl. 35; in LXVIII, LXXI., and in LXXII., with microscopic figures of the crystals.

<sup>2</sup> Hunter, VII. iii. p. 101.



the *Lepidosiren*, in which, as well as in the *Plagiostomes*, the whole labyrinth is buried in the thick basi-lateral walls of the cranium. In *Plagiostomes* the capsule conforms more closely in



Organ of hearing, Skate. LXVIII.

size and configuration to the membranous labyrinth; its passages and compartments are lined by a delicate perichondrium, from which filaments are detached to support the semicircular canal. The vestibule is divided in the *Skate* and *Tope* into three compartments, — the ‘*alveus communis*,’ fig. 228, *a*; the sac, *ib. b*, and the cysticule, *ib. c*; and it has also a small caecal appendage, called the ‘*utricule*,’ *ib. d*: the otolithic contents are like soft chalk, and are disposed in two masses; one very large, occupying the sac and the cysticule, the other

small, and lodged in the utricule. A canal extends in *Sharks* from the vestibular capsule to a foramen at the upper part of the occiput, which is closed by the skin. In the *Rays*, besides this ‘*fenestra capsulae*,’ *ib. e*, a membranous canal, *ib. o, p*, is produced from the vestibule itself, and, as *Hunter* well describes, ‘from the union of the two perpendicular canals, fig. 228, *p*; which is the case with all the *Ray* kind, the external orifice being small, and placed on the upper flat surface of the head.’ So minute and approximated are these ‘*outer ears*,’<sup>1</sup> that *Scarpa* may be pardoned for overlooking them, though scarcely for the warmth with which he repudiates their existence.<sup>2</sup> The ‘*meatus vestibuli*’ is provided at its bent extremity, fig. 228, *o*, with a special muscle, *ib. v*.

A true tympanic cavity and membrane, together with a cochlea, are absent in all *Fishes*. But in many osseous species a communication is established, either by tubular prolongations, or by chains of ossicles, between the acoustic labyrinth and the air-bladder. *Weber*<sup>3</sup> discovered the latter interesting structure in the *Carp*, *Loach*, and *Sheat-fish*. A canal is sent from the sac of each vestibule, fig. 229, *b*, to a common ‘*sinus impar*,’ *ib. h*, in the substance of the basi-occipital: this communicates on each

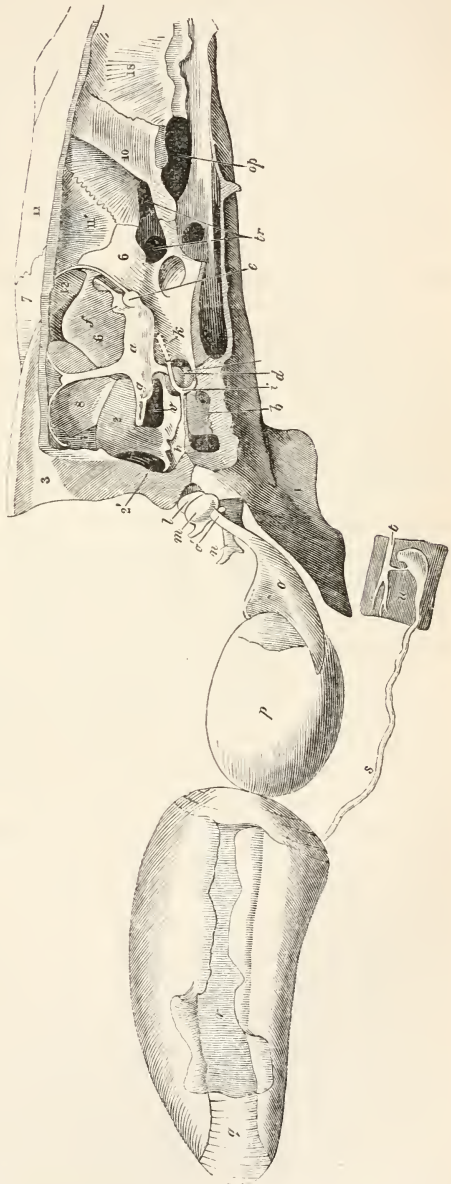
<sup>1</sup> XCII. p. 296. *Hunter*’s original memoir ‘On the Organ of Hearing in Fishes’ was printed in the volume of the *Philosophical Transactions* for 1782, not, as *Breschet* states, in the year 1786. (LVIII. p. 53.)

<sup>2</sup> ‘*Hunterum autem atque Monroum vehementer super hac re sibi hallucinatos fuisse.*’ (LX. pp. 1, 2.)

<sup>3</sup> LXXIII.

side by a small orifice with two subspherical 'atria,' on the body of the atlas, close to the foramen magnum, which 'atria' are supported externally by the ossicles *l* and *m*, and, by means of the large ossicle *o*, are brought into communication with the fore part of the air-bladder, *p*. Both the atria and common sinus are filled by the endolymph, and from the fore part of the sinus a 'canalis furcatus,' ib. *i*, is produced, the blind ends of which penetrate the alisphenoids. In the grovelling Loach (*Cobitis barbatula*), the air-bladder would seem to exist chiefly in subserviency to the organ of hearing. It is so small as to be wholly included within the singularly modified parapophyses of the second and third cervical vertebræ, which are expanded and coalesced so as to form a large 'bulla ossea' beneath their centrums.<sup>1</sup> The three ossicles on each side, which bring the air-bladder into communication with the 'atria' of the labyrinth, are also concealed by the fore part of the parapophysial bullæ: it is plain, therefore, that they are not dismemberments of those

229



Organ of Hearing in situ, with air-bladder and ossicles, Carp. LXXIII.

<sup>1</sup> xxxix. i. p. 380.

lateral or transverse apophyses of the vertebræ; and, with regard to their relation to the 'ossicula auditûs' of the tympanic cavity in Mammalia, Weber mistook a relation of analogy for one of homology, when he called them 'malleus,' 'incus,' and 'stapes.' They belong, like the capsules of the special organs of sense, to the 'splanchnoskeleton.' And since the vestibule is prolonged by the 'atria' into the neural canal of the atlas, this vertebra must be added, in the Cyprinoid and Siluroid Fishes, to the parts of the cranial vertebræ enumerated at p. 115, as entering into the formation of the chamber of the acoustic organ. In the Herring a tubular prolongation of the fore part of the air-bladder advances to the basioccipital, and bifurcates; each branch penetrates the side of the base of the skull, again bifurcates, and terminates in two blind sacs, which are in contact with similar cæcal processes of the labyrinth. In the *Holocentrum* and *Sargus*, cæcal processes of the swim-bladder also diverge, to attach themselves to the membrane closing the part of the otocrane containing the sac of the great otolite.

In Osseous Fishes the sonorous vibrations of their liquid element is communicated by the medium of the solid parts of their body, and in some species, also, through the vibrations of the air in the air-bladder, to the liquid contents of the labyrinth. In the Plagiostomous Fishes the resonance in the walls of their cartilaginous cranium is less than in the bony skull of ordinary fishes; but the labyrinth is wholly inclosed in the cartilage; and a further compensation is made by the prolongation of its chamber to the surface of the body in some, and by a similar prolongation of the membranous labyrinth itself in others. The position of the external orifices on the top of the head in the Skate tribe, may relate to the commonly prone position of these flat fishes at the bottom of the sea. Professor Müller concludes, from his experiments, 'that the air-bladder in fishes, in addition to other uses, serves the purpose of increasing by resonance the intensity of the sonorous undulations communicated from water to the body of the fish.'<sup>1</sup> The vibrations thus communicated to the peri- and endo-lymph of the labyrinth are doubtless made to beat more strongly upon the delicate extremities of the acoustic nerve, in Osseous Fishes, by their effect upon the suspended otolites: and it will be observed, that the chief portions of the nerve expand upon those chambers of the vestibule, which contain the otolites. The large size of the organ of hearing, and especially that of the hard otolites, also relate to the medium through which the sonorous vibrations are propagated

<sup>1</sup> LXXIII. p. 1245.

to the fish, and to the mode in which they are transmitted to the organ; in like manner as the eyeballs are expanded, in order to take in the utmost possible amount of light. The contracted encephalon harmonises with and suffices for the sensations and volitions, and the simple series of ideas daily repeated in the monotonous existence of the scaled inhabitants of the waters.

§ 67. *Organ of Hearing in Reptiles.*—The otocrane is large in proportion to the cranium, in the Perennibranchs, but is distinct from it: it is chiefly excavated in the alisphenoid and exoccipital. It includes a vestibule, three semicircular canals (*Proteus, Axelotes*), and the otolithic sac containing a cretaceous matter, which has more shape and consistency in the Axolotl than in the Newts and Salamanders. The external orifice of the acoustic capsule can now be recognised as a ‘vestibular’ one, or ‘fenestra ovalis,’ and it is closed by a cartilaginous plate representing the base of the stapes, connected with a slender ossicle in the Axolotl: but as yet there is no trace of tympanic cavity. The analogy of the ear to the eye, by the absence of the tympanic and conjunctivo-lacrymal forecourts in the respective organs of Fishes, is still kept up in the fish-like Reptilia.

The tympanic adjunct to the organ of hearing makes its first appearance, simultaneously with the development of eyelids and lacrymal organs, in the Batrachia which have quitted their aquatic for an aerial existence. Beyond the vestibular foramen is continued a short but wide passage outward, or ‘meatus,’ closed from the external air by a thin transparent vibratile membrane—the ‘tympanum’ or ear-drum. From the gristly plate closing the vestibular foramen a slender bony style is continued across the ‘tympanic cavity’ to a drum, to which it is attached by a capitular or spatulate cartilage, in which a small muscle is inserted. A wide vertical passage from the tympanic cavity to the fauces preserves the equilibrium between the air in that cavity and the atmosphere outside: it is called ‘eustachian tube.’ This tube will be found to bear relation to the size and exposed condition of the ear-drum, and perhaps, also, to its form, which, in the Frog and other air-breathing *Ovipara*, is convex externally. In the *Pipa* the bony meatus is long and tubular in shape, the eustachian tubes terminate by a single median and minute orifice on the palate: the ear-drum is concealed by a partial covering of skin. It is less conspicuous externally in all Toads than in Frogs: a small muscle acts on the cartilage connected with the ear-drum, and a second longer muscle is attached to the discoid piece closing the vestibular orifice. The labyrinth consists of *alveus communis*,



three semicircular canals, and otolithic sacculus containing a semi-fluid cretaceous substance: it is proportionally smallest in *Pipa*.

All serpents have the internal organ of hearing, similar in the main to the above: the base of the stapes closing the foramen vestibuli, is connected, in most serpents, by a long slender bony style, fig. 97, 16, through the medium of a cartilage and ligamentous fibres to the skin, which shows no sign of ear-drum or external meatus. No air is admitted by an eustachian canal to the cellular substance traversed by the tympanic ossicle; and of this there is no trace in *Tythlops* and *Rhinophis*.

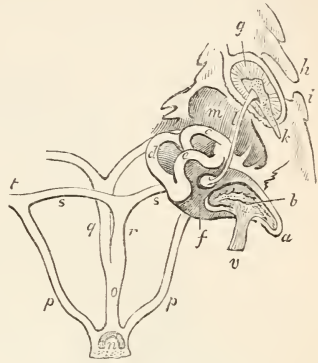
In Lacertians, the modification of part of the integument for the special reception of sonorous vibrations is resumed. In the Iguana, the ear-drum is partially protected by its oblique position and by a rising or fold of the skin at the back part of its circumference. It consists of the proper fibrous tissue of the tympanic membrane, covered externally by a thin layer of epithelium, and internally by the lining membrane of the tympanic cavity. The communication between the membrana vestibuli and membrana tympani is by the stapedia disc, the columelliform ossicle and the terminal or 'malleal' cartilage. The eustachian canal is relatively narrower, and its course more oblique than in the Frog: the otolite is a lenticular calcareous body, firmer than in the Frog.

In the Chelonia the ear-drum is again masked by unmodified integument; in the Turtle (*Chelone mydas*) it is covered by the second scale counting upward from the articulation of the lower jaw. The membrana tympani is, however, distinctly formed, thicker and more opaque than in *Batrachia* or *Lacertia*, and convex outwardly. The long columelliform ossicle fig. 92, 16', is connected with it by a discoid cartilage, and, at the opposite end, penetrates and closes the vestibular orifice by a sub-cartilaginous plate. The tympanic cavity is divided into two parts by a bony septum, intercommunicating at the columellar canal: the inner or antevestibular part also communicates with cells on the mastoid. The eustachian canal is narrow, and descends behind the articulation of the mandible; its palatal opening is more remote from that of the opposite ear than in other *Reptilia*. The proper capsule of the labyrinth is cartilaginous: besides the three semicircular canals and the otolithic capsule, there now buds from the vestibule a beginning of a cochlea, with a corresponding small opening into the tympanic cavity.

These approximations to the higher structure of the internal ear are more conspicuous in Crocodilia. The cochlear process is conical, with the apex, fig. 230, *a*, slightly bent; its cavity is

divided into two compartments by a double cartilaginous septum, *ib. b*, except at the apex, where they communicate; whilst, at the base, one compartment, 'scala vestibuli,' communicates with the vestibule, the other, 'scala tympani,' by a small orifice (foramen cochleæ, seu rotundum), with the tympanic cavity, in the dry skull, but closed by membrane in the living animal. The cochlear division of the acoustic nerve is shown at *v*, fig. 230. The semicircular canals are small compared with those of fishes: *c* is the anterior perpendicular, *d* the posterior perpendicular, and *e* the external or horizontal, canal which curves over the 'foramen ovale,' *f*. The membrana tympani, *g*, is lodged at the bottom of a deep fissure, and is protected by an opercular flap of the integument, *h*, fitting to a smaller fold below, *i*, and accurately closing the passage. This is the sole approach to an external ear known in existing Reptilia. The ear-drum is inclined downward and outward, adapted to the reception of sound from above, and also to the position of the overhanging flap. The gristly representation of the malleus, *k*, is well-marked, and the ear-drum is thickened at its place of attachment: the columellar part of the stapes, *l*, extends obliquely downward to the foramen ovale, seu vestibuli, *f*. The tympanic cavity, *m*, is singularly extended by air-cells, not only developed in the mastoid, but in the basi-, par-, and super-occipitals, fig. 94, 3, in the alisphenoid and parietal, *ib. 7*, bones. The communications between the tympanic cavity and fauces are more complex than in other animals,<sup>1</sup> although the eustachian faucial opening, *n*, is single, median, and common to both ears. It is situated a short way behind the posterior nostril; and from it is continued a median, *o*, and two lateral, *p*, canals. The median canal rises and enters a bony canal between the basioccipital and basisphenoid, which bifurcates, one branch, *q*, inclining forward into the basisphenoid, the other, *r*, continued vertically into the basioccipital, both in the medial plane. Each of these branches again bifurcates, transversely, one to the right, the other to the left, opening upon the floor of the tympanic cavity.

230



Organ of hearing, Crocodile.

<sup>1</sup> CLXXII.

The lateral membranous canals, *p, p*, from the eustachian outlet, diverge to the orifices of corresponding lateral bony canals, which ascend between the basioccipital and basisphenoid, and communicate each with the transverse subdivision, *s*, of the posterior or occipital branch of the median eustachian canal: a small rhomboidal sinus is formed at the point of union, from which a short canal, *t*, is continued to the tympanic cavity. The common inferior outlet, situated on a prominence, is partly closed by a valve, *n*, reducing its area to a crescentic form.<sup>1</sup>

§ 68. *Electric Organs of Fishes*.—Besides the modifications and appendages of the peripheral extremities of the nerves constituting organs of special sense, and those of which the function is still conjectural, there are nerves in fishes subject to more extraordinary combinations, and forming instruments, unknown in the higher vertebrate classes, having the property of accumulating and concentrating the subtle mode of force applicable to the communication of electric shocks. The faculty is limited to few genera, the most remarkable being *Torpedo* and *Gymnotus*, the species of which possess the electric organs in the highest state of development. In a minor degree the organs and power exist in *Malapterurus electricus*, *Mal. Beninensis*, *Mormyrus longipinnis*, *Mor. oxyrhynchus*, *Mor. dorsalis*, *Trichiurus electricus*, *Gymnarchus niloticus*, and *Tetraodon electricus*.

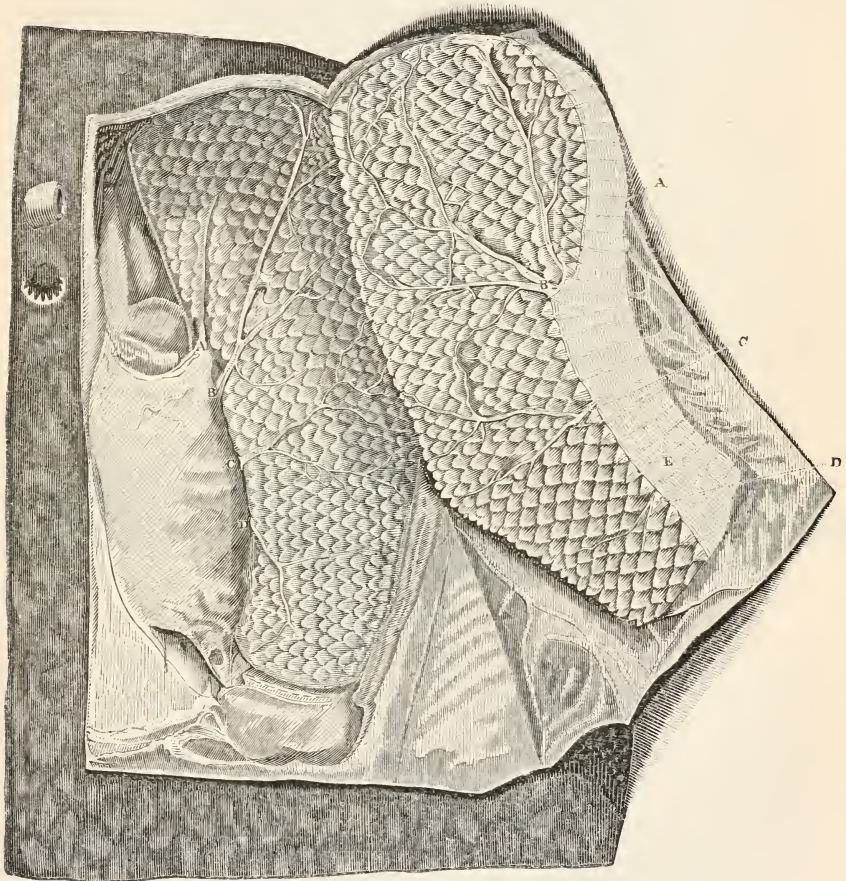
In the *Torpedo Galvanii* the organs are two in number, are large, flattened, reniform bodies, lodged on each side of the head and gills, and encompassed by these and by the anterior borders of the pectoral fins (fig. 139, E): they consist of a mass of vertical, for the most part hexagonal, prisms, the ends of which are covered by the dorsal and ventral integuments. Beneath these the organs are immediately coated by a thin glistening aponeurosis, which sends down partitions forming the chambers of the prismatic columns. Each column, when insulated in the recent fish, seems like a mass of clear trembling jelly; but consists of a series of delicate membranous plates inclosed by, or adherent by their margins to, a proper capsule, and separated from each other by a small quantity of a limpid albuminous fluid. Each flattened cell thus formed is lined by an epithelium of nucleated cells: the fibrous tissue of the plates and common capsule presents the microscopic characters of elastic tissue; between it and the epithelium is a clear unorganised layer, the seat of the ultimate ramifications of the vessels and nerves. The proper capsule adheres to the aponeurotic partition-walls which support the

<sup>1</sup> CLXXII. p. 521, pls. xl. xli. xlii.



columns and the larger branches of the nerves and vessels of the organ. Some of the vertical columns do not extend through the entire thickness of the organ; but are interrupted where the deep-seated nerves traverse the substance of the battery, fig. 231, A, D. The transverse plates of the vertical columns are shown

231



The right electrical organ, divided horizontally, at the place where the nerves enter, *Torpedo*. LXXXI.

at E. Hunter, who counted 470 columns in each organ, describes the partitions as being very vascular:—‘The arteries,’ he says, ‘are branches from the vessels of the gills, which convey the blood that has received the influence of respiration.’<sup>1</sup> But the

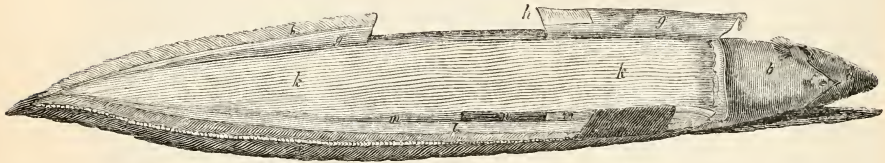
<sup>1</sup> LXXXI.



most characteristic feature of the organisation of the electric battery is its enormous supply of nervous matter. Each organ derives this supply from one branch of the trigeminal, fig. 231, A, and from four branches of the vagal nerves, ib., B, C, D; the four anterior nerves are each as thick as the spinal cord: the last nerve is a feeble branch of the vagus. The trigeminal and vagal enlargements of the olivary and restiform tracts coalesce on each side, forming the so-called 'electric lobes' of the medulla oblongata. The electric branch of the fifth nerve may be defined even at its origin, from the true ganglionic part of that nerve; and both this and the vagal branches consist entirely of the primitive nerve-fibres of animal life, as in fig. 164. The nerve-trunks are distributed by successive resolution into smaller and smaller fasciculi, until they finally penetrate the septa of the columns, and terminate thereon by meshes formed by loops, or by the return and anastomosis of the primitive nerve-fibres.<sup>1</sup>

In the eel-like *Gymnotus* the electric organs are four in number, and are situated two on each side the body, extending from behind the pectoral fins to near the end of the tail, fig. 232,

232



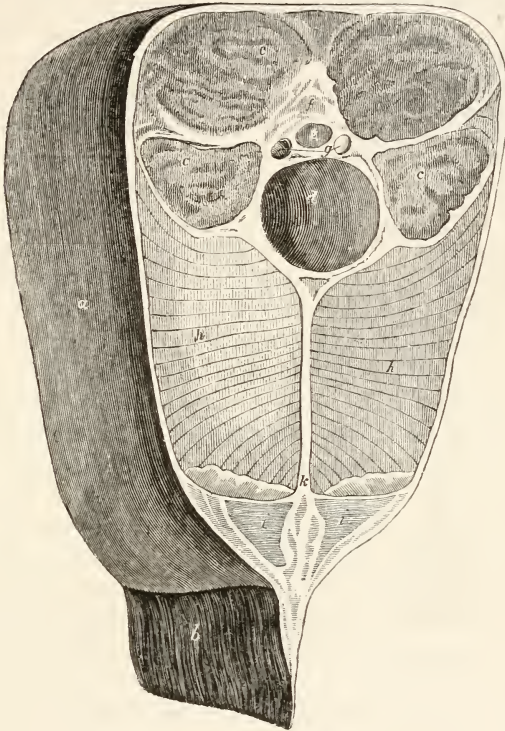
Right electrical organs, *Gymnotus* (reduced). CCXVII.

*k, l.* They occupy and almost constitute the whole lower half of the trunk, fig. 233; the upper organ, ib. *h*, being much larger than the lower one, ib. *i*, from which it is separated by a thin muscular and aponeurotic stratum. The organs of one side are separated from those of the other, above by the vertebral column and its muscles, ib. *c*, then by the air-bladder, ib. *d*, and below this by an aponeurotic septum, ib. *k*. From this septum, and from that covering the air-bladder, there extend outward, to be attached to the skin, a series of horizontal, or nearly horizontal, membranes, arranged in the longitudinal axis of the body nearly parallel to one another; they are of great but varying length, some being co-extensive with the whole organ, fig. 232, *k*: their breadth is almost that of the semidiameter of the plane of the body in

<sup>1</sup> LXXVI.

which they are situated, fig. 233, *h*. These membranes are about half a line apart at their outer borders; but, as they pass from the skin towards their inner attachments, they approach one

233



Vertical transverse section, *Gymnotus*, natural size. ccxv.

another. They are intersected transversely by more delicate vertical plates, extending from the skin to the median aponeurosis, and coextensive in length with the breadth of the septa between which they are placed. Hunter counted about 240 of these plates in a single inch of length of the horizontal membrane.<sup>1</sup> He compares those stronger membranes to the aponeurotic walls of the prisms of the *Torpedo*, and the intersecting delicate plates to the partitions of the prisms: and if we admit the analogy of these plates, and of those of the *Torpedo*, to the plates of the voltaic pile, we perceive that, in the

<sup>1</sup> LXXX.

Gymnotus, the batteries are horizontal and the plates vertical, fig. 233, *h*, whilst in the Torpedo the batteries are vertical and their plates horizontal, fig. 231, *E*. The situation of the organs is also very different in the two fishes; they extend from before the pectoral fins to the anterior part of the head in the one, fig. 139, *E*, and from behind the pectoral fins to near the end of the tail in the other, fig. 232, *h*. But a more important difference exists in the condition of the interspaces between the delicate transverse plates. In the Torpedo they simply contain a fluid. In the Gymnotus two strata of pyramidal cells diverge from a common basis traversing each interspace, and terminate freely, the one towards one plate, the other towards the opposite plate, and divide the fluid into a 'pre-cellular' and 'post-cellular' portion. The cellular basis is 'positive,' the post-cellular fluid and the partition-plate is negative, constituting the 'voltaic couple;' whilst the pre-cellular fluid is the conducting element between one 'couple' or plate and the next: the whole represents the ternary type of the voltaic pile. The Torpedo's structure is according to the binary type. Another remarkable difference is in the source of the nervous supply. In the Gymnotus the electric organs are supplied by the 'rami ventrales' of all the spinal nerves, about 200 pairs, that issue in the course of their extent; some of the filaments ramify upon the horizontal membranes from their cutaneous margins; but the greater part of the nerves come from the deeper-seated branches which descend upon the median aponeurotic partition-wall, and spread upon the septa of the organ from within outwards. Yet the nervus lateralis, which is derived from the same cerebral nerves as those which, in the Torpedo, supply the electric batteries, and which is formed by similar proportions of the trigeminal and vagus, extends the whole length of the electric organs in the Gymnotus without rendering them a filament; it is situated nearer the spine, and is of larger size than usual, but Hunter was not able to trace any nerves going from it to join those of the medulla spinalis, which run to the organ.<sup>1</sup> The quantity of nervous matter supplied to the batteries of the Gymnotus is less than in the Torpedo: but more substance enters into their composition.

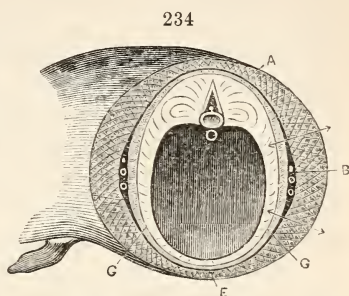
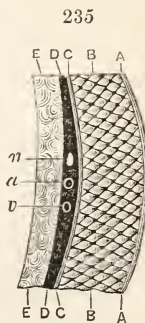
The proportional size of the electric organs is also much greater in the Gymnotus than in the Torpedo: indeed, the proper body of the Gymnotus is, as it were, a mere appendage tacked on

<sup>1</sup> LXXXI.

to the fore part of the enormous batteries; for the digestive and generative viscera, with the respiratory and circulating organs, the brain and organs of sense,—all, in fact, that constitute the proper animal,—are confined to that small segment of the entire body which is anterior to the electrical apparatus, fig. 232, *b*. The vent even opens beneath the head, in advance of the pectoral fins.

The electric organs of the *Malapterurus electricus*<sup>1</sup> form a layer fig. 234, *A*, immediately beneath the skin, enveloping the whole body except the head and fins, and separated from the muscles, *ib.* *G*, by a fascia with vessels and nerves, *ib.* *B*, and by a layer of adipose tissue, *ib.* *E*. The electric organ is divided by fine decussating membranes into minute lozenge-shaped cells, about a third of a line in diameter, fig. 235, *B*. It is supplied by a large nerve issuing from the beginning of the myelon and arising from a mass, in its substance, of ganglion-cells, like those in the electric lobes of the *Torpedo*. A considerable ganglion is also formed upon the nerve beyond its origin, from which the trunk is continued along the side of the body, like a ‘*nervus lateralis*,’ and distributes branches to the diffused organ. The structure of the organ is such that the electric currents run in all directions, and a discharge would take place from any point of its surface, whence, perhaps, the necessity for a layer of nonconducting substance, *E*, between the proper body of the fish and the organ. The shock delivered, wanting the concentration resulting from the structure in the *Torpedo*, is comparatively feeble, but suffices for defence; the fish being protected by its electrifying coat, as is the hedgehog by its spines.

In the *Mormyrus longipinnis* the electric organ consists of four series of membranous septa placed longitudinally on the tail, two on each side. Each series consists of about 150 septa with intervals of  $\frac{1}{30}$ th of a line, filled by albuminous fluid. The septa are stronger than those in the hexagonal columns of the *Torpedo*.<sup>2</sup>

<sup>1</sup> XCII. and CCXIX.<sup>2</sup> CCXX.Section of *Malapterurus electricus*. CCXIX.Section of electric organ, *Malapterurus*, CCXVIII. A, skin; B, electric cells; C, fascia; *n*, cellular tissue, with *a*, artery, *v*, vein, *n*, nerve; E, adipose tissue.



An animal must be in communication with the Torpedo by two distinct points, in order to receive the shock.<sup>1</sup> If an insulated frog's leg, fig. 207, c, touches the Torpedo by the end of the nerve only, no muscular contractions ensue on the discharge of the battery; but a second contact by a portion of muscle, or any other part of the leg, immediately produces them.<sup>2</sup>

The dorsal surface of the electric organ is positive, the ventral surface negative. The Torpedo has no power of otherwise directing the electric currents; but Matteucci found that wounding the electric lobes of the brain sometimes reversed the direction.<sup>3</sup> These currents, besides their effects on the living body, exercise all the other known powers of electricity; they render the needle magnetic,<sup>4</sup> decompose chemical compounds, and emit the spark.<sup>5</sup> The discharge of strong currents is usually accompanied by visible contraction of parts of the body, usually by a retraction of the eyes of the Torpedo, and one muscle, fig. 139, o, is arranged so as to constrict part of the circumference of each battery; but such consentaneous muscular action, though it may add to the force of the discharge, is not essential to its production. The benumbing effect seems to be produced by the rapid succession of shocks delivered by the recent and vigorous fish. Matteucci ascertained that, during the discharge, the nerves of the organ were not traversed by any electric current. Pacini,<sup>6</sup> from a minute comparison of the organs, deduces that the electricity in the Torpedo is produced by the dynamical conflict between the two polarities inherent in two sorts or different degrees of innervation, as it is evolved in the thermo-electric pile by the conflict of two polarities inherent in two different degrees of temperature; whilst in the Gymnotus it is produced, as in the voltaic pile, by the chemical conflict between the materials of the elements excited by the nervous influence.

Humboldt has given a lively narrative of the mode of capture

<sup>1</sup> When the Neapolitan fishermen pull their nets to shore, their first act usually is to wash the captured fishes by dashing over them bucketfuls of sea-water; and if a Torpedo be amongst them it makes its presence instantly felt by the shock transmitted to the arm discharging the bucket. If the fish be handled, the shock is too strong and painful to be willingly encountered a second time, and the arm continues long benumbed. Each repetition of the discharge, however, enfeebles its force, and the surface of the fish capable of communicating the shock progressively contracts, as life departs, to the region of the organs themselves. When the fisherman dashes the stream of water over the Torpedo, the electric current passes up from the dorsal surface of the batteries against the stream to the man's hand, and the circle is completed by the earth extending from the man's feet to the ventral surface of the prone fish.

<sup>2</sup> LXXVII. p. 148.

<sup>3</sup> *Ib.*

<sup>4</sup> LXXXII.

<sup>5</sup> LXXVII.

<sup>6</sup> CCXVIII.

of the Gymnoti, employed by the Indians of South America,<sup>1</sup> and all its circumstances establish the close general analogy between the Gymnotus and Torpedo in the vital phenomena attending the exercise of their extraordinary means of offence. It is voluntary and exhaustive of the nervous energy; like voluntary muscular effort, it needs repose and nourishment to produce a fresh accumulation.

In the experiments performed by Professor Faraday on a large living Gymnotus,<sup>2</sup> the most powerful shocks were received when one hand grasped the head and the other hand the tail, of which I had painful experience; especially at the wrists, the elbows, and across the back. But the nearer the hands were together within certain limits, the less powerful was the shock. It was demonstrated by the galvanometer that the direction of the electric current was from the anterior parts of the animal to the posterior parts, and that the person touching the fish with both hands received only the discharge of the parts of the organs included between the points of contact. Needles were converted into magnets: iodine was obtained by polar decomposition of iodide of potassium; and, availing himself of this test, Faraday showed that any given part of the organ is negative to other parts before it, and positive to such as are behind it. Finally, heat was evolved, and the electric spark obtained. The delicate plates

<sup>1</sup> They rouse the Gymnoti by driving horses and mules into the ponds which those fish inhabit, and harpoon them when they have exhausted their electricity upon the unhappy quadrupeds; 'I wished,' says Humboldt, 'that a clever artist could have depicted the most animated period of the attack: the groups of Indians surrounding the pond, the horses with their manes erect and eyeballs wild with pain and fright, striving to escape from the electric storm which they had roused, and driven back by the shouts and long whips of the excited Indians: the livid yellow eels, like great water-snakes, swimming near the surface and pursuing their enemy: all these objects presented a most picturesque and exciting *ensemble*. In less than five minutes two horses were killed. The eel, being more than five feet in length, glides beneath the body of the horse, and discharges the whole length of its electric organ. It attacks, at the same time, the heart, the digestive viscera, and, above all, the gastric plexus of nerves. I thought the scene would have a tragic termination, and expected to see most of the quadrupeds killed; but the Indians assured me the fishing would soon be finished, and that only the first attack of the Gymnoti was really formidable. In fact, after the conflict had lasted a quarter of an hour, the mules and horses appeared less alarmed; they no longer erected their manes, and their eyes expressed less pain and terror. One no longer saw them struck down in the water; and the eels, instead of swimming to the attack, retreated from their assailants, and approached the shore.' The Indians now began to use their missiles; and, by means of the long cord attached to the harpoon, jerked the fish out of the water, without receiving any shock so long as the cord was dry; but a less cautious assailant, who had climbed an overhanging bough, was brought down into the water, amidst the laughter of his companions, by the shock sent upwards from the wounded Gymnotus, along the wetted cord attached to the harpoon. CVII. p. 55.

<sup>2</sup> LXXXIII.

sustaining the terminal meshes of the nerves and vessels are horizontal in the *Torpedo*; the course of the electric current is from above downwards. The corresponding plates in the *Gymnotus* are vertical; the direction of the electric current is from before backwards: i. e. it is vertical to the planes of the plates in both cases.

The row of compressed cells constituting the electric prism of the *Torpedo* offers some analogy to the row of microscopic discs of which the elementary muscular filament appears to consist, fig. 128, B. The looped termination of the exciting nerve is common to muscular tissue and that of the electric organ. The electric, like the motory nerves, rise from the anterior myelonal tracts; and, though they have a special lobe at their origin, beyond that origin, in the *Torpedo*, they have no ganglion. An impression on any part of the body of the *Torpedo* is carried by the sensory nerves either directly, or through the posterior myelonal tracts, to the brain, excites there the act of volition, which is conveyed along the electric nerves to the organs, and produces the shock: in muscular contraction, the impression and volition take the same course to the muscular fibres. If the electric nerves are divided at their origin from the brain, the course of the stimulus is interrupted, and no irritant to the body has any effect on the electric organs any more than it would have under the like circumstances on the muscles. But, if the ends of the nerves in connection with the organ be irritated, the discharge of electricity takes place, just as irritating the end of the divided motor nerve in connection with the muscle would induce its contraction. If part of the electric nerves be left in connection with the brain, the stimulus of volition cannot, through these, excite the discharge of the whole organ, but only of that part of the organ to which the undivided nerves are distributed. So, likewise, the irritation of the end of a divided nerve in connection with the electric apparatus, excites the discharge of only that part to which such nerve is distributed. We have seen that the power of exciting the electric action, like that of exciting the muscular contraction, is exhausted by exercise and recovered by repose: it is also augmented by energetic circulation and respiration; and what is more significant of their close analogy, both powers are exalted by the direct action, on the nervous centres, of the drug 'strychnine:' its application causes simultaneously a tetanic state of the muscles of the fish, and a rapid succession of involuntary electric discharges.<sup>1</sup>

<sup>1</sup> LXXVII. p. 162.

## CHAPTER V.

## DIGESTIVE SYSTEM OF HÆMATOCRYA.

§ 69. *Dental Tissues*.—A tooth is a hard body attached to the mouth or commencement of the alimentary canal, partially exposed, when developed. Calcified teeth are peculiar to the Vertebrates, and may be defined as bodies primarily, if not permanently, distinct from the skeleton, consisting of a cellular and tubular basis of animal matter containing earthy particles, a fluid, and a vascular pulp.

In general, the earth is present in such quantity as to render the tooth harder than bone, in which case the animal basis is gelatinous, as in other hard parts where a great proportion of earth is combined with animal matter. In a very few instances, among the vertebrate animals, the hardening material exists in a much smaller proportion, and the animal basis is albuminous; the teeth here agree, in both chemical and physical qualities, with horn.

True teeth consist commonly of two or more tissues, characterised by the proportions of their earthy and animal constituents, and by the size, form, and direction of the cavities in the animal basis which contain the earth, the fluid, or the vascular pulp.

The tissue which forms the body of the tooth is called ‘dentine,’ (*dentinum*, Lat.; *zahnbein*, *zahnschubstanz*, Germ.; *l'ivoire*, Fr., fig. 236, *d*).

The tissue which forms the outer crust of the tooth is called ‘cement’ (*cæmentum*, *crusta petrosa*, Lat., *ib. e*).

The third tissue, when present, is situated between the dentine and cement, and is called ‘enamel’ (*encaustum*, *adamas*, Lat., *ib. e*).

‘Dentine’ consists of an organised animal basis and of earthy particles: the basis is disposed in the form of compartments or cells, fig. 237, *b*, and extremely minute tubes, *ib. a*: the earthy particles have a twofold arrangement, being either blended with the animal matter of the interspaces and parietes of the tubes, or contained in a minute granular state in their cavities. The density of the dentine arises principally from the proportion of earth in the first of these states of combination. The tubes contain, near the formative pulp, filamentary processes of that part<sup>1</sup>; and convey a

<sup>1</sup> CCXLVI. vol. iv. p. 929.



colourless fluid, probably transuded 'plasma': they thus relate not only to the mechanical conditions of the tooth, but to the vitality and nutrition of the dentine. This tissue has few or no canals large enough to admit capillary vessels with the red particles of blood, and it has been therefore called 'unvascular dentine.'

236



Magnified section of incisor, Horse;  
c cement, d dentine, e enamel. v.

'Cement' always closely corresponds in texture with the osseous tissue of the same animal; and wherever it occurs of sufficient thickness, as upon the teeth of the horse, sloth, or ruminant, it is also traversed, like bone, by vascular canals, fig. 236, c. When the osseous tissue is excavated, as in dentigerous Vertebrates above fishes, by minute radiated cells, forming with their contents the 'corpuscles of Purkinje,' fig. 15, these are likewise present, of similar size and form, in the 'cement,' and are its chief characteristic as a constituent of the tooth. The hardening material of the cement is partly segregated and combined with the parietes of the radiated cells and canals, and is partly contained in disgregated granules in the cells, which are thus rendered white and opaque, viewed by reflected light. The relative density of the dentine and cement varies according

to the proportion of the earthy material, and chiefly of that part which is combined with the animal matter in the walls of the cavities, as compared with the size and number of the cavities themselves. In the complex grinders of the elephant, the masked boar, and the capybara, the cement, which forms nearly half the mass of the tooth, wears down sooner than the dentine.

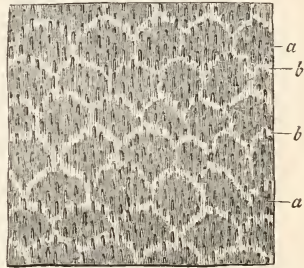
The 'enamel,' fig. 235, e, is the hardest constituent of a tooth, and, consequently, the hardest of animal tissues; but it consists, like the other dental substances, of earthy matter arranged by organic forces in an animal matrix. Here, however, the earth is mainly contained in the canals of the animal membrane; and, in mammals and reptiles, completely fills those canals, which are comparatively wide, whilst their parietes are of extreme tenuity. The

hardening salts of the enamel are not only present in far greater proportion than in the other dental tissues; but, in some animals, are peculiarly distinguished by the presence of fluato of lime.

Teeth vary in number, size, form, structure, modifications of tissue, position, and mode of attachment, in different animals. They are principally adapted for seizing, tearing, dividing, pounding, or grinding the food; in some they are modified to serve as weapons of offence and defence; in others, as aids in locomotion, means of anchorage, instruments for uprooting or cutting down trees, or for transport and working of building materials; they are characteristic of age and sex; and in man they have secondary relations subservient to beauty and to speech.

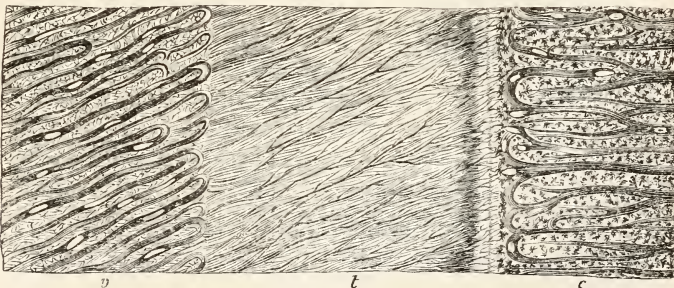
Teeth are always most intimately related to the food and habits of the animal, and are therefore highly interesting to the physiologist. They form for the same reason most important guides to the naturalist in the classification of animals; and their value, as zoological characters, is enhanced by the facility with which, from their position, they can be examined in living or recent animals. The durability of their tissues renders them not less available to

237



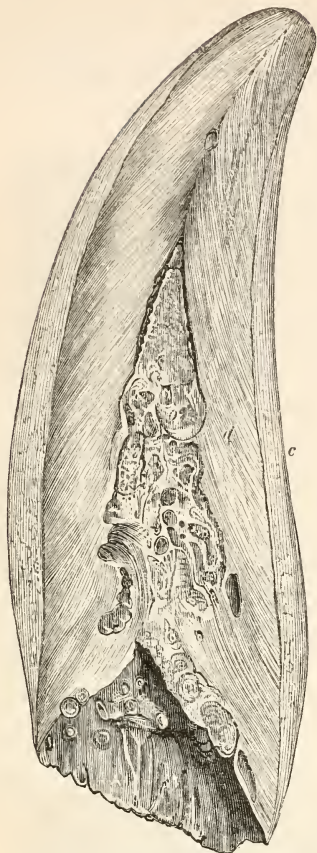
Section of tusk of Dugong, magn. v.

238

Magnified section of molar, Megatherium; *v* vasodentine, *t* dentine, *c* cement. VI.

the palæontologist in the determination of the nature and affinities of extinct species, of whose organisation they are often the sole remains discoverable in the deposits of former periods of the earth's history.

The simplest modification of dentine is that in which capillary tracts of the primitive vascular pulp remain uncalcified, and per-



Section of tooth of Cachalot, half natural size. v.

manently carry red blood into the substance of the tissue. These so-called 'medullary' or 'vascular' canals present various dispositions in the dentine which they modify, and which is called 'vaso-dentine.' It is often combined with true dentine in the same tooth; *e.g.* in the scalpriform incisors of certain Rodents,<sup>1</sup> the tusks of the Elephant,<sup>2</sup> the molars of the extinct *Megatherium*, fig. 238, v.

A third kind of dentine is where the cellular basis is arranged in concentric layers around the vascular canals, and contains 'radiated cells' like those of the osseous tissue: it is called 'osteodentine,' fig. 239, o. The transition from dentine to vaso-dentine, and from this to osteodentine, is gradual, and the resemblance of osteodentine to true bone is very close.

The chemical composition of teeth is exemplified in the subjoined analyses of those organs and their tissues from species of the different vertebrate classes:—

	MAN		LION		OX			CROCODILE		PIKE Large teeth of lower jaw
	Dentine	Enamel	Dentine	Enamel	Dentine	Enamel	Cement	Dentine	Cement	
Phosphate of lime, with a trace of fluato of lime . . . .	66.72	89.82	60.03	83.33	59.57	81.86	58.73	53.69	53.39	63.98
Carbonate of lime . . . .	3.36	4.37	3.00	2.94	7.00	9.33	7.22	6.30	6.29	2.54
Phosphate of magnesia . . . .	1.08	1.34	4.21	3.70	0.99	1.20	0.99	10.22	9.90	0.73
Salts . . . . .	0.83	0.88	0.77	0.64	0.91	0.93	0.82	1.34	1.42	0.97
Chondrine . . . . .	27.61	3.39	31.57	9.39	30.71	6.66	31.31	27.66	28.15	30.60
Fat . . . . .	0.40	0.20	0.42	atrace	0.82	0.02	0.93	0.79	0.76	1.18
	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

<sup>1</sup> v. p. 405.

<sup>2</sup> v. p. 643.



The examples are extremely few, and peculiar to the class *Pisces*, of calcified teeth which consist of a single tissue, and this is always a modification of dentine. The large pharyngeal teeth of the Wrasse (*Labrus*) consist of a very hard kind of unvascular dentine. Fig. 240 shows a vertical section of one of these teeth, supported upon the vascular osseous tissue of the pharyngeal bone: *p* is the pulp cavity.

The next stage of complexity is where a portion of the dentine is modified by vascular canals. Teeth, thus composed of dentine and vaso-dentine, are very common in fishes. The hard dentine is always external, and holds the place, and performs the office, of enamel in the teeth of higher animals; but it is only analogous to enamel, not the same tissue. Fig. 241 exemplifies this structure in a longitudinal section of the tooth of a Shark (*Lamna*).

The molars of the Dugong (*Halicore*) are composed of dentine and cement. the latter substance forming a thick outer layer, fig. 242, *c*.

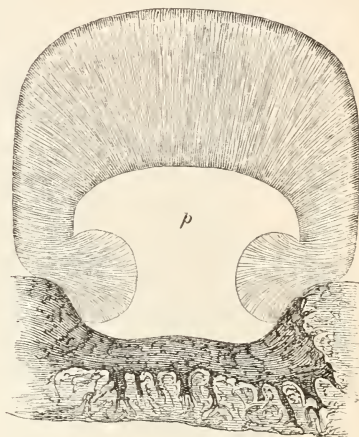
In the teeth of the Cachalot (*Physeter*) the pulp-cavity of the growing tooth becomes filled up by osteodentine, the result of a modified calcification of the dentinal pulp; when the tooth presents three tissues, as shown in fig. 239, in which *c* is the thick external cement, *d* the hard dentine, and *o* the osteodentine; sometimes developed in loose stalactitic-shaped nodules.

In the teeth of the Sloth, and its great extinct congener, the Megatherium, the hard dentine is reduced to a thin layer, fig. 238, *t*, and the chief bulk of the tooth is made up of a central body of vaso-dentine, *ib. v.*, and a thick external crust of cement, *ib. c*.

Besides the number of constituent tissues teeth become 'complex' in structure by the proportion and disposition, chiefly inflection, of more or fewer of those tissues.

Certain fishes and the extinct 'Labyrinthodont' reptiles exhibit this complexity in a remarkable degree. In fig. 243, the tooth of the *Labyrinthodon salamandroïdes* feebly indicates its singular structure by the longitudinal striæ. But every streak is

240

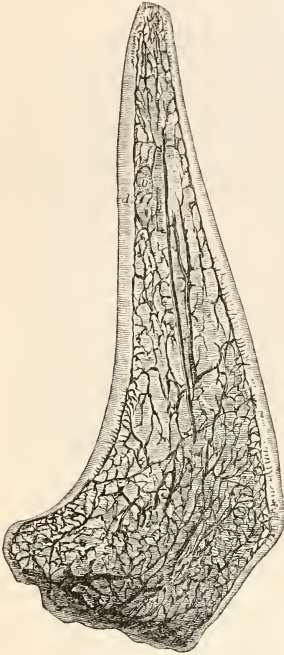


Section of pharyngeal tooth of *Labrus*, magnified. *v.*



a fissure, into which a thin outer layer of cement, fig. 244, *c*, is reflected into the body of the tooth, following the sinuous wavings of the lobes of dentine, *d*, which diverge from the central pulp-cavity, *a*.

241



Section of tooth of a Shark (*Lamna*), magn. ; *v* vaso-dentine, *d* gano-dentine. *v*.

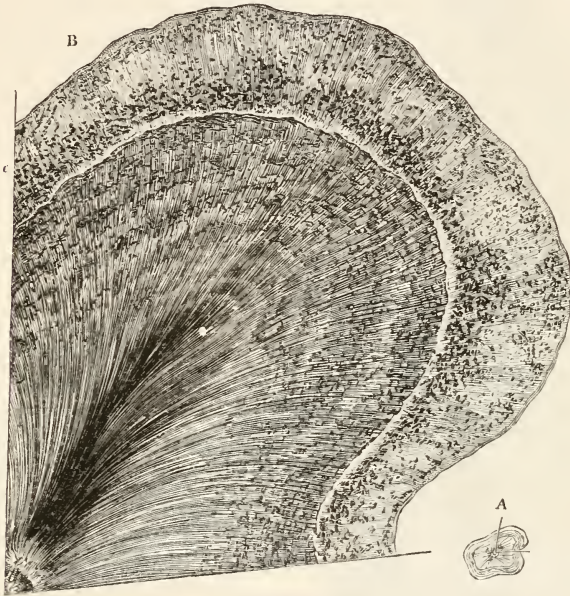
The inflected fold of cement, *c*, runs straight for about half a line, and then becomes wavy, the waves rapidly increasing in breadth as they recede from the periphery of the tooth; the first two, three, or four undulations are simple; then their contour itself becomes broken by smaller or secondary waves these become stronger as the fold approaches the centre of the tooth, when it increases in thickness, and finally terminates by a slight dilatation or loop close to the pulp-cavity, from which the free margin of the inflected fold of cement is separated by an extremely thin layer of dentine. The number of the inflected converging folds of dentine is about fifty at the middle of the crown of the tooth figured, but is greater at the base. All the inflected folds of cement at the base of the tooth have the same complicated disposition with increased extent; but, as they approach their termination towards the upper part of the tooth, they also gradually diminish in breadth, and consequently penetrate to a less distance into the substance of the tooth. Hence, in such a section as is delineated, fig. 244, it will be observed that some of the convoluted folds, as those marked *c*, extend near to the centre of the tooth; others, as those marked *c'*, reach only about half way to the centre; and those folds, *c''*, which, to use a geological expression, are 'cropping out,' penetrate to a very short distance into the dentine, and resemble, in their extent and simplicity, the converging folds of cement in the fangs of the tooth of the Ichthyosaurus and Lepidosteus.

The disposition of the dentine is still more complicated than that of the cement. It consists of a slender, central, conical column, excavated by a conical pulp-cavity for a certain distance from the base of the tooth; and this column sends radiating out-

wards, from its circumference, a series of vertical plates, which divide into two once or twice before they terminate at the periphery of the tooth.

Each of these diverging and dichotomising plates gives off throughout its course smaller processes, which stand at right

242



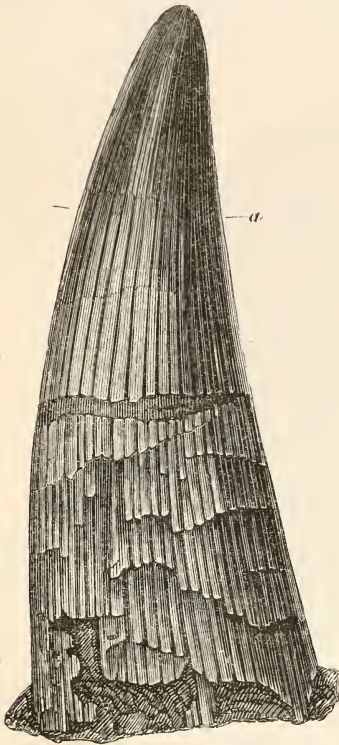
Section of tooth of Dugong; A, natural size; B, magnified; *d*, dentine; *c*, cement. v.

angles, or nearly so, to the main plate; they are generally opposite, but sometimes alternate; many of the secondary plates or processes, which are given off near the centre of the tooth, also divide into two before they terminate; and their contour is seen, in the transverse section, to partake of all the undulations of the folds of cement which invest and divide the dentinal plates and processes from each other.

The dental pulp-cavity is reduced to a mere line about the upper third of the tooth, but throughout its whole extent fissures radiate from it, corresponding in number with the radiating plates of dentine. Each fissure is continued along the middle of each plate, dividing where this divides, and extending along the middle of each bifurcation and process to within a short distance of the line of cement. The pulp-fissure commonly dilates into a canal

at the origin of the lateral processes of the radiating plates, before it divides to accompany and penetrate those processes.

243



Tooth of a *Labyrinthodon*, natural size; *a* line of section. v.

The main fissures or radiations of the pulp-cavity extend to within a line or half a line of the periphery of the tooth, and suddenly dilate at their terminations into spaces, which, in transverse section, are subcircular, oval, or pyriform, *p*: the branches of the radiating lines, which are continued into the lateral secondary plates or processes of the dentinal lamellæ, likewise dilate into similar, and generally smaller spaces. All these spaces, or canals, in the living tooth, must have been occupied by corresponding processes of the vascular pulp: they constitute as many centres of radiation of the fine tubes, which, with their uniting clear substance, constitute the dentine.<sup>1</sup>

An analogous complexity is produced by numerous fissures, radiating from a central mass of vasodentine, which more or less fills up the pulp cavity of the seemingly simple conical teeth, fig. 245, of the extinct 'Dendrodont' fishes.

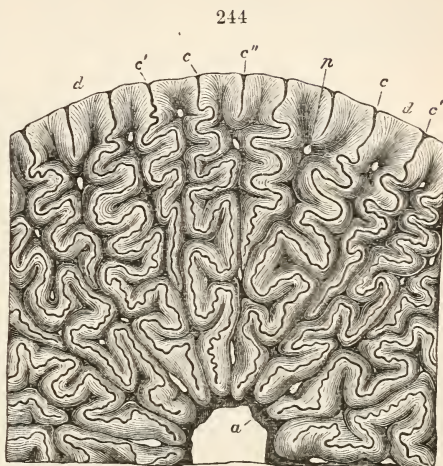
A portion of the transverse section, *a*, fig. 245, magnified, fig. 246, shows the fissures diverging from the pulp-cavity, *p*, and its reticulate extensions, and sending small branches into the dentinal lamellæ.

These lateral offsets subdivide into a few short ramifications, like the branches of a shrub, and terminate in irregular and somewhat angular dilatations, simulating leaves, but which resolve themselves into radiating fasciculi of dentinal tubes. There are from fifteen to twenty-five or thirty-six of these short and small lateral branches on each side of the main rays.



A third kind of complication is produced by an aggregation of many simple teeth into a single mass, fig. 247.

The examples of these truly compound teeth are most common in the class of Fishes, but the illustration here selected is from the Mammalian class. Each tooth of the Cape Ant-eater (*Orycteropus*) presents a simple form, is deeply set in the jaw, but without dividing into fangs; its broad and flat base is porous, like the section of a common cane. The canals to which these pores lead contain processes of a vascular pulp, and are the centres of ra-



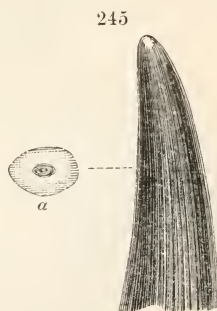
Portion of transverse section of tooth of *Labyrinthodon*, magn. v.

diation of as many independent series of dentinal tubules. Each tooth consists of a congeries of long and slender prismatic columns of dentine, cemented together by their ossified capsules. Fig. 247 is part of a transverse section of such compound tooth, showing *c* the cement, *d* the dentine, *p* the pulp-cavity of the denticles, and *d'* a section of one of the denticles just beyond its bifurcation.

In the series of tissues, 'cement' and 'dentine,' under its diverse modifications, rank with osteine. Enamel is a tissue *per se*: it might be compared to calcified epiderm; but, in the teeth of Fishes, there are intermediate gradations of structure which link enamel to dentine, and this to bone.

The general form of the matrix or formative organ of teeth, and the relative position of the dentinal pulp to its product, bear a close resemblance to the formative organ of hair and bristle. In these, however, the papilla or pulp is developed from the skin, in teeth from the mucous membrane.

Teeth further agree with the extravascular appendages of the skin in being shed and reproduced, sometimes once, sometimes frequently, during the lifetime of the individual. In some

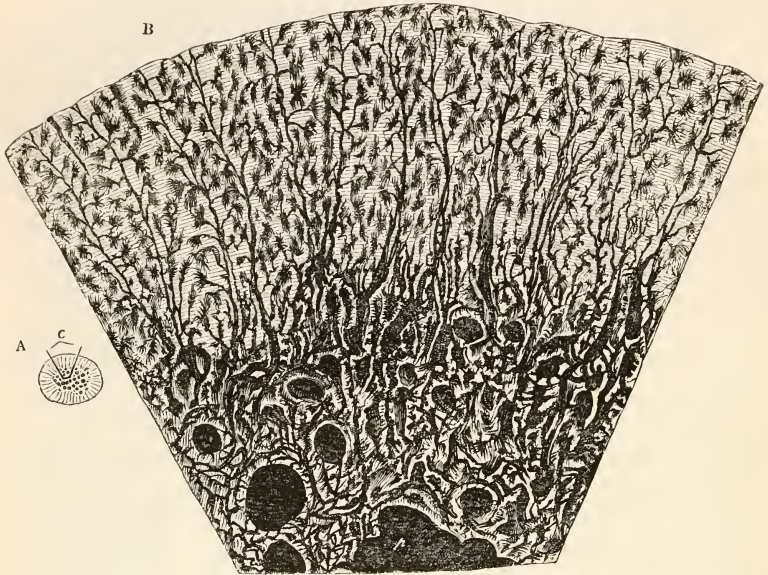


Tooth of a *Dendrodus*, natural size. v.



instances, as with certain dermal appendages, the reproduction of the tooth is uninterrupted, or continuous. A tooth, when fully formed, is subject to decay, but has no inherent power of reparation.

246



Portion of transverse section of tooth of a *Dendrodus*, magn. v.

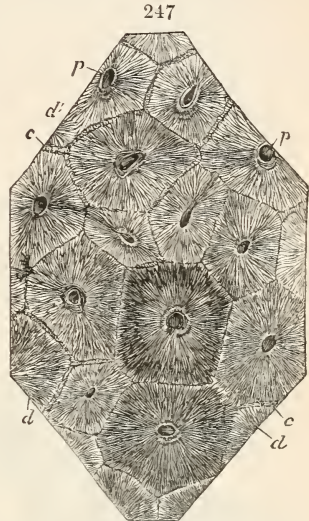
Thus teeth are analogous to epidermal and horny parts in their mode of development, in their shedding and reproduction, and in their exposure to outward influences; but the antlers of deer are similarly exposed, and are likewise shed and renewed, yet, like the teeth and horn-cores of the ox, they are classed with the osseous tissues.

§ 70. *Teeth of Fishes.*— In this class of Vertebrates the teeth, whether we study them in regard to their number, form, substance, structure, situation, or mode of attachment, offer a greater and more striking series of varieties than do those of any other class of Animals.

As to *number*, they range from zero to countless quantities. The Lancelet, the Ammocete, the Sturgeon, fig. 125, 22, 32, the Paddle-fish, and the whole order of *Lophobranchii*, are edentulous. The Myxinoids, fig. 248, have a single pointed tooth, *a*, on the roof of the mouth, and two serrated dental plates, *b*, on the tongue. The Tench has a single grinding-tooth on the occiput,

fig. 250, *c*, opposed to two dentigerous pharyngeal jaws, *d, d*, below. In the *Lepidosiren* a single maxillary dental plate, fig. 251, *a*, is opposed to a single mandibular one, *b*, and there are two small denticles on the nasal bone, *c*. In the extinct Sharks with crushing teeth, called *Ceratodus* and *Ctenodus*, the jaws were armed with four teeth, two above and two below.<sup>1</sup> In the *Chimæra* two mandibular teeth are opposed to four maxillary teeth.<sup>2</sup> From this low point the number in different Fishes is progressively multiplied until, in the Pike, the Siluroids, fig. 252, and many other fishes, the mouth becomes crowded with innumerable teeth.

With respect to *form*, I may premise that as organised beings withdraw themselves more and more, in their ascent in the scale of life, from the influence of common physical agents, so their parts progressively deviate from geometrical figures: it is only, therefore, in the lowest vertebrated class that we find teeth in the form of perfect cubes, and of prisms or plates with three sides (*Myletes*), four sides (*Scarus*), five, or six sides (*Myliobates*, fig. 249). The cone is the most common form in Fishes: such teeth may be slender, sharp-pointed, and so minute, numerous, and closely aggregated, as to resemble the plush or pile of velvet; these are called 'villiform teeth' (*dentes villiformes*, *dents en velours*<sup>3</sup>); all the teeth of the Perch are of this kind: when the teeth are equally fine and numerous, but longer, they are called 'ciliiform' (*dentes ciliiformes*): when the teeth are similar to, but rather stronger than these, they are called 'setiform' (*dentes setiformes*, *dents en brosse*): conical teeth, as close set and sharp pointed as the villiform teeth, but of larger size, are called 'rasp-teeth' (*dentes raduliformes*, *dents en rape* or *en cardes*, fig. 252); the Pike presents such teeth on the back part of the vomer: the teeth of the Sheat-fish (*Silurus glanis*) present all the gradations



Transverse section of tooth of *Orycteropus*, magn. v.



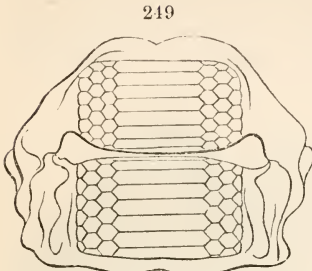
Teeth of *Myxine*. xxi.

<sup>1</sup> v. pl. 22.

<sup>2</sup> v. pl. 28.

<sup>3</sup> The French terms are those used by Cuvier in xxiii. *passim*.

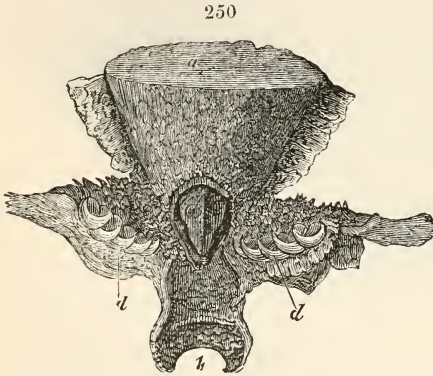
between the villiform and raduliform types. Setiform teeth are common in the Fishes thence called Chaetodonts;<sup>1</sup> in the genus *Citharina* they bifurcate at their free extremities; in the genus *Platax* they end there in three diverging points, and the cone here merges into the long and slender cylinder, fig. 253.



Jaws and teeth (*Myliobates*).

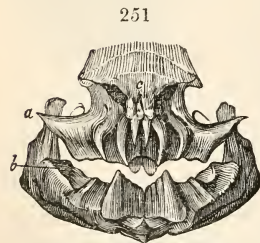
may be bent upon itself, like a tenterhook, as in the fishes thence called Goniodonts.<sup>2</sup> In the Bonito may be perceived a progressive

thickening of the base of the conical teeth: and this being combined in other predatory fishes with increased size and recurved direction, they then resemble the laniary or canine teeth of carnivorous quadrupeds, as we see in the large teeth of the Pike, in the *Lophius*, fig. 260, and in certain sharks, fig. 263.



Teeth of Trench. v.

and by progressive blunting, flattening, and expansion of the apex, observable in different fishes, the cone gradually changes to the thick and short cylinder, such as is seen in the back teeth of the wolf-fish, and in similar grinding and crushing teeth in other genera, whether feeders on sea-weeds or on crustaceous and testaceous animals. The grinding surface of these short cylindrical teeth may be convex, as in the Sheep's-head fish (*Sargus*); or flattened, as in the



Teeth of *Lepidosiren*. xxxiii.

pharyngeal teeth of the Wrasse (*Labrus*, fig. 254). Sometimes the hemispheric teeth are so numerous, and spread over so broad a

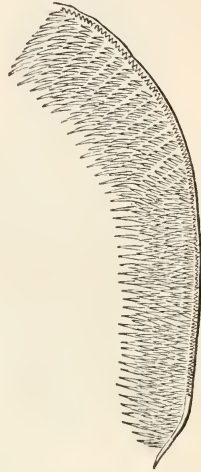
<sup>1</sup> Χαίτη, a bristle; ὀδὸς, a tooth.

<sup>2</sup> Γωνία, an angle; ὀδὸς, a tooth.



surface, as to resemble a pavement, as in the pharyngeal bones of the Wrasse or Rock-fish (*Labrus*, fig. 254); or they may be so small, as well as numerous (*dentes graniformes*), as to give a granulated surface to the part of the mouth to which they are attached (premaxillaries of *Cossyphus*).<sup>1</sup> A progressive increase of the transverse over the vertical diameter may be traced in the molar teeth of different fishes, and sometimes in those of the same individual, as in *Labrus*, until the cylindrical form is exchanged for that of the depressed plate. Such dental plates (*dentes lamelliformes*) may be found, not only circular, but elliptical, oval, semilunar, sigmoid, oblong, or even square, hexagonal, pentagonal, or triangular; and the grinding surface may present various and beautiful kinds of sculpturing. The broadest and thinnest lamelliform teeth are those that form the complex grinding tubercle of the Diodon, fig. 257, *b*. The front teeth of the Flounder and Sargus present the form of compressed plates, at least in the crown, and are *dentes incisivi*. Numerous wedge-shaped dental plates (*dentes cuneati*) are set vertically in the

252



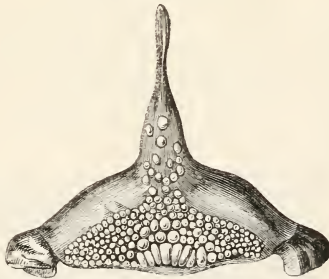
Palatine bone and teeth  
(*Siturus*). v.

253



Mandibular teeth,  
magnified (*Platax*). v.

254



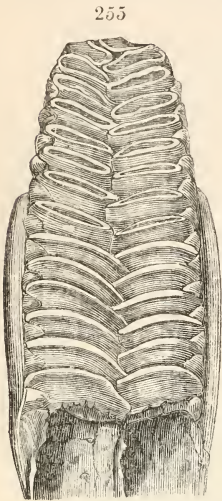
Inferior pharyngeal bone and teeth (*Labrus*). v.

upper pharyngeal bone of the Parrot-fish (*Scarus*, fig. 255). A thin lamella, slightly curved like a finger-nail, is the singular form of tooth in an extinct genus of fishes, thence called *Petalodus*. Sometimes the incisive form of tooth is notched in the middle of the cutting edge, as in *Sargus unimaculatus*. Sometimes the edge of the crown is trilobate (*Aplodactylus*, fig. 256). Sometimes it is made quinquelobate by a double

<sup>1</sup> v. pl. 45, fig. 1.



notch on each side of the large middle lobe (*Boops*). In the formidable Sea-pike (*Sphyræna Barracuda*) the crown of each tooth, large and small, is produced into a compressed and sharp point, and resembles a lancet. Sometimes the edges of such lancet-shaped teeth are finely serrated, as in *Priodon*, and the great Sharks of the genus *Carcharias*, the fossil teeth of which indicate a species (*Carch. Megalodon*) sixty or seventy feet in length.



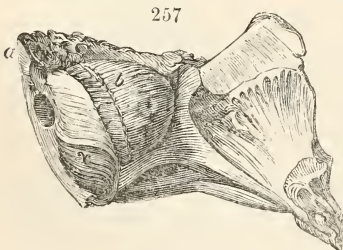
Superior pharyngeal bones and teeth (*Scarus*). v.

The lancetted form is exchanged for the stronger spear-shaped tooth in the Sharks of the genus *Lamna*, fig. 260; and in the allied great extinct *Otodus*, as in the small Porbeagle, similarly shaped, but stronger, piercing and cutting teeth were complicated by one or more accessory compressed cusps on each side of their base, like the Malay crease. With respect to *situation*, the teeth, in Sharks and Rays, are limited to the bones (maxillary and mandibular), which form the anterior aperture of the mouth: in the Carp and other Cyprinoids the teeth are confined to the bones (pharyngeal and basioccipital) which circumscribe the posterior aperture of the mouth. The Wrasses (*Labrus*) and the Parrot-fishes (*Scarus*) have teeth on the pre-maxillary and pre-mandibular, as well as on the upper and lower pharyngeals; both the anterior and posterior apertures of the mouth being thus provided with instruments for seizing, dividing, or comminuting the food, the grinders being situated at the pharynx. In most fishes teeth are developed also in the intermediate parts of the oral cavity, as on the palatines, the vomer, the hyoid bones,



Front teeth of *Aplo-dactylus*. v.

the branchial arches; and, though less commonly, on the pterygoids, the entopterygoids and the sphenoids. It is very rare to find teeth developed on the true superior maxillary bones; but the Herring and Salmon tribes, some of the Ganoid Fishes, and the great *Sudis*, fig. 86, 21, are examples of this approach to the higher Vertebrates. Among the anomalous positions of teeth may



Section of the jaw and teeth of the Globe-fish (*Diodon*). v.

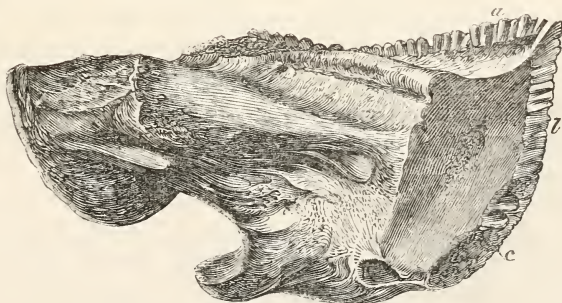
be cited, besides the nasal teeth of the *Lepidosiren*, fig. 251, *c*, and the occipital alveolus of the Carp and Tench, fig. 250, the marginal alveoli of the prolonged, depressed, well ossified rostrum of the Saw-fish (*Pristis*, fig. 65). In the Lampreys, fig. 138, and in *Helostomus* (an osseous fish), most of the teeth are attached to the lips. Lastly, it is peculiar to the class *Pisces*, amongst Vertebrates, to offer examples of teeth developed in the median line of the mouth, as in the palate of the *Myxines*, fig. 248, *a*; or crossing the symphysis of the jaw, as in *Notidanus*, *Scymnus*, and *Myliobates*, fig. 249.

Nor is the mode less varied than the place of attachment. The teeth of *Lophius*, *Pæcilia*, *Anableps*, are always moveable. In most fishes they are ankylosed to the jaws by continuous ossification from the base of the dental pulp. Sometimes we find, not the base, but one side, of the tooth ankylosed to the alveolar border of the

258

Beak of Parrot-fish (*Scarus muricatus*). v.

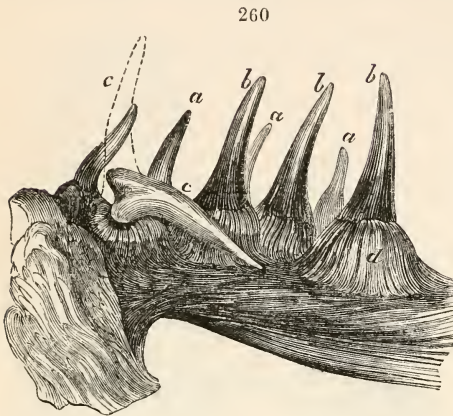
259



Section of the jaw of the Parrot-fish, showing the progress of dentition. v.

jaw; and the teeth oppose each other by their sides instead

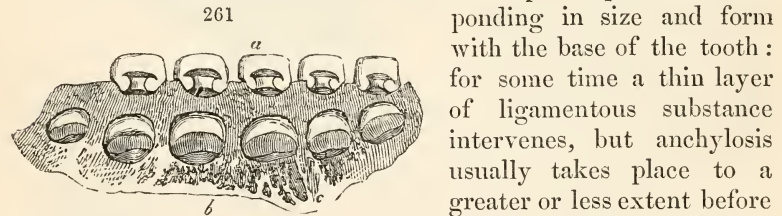
of their summits (*Scarus*, fig. 259); in *Pimelodus*, however, where the teeth are thus attached, the crown is bent down in the upper teeth, and bent up in the lower ones, at right angles



Portion of the jaw of *Lophius piscatorius*, showing the ligamentous attachment of the teeth. v.

to the fang, so that they oppose each other by the normal surfaces. Certain teeth of recent and fossil cartilaginous fishes have their base divided into processes like fangs, but these serve for the attachment of ligaments, and are not set in bony sockets like the true fangs or roots of the teeth of Mammals.

The base of anchylosed teeth is, at first, attached to the jawbone by liga-



Teeth of the Wrasse (*Crenilabrus*). v.

ment; and in the Cod-fish, Wolf-fish, and some other species, as calcification of the tooth progresses towards its base, the subjacent portion of the jawbone receives a stimulus, and develops a process corresponding in size and form with the base of the tooth: for some time a thin layer of ligamentous substance intervenes, but anchylosis usually takes place to a greater or less extent before the tooth is shed. Most of the teeth of the *Lophius* retain the primitive connection; the ligaments, fig. 260, *d*, of the large internal or posterior teeth of the upper and lower jaws, radiate on the corresponding sides of the bone, the base of the tooth resting on a conformable alveolar process. The ligaments do not permit the tooth to be bent outward beyond the vertical position, but yield to pressure in the contrary direction, by which the point of the tooth may be directed towards the back of the mouth, as at *c*; the instant, however, that the pressure is remitted, the tooth returns through the elasticity of the bent ligaments, as by the action of a spring, into its usual erect position, *b*; the deglutition of the prey of this voracious fish is thus facilitated, and its escape



prevented. The broad and generally bifurcate bony base of the teeth of Sharks is attached by ligament to the semio ossified crust of the cartilaginous jaws, fig. 263; but they have no power of erecting or depressing the teeth at will. The small and closely crowded teeth of Rays are also connected by ligaments to the subjacent maxillary and mandibular membranes. The broad teselated teeth of the *Myliobates* have their attached surface longitudinally grooved to afford them better hold-fast, and the sides of the contiguous teeth are articulated together by serrated or finely undulating sutures, a structure unique in dental organisation. The teeth of the *Sphyræna* are examples of the ordinary implantation in sockets, with the addition of a slight ankylosis of the base of the fully-formed tooth with the alveolar parietes; and the compressed rostral teeth of the Saw-fish, fig. 65, are deeply implanted in sockets. In the latter the hind margin of their base is grooved, and a corresponding ridge from the back part of the socket fits into the groove, and gives additional fixation to the tooth. Some implanted teeth in the present class have their hollow base further supported, like the claws of the feline tribe, upon a bony process arising from the base of the socket; the incisors of the *Balistes*, e. g. afford an example of this double or reciprocal gomphosis.<sup>1</sup> In fact, the whole of this part of the organisation of fishes is replete with beautiful instances of design and instructive illustrations of animal mechanics. The vertical section of a pharyngeal jaw and teeth of the Wrasse (*Labrus*) would afford the architect a model of a dome of unusual strength, and so supported as to relieve from pressure the floor of a vaulted chamber beneath. The base of the dome-shaped tooth, fig. 240, *p*, is slightly contracted, and is implanted in a shallow circular cavity; the rounded margin of which is adapted to a circular groove in the contracted part of the base; the margin of the tooth which immediately transmits the pressure of the bone, is strengthened by an inwardly projecting convex ridge. The masonry of this inner buttress, and of the dome itself, is composed of hollow columns, every one of which is placed so as best to resist or transmit in the due direction the external pressure. The floor of the alveolus is thus relieved from the office of sustaining the tooth: it forms, in fact, the roof of a lower vault, in which the germ of a successional tooth, fig. 261, *b*, is in course of development. The superincumbent pressure is exclusively sustained by the border of the alveolus, whence it is transferred to

<sup>1</sup> v. p. 82, pl. 40.



the walls dividing the vaulted cavities containing the germs of the new teeth; the roofs of these cavities yield to the absorbent process consequent on the growth of the new teeth without materially weakening the attachment of the old teeth, and without the new teeth being subjected to any pressure until their growth is sufficiently advanced to enable them to bear it with safety; by this time the sustaining borders of the old alveolus are undermined, and the old worn-down tooth is shed.

The dental system of the Wolf-fish (*Anarrhichas Lupus*), is adapted for feeding on hard crustacea and testacea. But, in order to secure the capture of the shell-fish, the teeth of the Wolf-fish are not all crushers; some present the laniary type, with the apices more or less recurved and blunted by use, and consist of strong cones spread abroad, like grappling-hooks, at the anterior part of the mouth.<sup>1</sup>

The premaxillary teeth are conical, and arranged in two rows. There are three large, strong, diverging laniaries at the anterior end of each premandibular bone, and immediately behind these an irregular number of shorter and smaller conical teeth, which gradually exchange this form for that of large obtuse tubercles; these extend backward, in a double alternate series, along a great part of the alveolar border of the bone. Each palatine bone supports a double row of teeth, the outer ones being conical and straight, and from four to six in number; the inner ones two, three, or four in number, and tuberculate. The lower surface of the vomer is covered by a double irregularly alternate series of the same kind of large crushing teeth as those at the middle of the premandibular. All the teeth are anchylosed to more or less developed alveolar eminences, like the anterior teeth of the *Lophius*.

From the enormous development of the muscles of the jaws, and the strength of the shells of the whelks and other testacea which are cracked and crushed by the teeth, their fracture and displacement must obviously be no unfrequent occurrence; and most specimens of the jaws of the Wolf-fish exhibit some of the teeth separated at the line of anchylosis, or broken off above the base.

With regard to the *substance* of the teeth of Fishes, the modifications of dentine, called vaso-dentine and osteo-dentine, predominate much more than in the higher Vertebrates, and they thus more closely resemble the bones which support them. The

<sup>1</sup> v. pl. 60, 61.

teeth of most of the Chætodonts are flexible, elastic, and composed of a yellowish subtransparent albuminous tissue; such, likewise, are the labial teeth of the Helostome, the premaxillary and mandibular teeth of the Goniodonts, and of the percoid genus *Trichodon*. In the Cyclostomes the teeth consist of a denser albuminous substance. The upper pharyngeal molar of the Carp consists of a peculiar brown and semitransparent tissue, hardened by salts of lime and magnesia. The teeth of the Flying-fish (*Exocætus*) and Sucking-fish (*Remora*) consist of osteo-dentine. In many Fishes, e. g. the *Acanthurus*, *Sphyræna*, and certain Sharks (*Lamna*, fig. 241), a base, or body of osteo-dentine, is coated by a layer of true dentine, *d*, but of unusual hardness, like enamel: in *Prionodon* this hard tissue predominates. In the *Labrus* the pharyngeal crushing teeth consist wholly of hard or unvascular dentine, fig. 240. In most Pycnodonts and Cestractions, and many other Fishes, the body of the tooth consists of ordinary unvascular dentine, covered by a modification of ganodentine. In *Sargus* and *Balistes* the body of the tooth consists of true dentine, and the crown is covered by a thick layer of a denser tissue, differing from the 'enamel' of Mammalia only in the more complicated and organised mode of deposition of the earthy salts. The ossification of the capsule of the complex matrix of these teeth covers the enamel with a thin coating of 'cement.' In the pharyngeal teeth of the *Scarus* a fourth substance is added by the ossification of the base of the pulp after its summit and periphery have been converted into hard dentine; and the teeth, fig. 262, thus composed of cement, *c*, enamel, *e*, dentine, *d*, and osteo-dentine, are the most complex in regard to their substance that have yet been discovered in the animal kingdom.

The tubes which convey the capillary vessels through the substance of the osteo- and vaso-dentine of the teeth of Fishes were early recognised, on account of their comparatively large size; as by André, e. g. in the teeth of *Acanthurus*,<sup>1</sup> and by Cuvier and Von Born in the teeth of the wolf-fish and other species. Leeuwenhoek had also detected the much finer tubes of the peripheral dentine of the teeth of the haddock.<sup>2</sup> These 'dentinal tubuli' are given off from the parietes of the vascular canals, and bend, divide, and subdivide rapidly in the hard basis-tissue of the interspaces of those canals in osteo-dentine; the dentinal tubuli alone are found in true dentine, and they have a

<sup>1</sup> CCXLVII.<sup>2</sup> CCXLVIII, p. 1003.

straighter and more parallel course, usually at right angles to the outer surface of the dentine. Those conical teeth which, when fully formed, consist wholly or in great part of osteo-dentine or vaso-dentine, always first appear with an apex of hard or true dentine. In some Fishes the simple central basal pulp-cavity of such teeth, instead of breaking up into irregular or parallel canals, sends out a series of vertical plates from its periphery, which, when calcified, give a fluted character to the base of the tooth, e. g. in *Lepidosteus oxyurus*.<sup>1</sup> This is the first step in the pattern of complication which attains its maximum in Labyrinthodonts and Dendrodonts, figs. 244, 246.

Thus, with reference to the main tissue of tooth, we find not fewer than six leading modifications in Fishes: hard or true dentine (*Sparoids*, *Labroids*, *Lophius*, *Balistes*, *Pycnodonts*, *Prionodon*, *Sphyræna*, *Megalichthys*, *Rhizodus*, *Diodon*, *Scarus*), osteo-dentine (*Cestracion*, *Acrodus*, *Lepidosiren*, *Ctenodus*, *Hybodus*, *Percoids*, *Sciænoids*, *Cottoids*, *Gobioids*, and many others), vaso-dentine (*Psammodus*, *Chimæroids*, *Pristis*, *Myliobates*), plici-dentine (*Lophius*, *Holoptychius*, *Lepidosteus oxyurus*, at the base of the teeth), labyrintho-dentine (*Lepidosteus platyrhinus*, *Bothriolepis*), and dendro-dentine (*Dendrodus*); besides the compound teeth of the *Scarus* and *Diodon*.

One structural modification may prevail in some teeth, another in other teeth, of the same fish; and two or more modifications may be present in the same tooth, arising from changes in the process of calcification and a persistency of portions or processes of the primitive vascular pulp or matrix of the dentine.

The dense covering of the beak-like jaws of the Parrot-fishes (*Scarus*, figs. 258, 259) consists of a stratum of prismatic denticles, standing almost vertically to the external surface of the jaw-bone. It is peculiarly adapted to the habits and exigences of a tribe of Fishes which browse upon the lithophytes that clothe, as with a richly tinted carpet, the bottom of the sea, just as the Ruminant quadrupeds crop the herbage of the dry land.

The irritable bodies of the gelatinous polypes which constitute the food of these Fishes retract, when touched, into their star-shaped stony shells, and the Scari consequently require a dental apparatus strong enough to break off or scoop out these calcareous recesses. The jaws are, therefore, prominent, short, and stout, and the exposed portions of the premaxillaries and premandibulars

<sup>1</sup> Wyman, American Journal of Natural Sciences, Oct. 1843. Cuvier has given an accurate view of the plaited structure of the base of the Wolf-fish's teeth in pl. 32, fig. 7, of his *Leçons d'Anatomie Comparée*, 1805.

are encased by the above-described complicated dental covering. The polypes and their cells are reduced to a pulp by the action of the pharyngeal jaws and teeth, that close the posterior aperture of the mouth. The superior dentigerous pharyngeals, fig. 255, present the form of an elongated, vertical, inequilateral, triangular plate: the upper and anterior margin forms a thickened articular surface, convex from side to side, and playing in a corresponding groove or concavity upon the base of the skull; the inferior boundary of the triangle is the longest, and also the broadest; it is convex in the antero-posterior direction, and flat from side to side. On this surface the teeth are implanted, and in most species they form two rows: the outer one consisting of very small, the inner one of large, dental plates, which are set nearly transversely across the lower surface of the upper pharyngeal bones and teeth, in close apposition, one behind the other: their internal angles are produced beyond the margin of the bone, and interlock with those of the adjoining bone when the pharyngeals are in their natural position; the smaller denticles of the outer row are set in the external interspaces of those of the inner row. The single inferior pharyngeal bone consists principally of an oblong dentigerous plate,<sup>1</sup> supported by a strong, slightly curved, transverse, osseous bar, the extremities of which expand into thick obtuse processes for the implantation of the triturating muscles. A longitudinal row of small oval teeth alternating with the large lamelliform teeth, like those of the superior pharyngeals, bounds the dentigerous plate on each side; the intermediate space is occupied exclusively by the larger wedge-shaped teeth, set vertically in the bone, and arranged transversely in alternate and pretty close-set series.

The dental plates are developed in wide and deep cavities in the substance of the posterior part of the lower, and of the anterior part of the upper pharyngeal bones. The teeth exhibit progressive stages of formation as they approach those in use; and, as their formation advances to completion they become soldered together by ossification of their respective capsules into one compound tooth, which soon becomes ankylosed by ossification of the dental pulp to the pharyngeal bone itself.

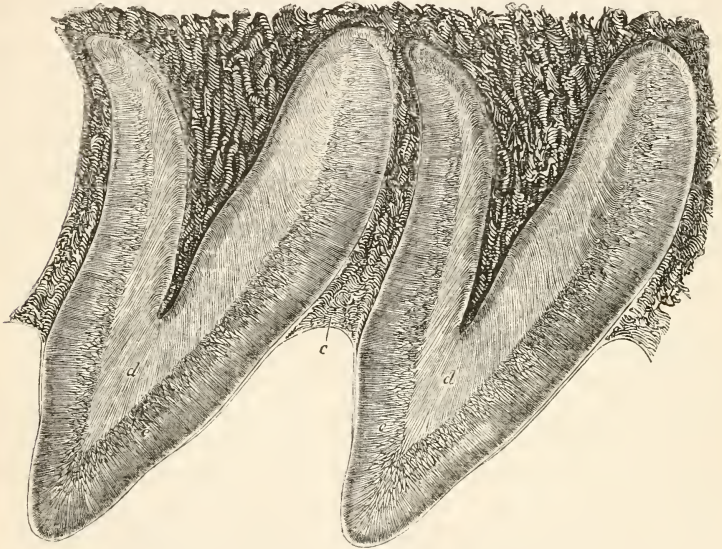
In the dentine of the pharyngeal teeth of the *Scarus* the dentinal tubes average a diameter of  $\frac{1}{20000}$  of an inch, and are separated by interspaces equal to twice their own diameter. The course of these tubes is shown in fig. 262, *d*, in which they are

<sup>1</sup> v. pl. 51, fig. 3.



exposed by a vertical section through the middle of two of the superior denticles. Each tube is minutely undulated: it dichotomises three or four times near its termination, sends off many fine lateral branches into the clear uniting substance, and finally terminates in a series of minute cells and inosculating loops at the line of junction with the enamel. This substance, fig. 262, *e*, is as thick as the dentine, and consists of a similar combination of minute tubes and a clear connecting substance. The tubes may be described as commencing from the peripheral surface of the tooth to which they

262



Two of the upper pharyngeal teeth (*Scarus*), magn.  $\times$ .

stand at right angles, and, having proceeded parallel to each other halfway towards the dentine, they then begin to divide and subdivide, the branches crossing each other obliquely, and finally terminating in the cellular boundary between the enamel and dentine.

In the progress of attrition, the thin coat of cement resulting from the ossification of the capsule is first removed from the apex of the tooth, then the enamel constituting that apex, next the dentine, and, finally, the coarse central cellular bone, supporting the hollow tooth: and thus is produced a triturating surface of four substances of different degrees of density. The enamel,

being the hardest element, appears in the form of elliptical transverse ridges, inclosing the dentine and central bone: and external to the enamel is the cement, *c*, which binds together the different denticles.

There is a close analogy between the dental mass of the *Scarus* and the complicated grinders of the Elephant, both in form, structure, and in the reproduction of the component denticles in horizontal succession. But in the fish the complexity of the triturating surface is greater than in the mammal, since, from the mode in which the wedge-shaped denticles of the *Scarus* are implanted upon, and ankylosed to, the processes of the supporting bone, this likewise enters into the formation of the masticatory surface when the tooth is worn down to a certain point.

The proof of the efficacy of the complex masticatory apparatus above described is afforded by the contents of the alimentary canal of the *Scari*. The intestines are usually laden with a chalky pulp, to which the coral dwellings have been reduced.

*Development.*—As might be supposed, by the above-defined varied and predominating vascular organisation in the teeth of Fishes, and the passage from non-vascular dentine to vascular dentine in the same tooth, the developement of dentine by centripetal metamorphosis and calcification of the pulp was determined by observations made on the developement of the teeth in the present class.<sup>1</sup>

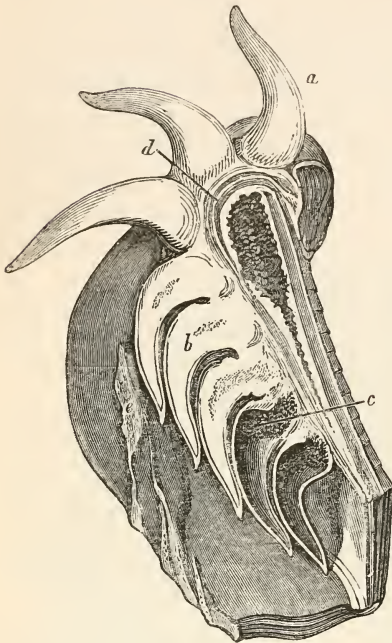
It is interesting to observe in it the process arrested at each of the well-marked stages through which the developement of a Mammalian tooth passes. In all Fishes the first step is the simple production of a soft vascular papilla from the free surface of the buccal membrane: in Sharks and Rays these papillæ, fig. 382, *c*, do not proceed to sink into the substance of the gum, but are covered by caps of an opposite free fold of the buccal membrane: these caps do not contract any organic connection with the papilliform matrix, but, as this is converted into dental tissue, ib. *b*, the tooth is gradually withdrawn from the extraneous protecting cap, to take its place and assume the erect position on the margin of the jaw, fig. 263, *a*. Here, therefore, is represented the first and transitory ‘papillary’ stage of dental developement in Mammals: and the simple crescentic cartilaginous maxillary plate, *d*, with the open groove behind containing the germinal papillæ of the teeth, offers in the Shark a magnified representation of the earliest condition of the jaws and teeth in the human embryo.

In many Fishes, e. g. *Lophius*, *Esox*, the dental papillæ become

<sup>1</sup> LXXXIX. p. 784.

buried in the membrane from which they rise, and the surface to which their basis is attached becomes the bottom of a closed sac: but this sac

263



Vertical section of jaw and teeth (*Lamna*). v.

does not become inclosed in the substance of the jaw; so that teeth at different stages of growth are brought away with the thick and soft gum, when it is stripped from the jaw-bone. The final fixation of teeth, so formed, is effected by the development of ligamentous fibres in the submucous tissue between the jaw and the base of the tooth, which fibres become the medium of connection between those parts, either as elastic ligaments or by continuous ossification. Here, therefore, is represented the 'follicular' stage of the development of a Mammalian tooth: but the 'eruptive' stage takes place without previous

inclosure of the follicle and matrix in the substance of the jaw-bone.

In *Balistes*, *Scarus*, *Sphyræna*, the Sparoids, and many other Fishes, the formation of the teeth presents all the usual stages which have been observed to succeed each other in the dentition of the higher Vertebrates: the papilla sinks into a follicle, becomes surrounded by a capsule, and is then included within a closed alveolus of the growing jaw, figs. 259, 261, *c*, where the development of the tooth takes place and is followed by the usual eruptive stages. A distinct enamel-pulp is developed from the inner surface of the capsule in *Balistes*, *Scarus*, *Sargus*, and *Chryso-phrys*.

In the formidable Barracuda (*Sphyræna*) the loss or fracture of the lancet-shaped teeth, in the conflict with a struggling prey, is repaired by an uninterrupted succession of new pulps and teeth. The existence of these is indicated by the foramina, which are



situated immediately posterior to, or on the inner margin of, the sockets of the teeth in place: these foramina lead to alveoli of reserve, in which the crowns of the new teeth, in different stages of development, are loosely embedded. It is in this position of the germs of the teeth that the Sphyrænoïd fishes, both recent and fossil, mainly differ, as to their dental characters, from the rest of the Scomberoid family.

It is interesting to observe that the alternate teeth are, in general, contemporaneously shed: so that the maxillary armour is thus preserved in an effective state. The relative position of the new teeth to their predecessors, and their influence upon them, resembles, in the *Sphyræna*, some of the phenomena which will be described in the dentition of the Crocodilian Reptiles. To the Crocodiles the present voracious Fish also approximates in the alveolar lodgement of the teeth: but it manifests its ichthyic character in the ankylosis of the fully-developed teeth to their sockets, and still more strikingly in the intimate structure of the teeth.

In all Fishes the teeth are shed and renewed, not once only, as in Mammals, but frequently, during the whole course of their lives. The maxillary dental plates of *Lepidosiren*, the cylindrical dental masses of the Chimæroid and Edaphodont Fishes, and the rostral teeth of *Pristis* (if these modified dermal spines may be so called), are, perhaps, the sole examples of 'permanent teeth' to be met with in the whole class.

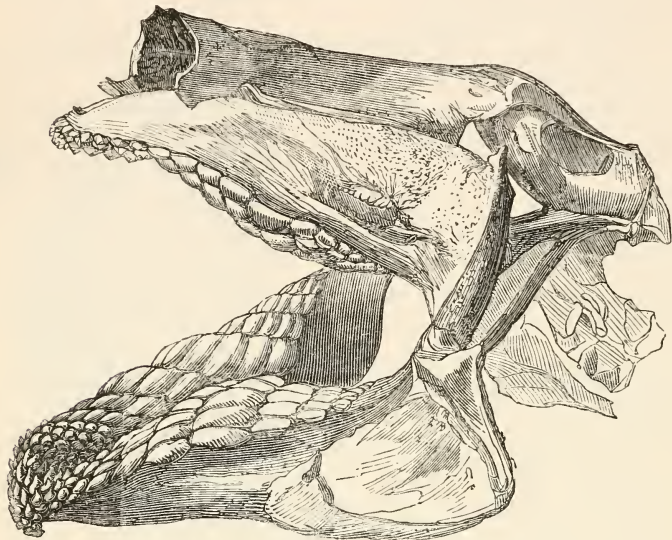
When the teeth are developed in alveolar cavities, they are usually succeeded by others in the vertical direction, as in the pharyngeal bones of the Labroids, fig. 261: but sometimes they follow one after the other, side by side, as in the Scaroids, fig. 259, *c*. In Reptiles and Mammals the successional teeth owe the origin of their matrix to the budding out from the capsule of their predecessors of a cæcal process, in which the papillary rudiment of the dentinal pulp is developed; but, in the great majority of Fishes, the germs of the new teeth are developed, like those of the old, from the free surface of the buccal membrane throughout the entire period of succession: a circumstance peculiar to the present class. The Angler, the Pike, and most of our common Fishes, illustrate this mode of dental reproduction; it is very conspicuous in the cartilaginous Fishes, figs. 263 and 264, in which the whole phalanx of their numerous teeth is ever marching slowly forwards in rotatory progress over the alveolar border of the jaw, the teeth being successively cast off as they reach the outer margin, and new



teeth rising from the mucuous membrane behind the rear rank of the phalanx.

This endless succession and decadence of the teeth, together with the vast numbers in which they often coexist in the same

264



Skull and jaws of Port Jackson Shark (*Cestracion Phillipii*), showing the forms and arrangement of the teeth. v.

Fish, illustrate the law of Vegetative or Irrelative Repetition,<sup>1</sup> as it manifests itself on the first introduction of new organs in the Animal Kingdom, under which light we must view the above-described organised and calcified preparatory instruments of digestion in the lowest class of the vertebrate series.

At the extreme limit of the class of Fishes, and connecting that class with the Reptiles, stands the very remarkable genus, the dental system of which is figured in cut 251. This consists of two small, slender, conical, sharp-pointed, and slightly recurved teeth, which project downward from the nasal bone, *c*, and of strong trenchant dental plates, anchylosed with the alveolar border of the upper, *a*, and lower, *b*, jaws, in each of which the plate is divided at the middle, or symphysial line, so as to form two distinct lateral teeth. The office of the two laniariform teeth is to pierce and retain the nutritive substance or prey which is

<sup>1</sup> CCXLIX.

afterwards divided and comminuted by the strong maxillary dental plates.

§ 71. *Teeth of Reptiles.*— If we compare the dental system of *Lepidosiren* with that in Batrachia, it is to the larval state of the Anourans that an analogy may be found: the tadpole of the Frog having its maxilla and mandibula each sheathed with a continuous horny trenchant covering. Were this sheath actually dental in tissue and united to the jaw-bone, the resemblance to the *Lepidosiren* would be closer: but it is never calcified, and is shed during the progress of the metamorphosis.<sup>1</sup> The Siren alone, among the perennibranchiates, retains the sheath upon the extremity of the upper and lower jaws; it consists of a firm albuminous tissue, and becomes harder than horn. But these trenchant mandibles, which play upon one another like the blades of a pair of curved scissors, are associated with numerous small but distinct true teeth, which are grouped together to form a rasp-like surface on each half of the divided vomer, and which beset the alveolar border of the splenial element of the mandible below.

The whole order of Chelonia is edentulous, as well as the family of Toads (*Bufo*idæ) in the order Batrachia; certain extinct genera of Saurians were likewise edentulous, e. g. *Rhynchosaurus* and *Oudenodon*.<sup>2</sup>

In the Tortoises and Turtles the jaws are covered by a sheath of horn, which in some species is very dense; its working surface is trenchant in the carnivorous species, but is thick, variously sculptured, and adapted for both cutting and bruising in the vegetable feeders. The development of the continuous horny maxillary sheath commences, as in the Parrot tribe, from a series of distinct papillæ, which sink into alveolar cavities, regularly arranged (in *Trionyx*) along the margins of the upper and lower jaw-bones: these alveoli are indicated by the persistence of vascular canals long after the originally separate tooth-like cones have become confluent, and the horny sheath completed.

The teeth of the dentigerous Saurian, Ophidian, and Batrachian Reptiles are, for the most part, simple and adapted for seizing and holding, but not for dividing or masticating, their food. The Siren alone combines true teeth with a horny maxillary trenchant sheath, like that of the Chelonian Reptiles.

<sup>1</sup> The large dental plates of *Lepidosiren* have their nearest homologues in those of the extinct fish called *Ceratodus* (v. pl. 22, fig. 2).

<sup>2</sup> CCXXIII. p. 54, pl. I. fig. 1.

With respect to *number*, in no existing Reptile are the teeth reduced so low as in certain Mammals and Fishes; nor, on the other hand, are they ever so multiplied as in many of the latter class. *Myobatrachus paradoxus*, an Australian Frog, has but two teeth in the premaxillary bones. The extinct Dicynodont Reptiles of South Africa had two long tusks implanted in the upper jaw, fig. 271.<sup>1</sup> Some species of *Amphisbæna* (*A. alba*), with fifteen teeth in the upper jaw and fourteen in the lower jaw, and certain Monitors (*Varanus*), with sixteen teeth in the upper and fourteen in the lower jaw exemplify a low number of teeth amongst existing Reptiles; and certain Batrachians, with teeth 'en cardes' at the roof of the mouth, or which have upwards of eighty teeth in each lateral maxillary series, present the opposite extreme. Rarely, however, is the number of the teeth so fixed and determinate in any Reptile as to be characteristic of the species, and still more rarely have the individual teeth such characters as to be determined homologically from one species to another.

With respect to *situation*, the teeth may be present on the jaws only, i. e. the maxillary, the premaxillary, and mandibular bones, as in the Crocodiles, fig. 95, and many Lizards: or upon the jaws and roof of the mouth: and here either upon the pterygoid bones, as in the Iguana, fig. 98, D, 24, and Mosasaur; or upon both palatine and pterygoid bones, as in most Serpents, fig. 266, 20, 24; or upon the vomer, as in most Batrachians, fig. 265, *l*; or upon both vomerine and pterygoid bones, as in the Axolotl; or upon the vomerine and sphenoid bones, as in *Salamandra glutinosa*. With respect to the marginal or jaw teeth, these may be absent in the premaxillary bones, as in many Serpents, fig. 266, 22: or they may be present in the upper and not in the lower jaw, as in most Frogs: or in both upper and lower jaws, as in the tailed Batrachians: and among these they may be supported, upon the lower jaw, by the premandibular or dentary piece, as in the Salamanders, Menopome, Amphiume, Proteus: or upon the splenial piece, as in the Siren: or upon both splenial and premandibular bones, as in the Axolotl. The palatine and pterygoid teeth may, in the Batrachians, be arranged in several rows, like the 'dents en cardes' of Fishes. The sphenoid and splenial teeth are always so arranged in the few species that possess them. The intermaxillary, maxillary, and premandibular teeth are uniserial, or in one row, with the exception of the Cæcilia and the extinct

<sup>1</sup> CLVIII. vol. vii. p. 59.

Labyrinthodonts, which have a double row of teeth at the anterior part of the lower jaw.

The teeth of Reptiles, with few exceptions, present a simple conical *form*, with the crown more or less curved, and the apex more or less acute. The cone varies in length and thickness; its transverse section is sometimes circular, but more commonly elliptical or oval: and this modification of the cone may be traced through every gradation, from the thick, round, canine-like tooth of the Crocodile to the sabre-shaped fang of the Varanus, the Megalosaur, and the Cladeiodon.<sup>1</sup> Sometimes, as in the fully formed teeth of the Megalosaur, one of the margins of the compressed crown of the tooth is trenchant, sometimes both are so; and these may be simply sharp-edged, as in the Varanus of Timor, or finely serrated, as in the great Varanus, the Cladeiodon, and the Megalosaur.<sup>2</sup>

The outer surface of the crown of the tooth is usually smooth; it may be polished, as in the Leiodon, or impressed with fine lines, as in the Labyrinthodon, fig. 243, or raised into many narrow ridges, as in the Pleiosaur and Polyptychodon, or broken by a few broad ridges, as in the Iguanodon, fig. 273, or grooved by a single longitudinal furrow, as in some Serpents, fig. 269, c.<sup>3</sup>

The cone is longest and its summit sharpest in the Serpents: from these may be traced, chiefly in the Lizard tribe, a progressive shortening, expansion of the base, and blunting of the apex of the tooth, until the cone is reduced to a hemispherical tubercle, or plate, as in *Cyclodus*, fig. 272, and, in a more remarkable degree, in the extinct shellfish-eating Saurian, called *Placodus*.<sup>4</sup>

In the Pleiosaur the dental cone is three-sided, with one of the angles rounded off. The posterior subcompressed teeth of the Alligator, fig. 275, present a new modification of form; here they terminate in a mammillate summit, supported by a slightly constricted neck. In the tooth of the Hylæosaur the expanded summit is flattened, bent, and spear-shaped, with the edges blunted. But the expansion of the crown is greatest in the subcompressed teeth of the extinct *Cardiodon* and the existing Iguanas, the teeth of which are farther complicated by having the margins notched. The great Iguanodon had the crown of the tooth expanded both in length and breadth, and combining

<sup>1</sup> v. pl. 62 A, fig. 4.

<sup>2</sup> Ib. fig. 6 c.

<sup>3</sup> Ib. pl. 65. CCL. vol. iv. figs. 209, 210.

<sup>4</sup> CXLIII. p. 169.



marginal dentations with longitudinal ridges: this tooth, fig. 273, presents the most complicated external form as yet discovered in the class of Reptiles.

In no Reptile does the base of the tooth ever branch into fangs.

*Attachment.*—As a general rule, the teeth of Reptiles are anchylosed to the bone which supports them. When they continue distinct, they may be lodged either in a continuous groove, as in the Ichthyosaur,<sup>1</sup> or in separate sockets, as in the Plesiosaur and Crocodilians, fig. 275. The base of the tooth is anchylosed to the wall of a moderately deep socket in the extinct Megalosaur and Thecodon. In the Labyrinthodonts and Cæciliæ, among the Batrachians, in most Ophidians, and in the Geckos, Agamians, and Varanians, among the Saurians, the base of the tooth is imbedded in a shallow socket, and is confluent therewith.

In the Scincoids, the Safeguards (*Tejus*), in most Iguanians, in the Chameleons and many Lacertian reptiles, the tooth is anchylosed by an oblique surface extending from the base more or less upon the outer side of the crown to an external alveolar plate of bone,<sup>2</sup> the inner alveolar plate not being developed. In the Frogs the teeth are similarly but less firmly attached to an external parapet of bone. The Lizards which have their teeth thus attached to the side of the jaw are termed ‘Pleurodonts.’ In a few Iguanians, as the Istiures and Rhynchocephalus, the teeth are soldered to the margins of the jaws; and in some large extinct Lacertians, e. g. the Mosasaur and Leiodon, each tooth is fixed upon a conical process of the alveolar border: these Sauria are termed ‘Acrodonts.’

Such modifications of the attachment of the teeth of Reptiles are adapted to the habits and food of the species; and they likewise offer an analogy to some of the transitory conditions of the human teeth. There is a period, for example, when the primitive dental papillæ are not defended by either an outer or an inner alveolar process, any more than their calcified homologues, which are confluent with the margin of the jaw in the Rhynchocephalus.<sup>3</sup> There is another stage in which the groove containing the dental germs is defended by a single external cartilaginous alveolar ridge; this condition is permanently typified in the *Cyclodus*, fig. 272, and most existing Lizards. Next there is developed in the human embryo an internal alveolar plate, and the sacs and pulps of the teeth sink into a deep but continuous groove, in which traces of transverse partitions soon make their appear-

<sup>1</sup> v. pl. 13, fig. 9.

<sup>2</sup> v. pl. 67.

<sup>3</sup> CLVIII. pt. 2, pl. 6, figs. 5 & 6, p. 83.

ance; in the ancient Ichthyosaur the relation of the jaws to the teeth never advanced beyond this stage. Finally, the dental groove is divided by complete partitions, and a separate socket is formed for each tooth; and this stage of development is attained in the highest-organised Reptiles, e. g. the Crocodiles, figs. 95, 275.

*Substance.*— This may be four-fold, and a single tooth may be composed of dentine, cement, enamel, and bone: but the dentine and cement are present in the teeth of all Reptiles.

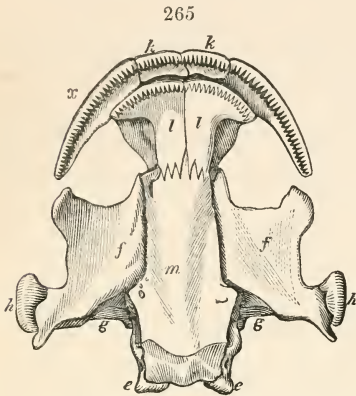
In the Batrachians and Ophidians a thin layer of cement invests the central body of dentine, and, as usual, follows any inflections or sinuosities that may characterise its surface. Besides the outer coat of cement, which is thickest at the base, a generally thin coat of enamel defends the crown of the tooth in most Saurians, and the last remains of the pulp are not unfrequently converted into a coarse bone, both in the teeth which are anchylosed to the jaw, and in some teeth, as those of the Ichthyosaur, which remain free. The modification called ‘vaso-dentine’ is peculiar in the present class to the teeth of the Iguanodon.<sup>1</sup>

*Structure.*— The varieties of dental structure are few in the Reptiles as compared with Fishes or Mammals, and its most complicated condition arises from interblending of the dental and other substances rather than from modifications of the tissues themselves. In the teeth of most Reptiles the intimate structure of the dentine is of the hard or unvascular kind, presenting only plasmatic or dental tubes, diverging from the pulp cavity, at right angles to the external surface of the tooth. Such dentine may be folded inwardly upon itself, so as to produce a deep longitudinal indentation on one side of the tooth; it is the expansion of the bottom of such a longitudinal deep fold that forms the central canal of the venom-fang of the Serpent: but its structure remains unaltered; and although the pulp-cavity, fig. 270, *p*, is reduced to the form of a crescentic fissure, the dental tubes continue to radiate from it according to the usual law. By a similar inflection of many vertical longitudinal folds of the cement and external surface of the tooth at regular intervals around the entire circumference of the tooth, and by a corresponding extension of radiated processes of the pulp-cavity and dentine into the interspaces of such inflected and converging folds, a modification of dental structure is established in certain extinct Reptiles, which,

<sup>1</sup> v. pl. 71, Iguanodon.

by the various sinuosities of the interblended folds of cement and processes of dentine, with the partial dilatations of the radiated pulp-cavity, produces the complicated structure which is described at p. 365, and figured in cut 244.

*Development.*—The teeth of Reptiles are never completed at the first or papillary stage; the pulp sinks into a follicle, and becomes inclosed by a capsule; and in certain reptiles this becomes more or less surrounded by bone; but the ‘eruptive’ stage, in the sense in which this is usually understood, as signifying the extrication of the young tooth from a closed alveolus, is not exemplified in recent Reptiles, and was rare in extinct ones.<sup>1</sup>



Teeth of Menopome; *k* premaxillary, *l* vomerrine, *x* maxillary

The completion of a tooth, with the exception of the Diconodont Reptiles, is soon followed by preparation for its

removal and succession; the faculty of developing new tooth-germs seems to be unlimited in the present class, and the phenomena of dental decadence and replacement are manifested at every period of life; the number of teeth is generally the same in each successive series, and the difference of size presented by the teeth of different and distant series in the same individual is considerable.

The new germ is always developed, in the first instance, at the side of the base of the old tooth, never in the cavity of the base; the crocodiles form no exception to this rule. The poison-fangs of serpents succeed each other from behind forwards; in almost every other instance the germ of the successional tooth is developed at the inner side of the base of its predecessor. In the Frog the dental germ makes its appearance in the form of a papilla developed from the bottom and towards the outer side of a small fissure in the mucous membrane or gum that fills up the shallow groove at the inner side of the alveolar parapet and its adherent teeth: the papilla is soon enveloped by a capsular process of the surrounding membrane. As the tooth acquires hardness and size, it presses against the

<sup>1</sup> CXLIII. p. 178, pl. ix., fig. 4, a'.

base of the contiguous attached tooth, causes a progressive absorption of that part, and finally undermines, displaces, and replaces its predecessor. The number of nascent matrices of the successional teeth is so great in the Frog, and they are crowded so close together, that it is not unusual to find the capsules of contiguous tooth-germs becoming adherent together, as their ossification proceeds. After a brief maceration, the soft gum may be stripped from the shallow alveolar depression, and the younger tooth-germs in different stages of growth are brought away with it.

The mode of development of the teeth of serpents does not differ essentially from that of the teeth of the Batrachian above described, except in the relation of the papillæ of the successional poison-fangs to the branch of the poison-duct that traverses the cavity of the loose mucous gum in which they are developed.

Some of the peculiarities of the dentition of the Batrachians have already been noticed, as in the comparison of the *Siren* with the *Lepidosiren*, in which the true amphibian was shown to have numerous teeth on the palate and lower jaw.<sup>1</sup> The piscine character of rasp-like teeth aggregated in numerous series, is manifested also in the Axolotl,<sup>2</sup> upon the palatal region of the mouth, and upon the splenial or opercular element of the lower jaw; but the superior maxillary bones are here developed, and also support teeth. The premandibular and the premaxillary bones, instead of preserving the larval condition of the horny sheath, have their alveolar border armed with a single row of small, equal, fine and sharp-pointed denticles, which are continued above, along the maxillaries; thus establishing the commencement of the ordinary Batrachian condition of the marginal teeth of the buccal cavity. The dentigerous bones of the palate consist of two plates on each side, as in the *Siren*; the anterior pair, or vomerine bones, converge and meet at their anterior extremities; the minute denticles which they support are arranged quincuncially; the posterior pair of bones are continued backwards according to the usual disposition of the pterygoids, to abut against the tympanic bones; the denticles are confined to the anterior part of their oral surface, and resemble in their arrangement and anchylosed attachment those of the vomerine series, of which they form the posterior termination.

In the Menopome, fig. 265, the teeth are small, pointed, in a

<sup>1</sup> v. pl. 62, figs. 5 & 6.

<sup>2</sup> Ib. pl. 62, fig. 4.



single row, in each bone; describing a semicircle, upon the premaxillary, *h*, and maxillary, *x*, bones: a shorter parallel series is supported on the vomerine bones, *l*.<sup>1</sup> The mandibular series is received into the interspace of the two rows in the upper jaw.

The Frogs (*Rana*)<sup>2</sup> have no teeth on the lower jaw; but in some species the alveolar edge of this bone is finely notched or dentated, as in the horned Frogs (*Ceratophrys*). *Dactylethra* has maxillary teeth only; *Myobatrachus* has but two horizontal premaxillary teeth. Both premaxillary and maxillary bones usually support a long, close-set, single series of small, conical, hollow teeth, of which the apices only project beyond the external alveolar ridge to which they are attached. A short transverse row of similar but smaller teeth extends along the posterior border of each vomer. Other dispositions of the vomerine teeth help to characterise the genera of *Ranidæ*, in a few of which they are wanting; as, e.g., in *Uperoleia*, in the slender-armed Frogs (*Leptobrachium*), in *Oxyglossus*, and in some of the Tree Frogs (e.g. *Eucnemis*), in which the roof of the mouth is edentulous.

Amongst the most extraordinary examples of extinct reptiles are those which are characterised by the labyrinthic modification of the dental structure above described, and which, with some affinities to Saurians, combine characters which are essentially those of the order Batrachia. In *Labyrinthodon leptognathus*, the upper jaw contains a single row of small teeth, about sixty in number, anterior to which are three or four large conical tusks. The apical two thirds of each tooth is smooth, but the basal third is fluted and ankylosed to the outer wall of the socket. The osseous roof of the mouth is principally composed of a pair of broad and flat bones, homologous with the divided vomer in Batrachia, but of much greater relative extent. Each bone supports anteriorly three median small teeth and two outer larger ones, from which a longitudinal row of small and equal-sized teeth is continued backward along the exterior margin of the vomer. The whole of this series of vomerine teeth is nearly concentric with the maxillary teeth.

In Lacertine reptiles the examples of a row of palatal teeth are rare, and, when present, it is short, and situated upon the pterygoid bones, as in the Iguana and Mosasaur. In Batrachians the most common disposition of the palatal teeth is a transverse row placed at the anterior part of the divided vomer, as in Frogs, and the Menopome. In the Amphiume, the vomerine teeth form a nearly longitudinal series along the outer margin of the palatine bones.

<sup>1</sup> v. pl. 62, fig. 10.

<sup>2</sup> Ib. pl. 62, fig. 10.

The *Labyrinthodon* combines both these dispositions of the palatal teeth. The lower jaw, like the upper, contains a series of small teeth, with a few larger tusks anterior to them. The sockets of the teeth are shallower than in the upper jaw; the outer wall is more developed than the inner, and the anchylosed bases of the teeth more nearly resemble, in their oblique position, those of existing Batrachia. Between the apex and the part where the inflected vertical folds of the cement commence, the tooth of the *Labyrinthodon* resembles, in the simplicity of its intimate structure, that of the entire tooth of ordinary Batrachia and most reptiles; and in the lower or basal half of the tooth the labyrinthic structure above described commences, and gradually increases in complexity.

In the genus *Deirodon*,<sup>1</sup> the teeth of the ordinary bones of the mouth are so small as to be scarcely perceptible; and they appear to be soon lost. An acquaintance with the habits and food of this species has shown how admirably this apparent defect is adapted to its well-being. Its business is to restrain the undue increase of the smaller birds by devouring their eggs. Now if the teeth had existed of the ordinary form and proportions in the maxillary and palatal regions, the egg would have been broken as soon as it was seized, and much of the nutritious contents would have escaped from the lipless mouth of the snake in the act of deglutition; but, owing to the almost edentulous state of the jaws, the egg glides along the expanded opening unbroken; and it is not until it has reached the gullet, and the closed mouth prevents any escape of the nutritious matter, that the egg becomes exposed to instruments adapted for its perforation. These instruments consist of the hypapophyses of the seven or eight posterior cervical vertebræ, the extremities of which are capped by a layer of hard cement, and penetrate the dorsal parietes of the œsophagus.<sup>2</sup> They may be readily seen, even in very small subjects, in the interior of that tube, in which their points are directed backwards. The shell being sawed open longitudinally by these vertebral teeth, the egg is crushed by the contractions of the gullet, and is carried to the stomach, where the shell is no doubt soon dissolved by the acid gastric juice.

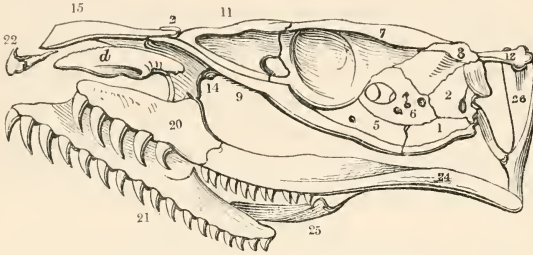
In the Boa and Pythons, fig. 266, the teeth are slender, conical, bent backward and inward above their base of attachment. The premaxillary bone in some, ib. 22, is edentulous; in most it supports four small teeth; each maxillary bone, ib. 21, has a row

<sup>1</sup> The *Coluber scaber* of Linnæus; an arboreal serpent of South Africa.

<sup>2</sup> Jourdan, in CCXLII, t. vi. p. 160.

of larger ones, which gradually decrease in size as they are placed further back. There are teeth of similar size and proportions in each premandibular bone. These teeth are separated by intervals,

266

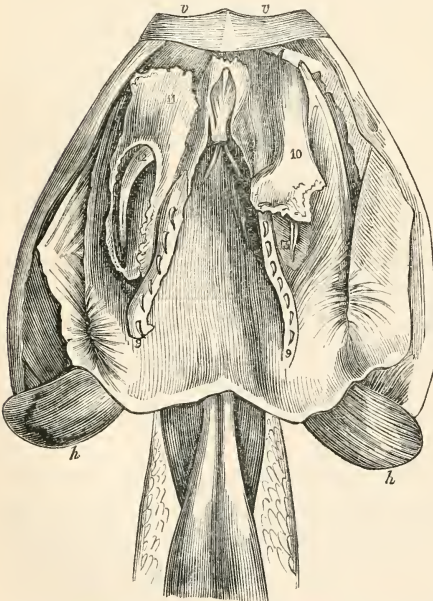


Dentition, upper jaw, Python. CCL.

from which other teeth, similar to those in place, have been detached. The base of each is anchylosed to a shallow alveolus, extending obliquely across the alveolar groove, of which the outer is higher than the inner wall.

The palatine teeth, ib. 20, are as large as the maxillary, and are similarly attached. The pterygoid teeth, ib. 24, which complete the internal dental series on the roof of the mouth, are of smaller size, and gradually diminish as they recede backward. In the interspaces of the fixed teeth in both of these bones, the places of attachment of the shed teeth are always visible; so that the dental formula, if it included the vacated with the occupied sockets, would express a greater number of teeth than are ever in place and use at the same time.

267



Roof of the mouth of the Rattlesnake, showing the poison-fangs, 10, 11, and pterygoid teeth, 9. CCL.

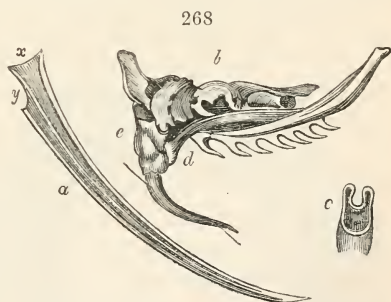
The smaller non-venomous serpents, *Colubridæ*, e. g. have two rows of teeth on the roof of the mouth,

extending along the palatines and pterygoids. The genus *Oligodon* appears to form the sole exception to this rule. In the *Dryinus nasutus*, a few small teeth are present on the ectopterygoid as well as on the pterygoid.

In *Dryophis*, *Dipsas*, and *Bucephalus*, in which the maxillary teeth increase in size towards the posterior part of the bone, the large terminal teeth of the series are traversed along their anterior and convex side by a longitudinal groove. In the *Bucephalus capensis*, the two or three posterior maxillary teeth present this structure, and are much larger than the anterior teeth, or those of the palatine and premandibular series. They add materially, therefore, to the power of retaining the prey, and may conduct into the wounds which they inflict an acrid saliva; but they are not in connection with the duct of an express poison-gland. The long grooved fangs are either firmly fixed to the maxillary bones, or are slightly moveable, according to their period of growth. They are concealed by a sheath of thick and soft gum, and their points are directed backward. The sheath always contains loose recumbent grooved teeth, ready to succeed those in place.

In most of the *Colubri*, each maxillary and premandibular bone includes from twenty to twenty-five teeth. They are less numerous in the genera *Tortrix* and *Homalopsis*, and are reduced to a still smaller number in the poisonous serpents, in the typical genera of which the short maxillary bone supports only a single perforated fang.

The maxillary, fig. 268, *e*, diminishes in length with the decreasing number of teeth which it supports: the ectopterygoid, *d*, elongates in the same ratio, so as to retain its position as an abutment against the shortened maxillary; and the muscles implanted into



Structure of the poison-teeth of the Rattle-snake

the ectopterygoid communicate through it to the maxillary bone the hinge-like movements backward and forward upon the ginglymoid articulations connecting that bone with the prefrontal and palatine bones. As the fully developed poison-fangs are attached by the same firm basal anchylosis to maxillary sockets, which forms the characteristic mode of attachment of the simple or solid teeth, they necessarily follow all the movements of the superior maxillary bone. When the external pterygoid is re-



tracted, the superior maxillary rotates backward, and the poison-fang is concealed in the lax mucous gum, with its point turned backward, fig. 267, 10. When the muscles draw forward the external pterygoid, the maxillary bone is pushed forward, and the recumbent fang withdrawn from its concealment and erected.

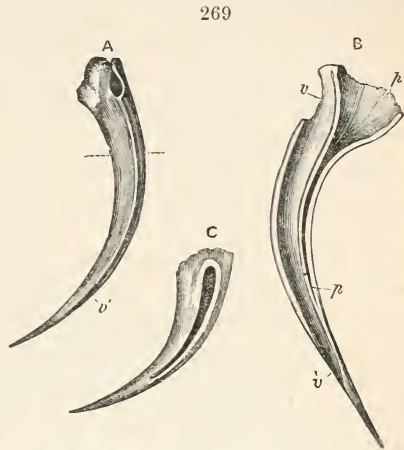
In this power of changing the direction of a large tooth, so that it may not impede the passage of food through the mouth, we may perceive an analogy between the viper and the *Lophius*; but in the fish the movement is confined to the tooth alone, and is dependent on the mere physical property of the elastic medium of attachment; in the serpent the tooth has no independent motion, but rotates with the jaw, whose movements are governed by muscular actions. In the fish the great teeth are erect, except when pressed down by some extraneous force. In the serpent the habitual position of the fang is the recumbent one, and its erection takes place only when the envenomed blow is to be struck.

A true idea of the structure of a poison-fang will be formed by supposing the crown of a simple tooth, as that of a boa, to be pressed flat, and its edges to be then bent towards each other, and soldered together so as to form a hollow cylinder, or rather cone, open at both ends. The flattening of the fang and its inflection around the poison-duct commences immediately above the base, and the suture of the inflected margins runs along the anterior and convex side of the recurved fang, as shown in fig. 269, A: the poison-canal is thus in front of the pulp-cavity, as shown in the longitudinal section of the fang, fig. 268, *y*, and fig. 269, B. The basal aperture of the poison-canal, *ib. v*, is oblique, and its opposite outlet *v'* is still more so, presenting the form of a narrow elliptical longitudinal fissure, terminating at a short distance from the apex of the fang. In fig. 268, a fine hair is represented as passing through the poison-canal by the duct of the fang.

The secretion of the poison-gland is conveyed to the basal aperture of the poison-canal of the fang. We may suppose, that as the analogous lacrymal and salivary glands in other animals are most active during particular emotions, so the rage which stimulates the venom-snake to use its deadly weapon must be accompanied with an increased secretion and great distension of the poison-glands; and as the action of the compressing muscles is contemporaneous with the blow by which the serpent inflicts the wound, the poison is at the same moment injected with force into the wound from the apical outlet of the perforated fang.

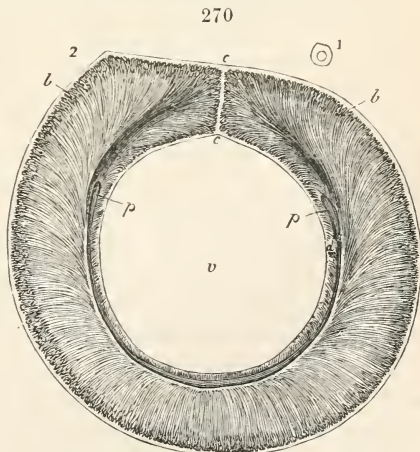
The duct which conveys the poison, although it runs through

the centre of a great part of the tooth, is really on the outside of the tooth, the canal in which it is lodged and protected being formed by a longitudinal inflection of the dentinal parietes of the pulp-cavity, fig. 270, *c*. This inflection commences a little beyond the base of the tooth, where its nature is readily appreciated, as the poison-duct there rests in a slight groove or longitudinal indentation on the convex side of the fang, fig. 269, A, B, *v*; as it proceeds it sinks deeper into the substance of the tooth, and the sides of the groove meet and seem to coalesce, so that the trace of the inflected fold ceases, in some species, to be perceptible to the naked eye; and the fang appears, as it is commonly described, to be perforated by the duct of the poison-gland. In the *Hydrophis* the groove remains permanently open, as in fig. 269, *c*.



Poison-fangs of A, Viper; B, Cobra (in section);  
C, *Hydrophis*. v.

From the position of the poison-canal it follows that the transverse section of the tooth varies in form in different parts of the tooth: at the base it is oblong, with a large pulp-cavity of a corresponding form, with an entering notch at the anterior surface, fig. 268, *c*; farther on, the transverse section presents the form of a horseshoe, and the pulp-cavity that of a crescent, the horns of which extend into the sides of the deep cavity of the poison-fang: a little beyond this part the section of the tooth itself is crescentic, with the horns obtuse and in contact, so as to circumscribe the poison-canal; and along the whole of the middle four



Section of poison-fang of Cobra, magn. v.

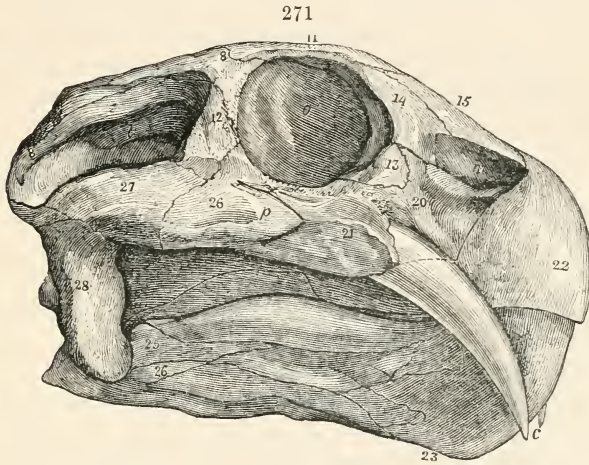
sixths of the tooth, the section, of which a magnified view is given in fig. 270, shows the dentine of the fang inclosing the poison-canal, and having its own centre or pulp-canal,  $p, p$ , in the form of a crescentic fissure, situated close to the concave border of the inflected surface of the tooth. The pulp-cavity disappears, and the poison-canal again resumes the form of a groove near the apex of the fang, fig. 269,  $A, B, v'$ , and terminates on the anterior surface in an elongated fissure.

The venom-fangs of the viper, rattle-snake, and the *Fer-de-lance* are coated only with a thin layer of a subtransparent and minutely cellular cement. The disposition of the dentinal tubes is obedient to the general law of verticality to the external surface of the tooth; it is represented as seen in the transverse section from the middle of the fang in fig. 270. Since the inflected surface of the tooth can be exposed to no other pressure than that of the turgescient duct with which it is in contact, the tubes which proceed to the central surface, while maintaining their normal relation of the right angle to it, are extremely short; and the layer of dentine separating the poison-tube from the pulp-cavity is proportionally thin. The dentinal tubes that radiate from the opposite side of the pulp-cavity to the exposed surface  $b$  of the tooth are disproportionately long.

The teeth of Ophidians are developed and completed in that part which forms the original seat of the tooth-germs in all animals; viz. the mucous membrane or gum covering the alveolar border of the dentigerous bones. The primitive dental papilla in the common harmless snake very soon sinks into the substance of the gum, and becomes enclosed by a capsule. As soon as the deposition of the calcareous salts commences in the apex of the papilla, the capsule covering that part becomes ossified and adherent to the dentine, and the tooth begins to pierce and emerge from the gum before its mould, the pulp, is half completed. Fresh layers of cells are successively added to the base of the pulp, and converted, by their confluence and calcification, into the tubular dentine, until the full size of the tooth is attained, when its situation in the gum is gradually changed, and its base becomes ankylosed to the shallow cavity of the alveolar surface of the bone. In the posterior part of the large mucous sheath of the poison-fang, the successors of this tooth are always to be found in different stages of development; the pulp is at first a simple papilla, and when it has sunk into the gum the succeeding portion presents a depression along its

inferior surface, as it lies horizontally, with the apex directed backward; the capsule adheres to this inflected surface of the pulp; and the base of the groove of the loose growing poison-fang is brought into the same relation with the duct of the poison gland as the displaced fang, which has been severed from the duct.

The existing species of Lizards differ from those of Crocodiles in the anchylosed condition of the teeth, which present few modifications of importance: those that yield most fruit to physiology, and which have most expanded our ideas of the extent of the



Skull of *Dicynodon lacerticeps*, one third natural size

resources of Nature and the exceptional deviations from what was deemed the rule of structure in the Saurian dentition, have been discovered by the study of the fossil teeth of extinct forms of the order. Amongst these the most extraordinary are those called ‘*Dicynodonts*,’<sup>1</sup> from their dentition being reduced to one long and large canine tooth on each side of the upper jaw. These teeth recall, at first sight, the character which the long poison-fangs give, when erected, to the upper jaw of the Rattle snake. The alveolar border of the lower jaw and of the premaxillary part of the upper jaw is trenchant, and seems to have been sheathed with horn. The maxillary, fig. 271, 21, is excavated by a wide and deep alveolus, with a circular area, and lodges a long and strong, slightly curved, and sharp-pointed tusk, which projects about two thirds of its length from

<sup>1</sup> From *δύς*, two, and *κυνόδους*, the name given by Hippocrates to the *canine teeth*, and signifying the same idea as their common English denomination.



the open extremity of the socket; the two converging, as they descend along the outer side of the compressed symphysis of the lower jaw. The tusk is principally composed of a body of compact unvascular dentine. The base is excavated by a wide conical pulp-cavity with the apex extending to about one half of the implanted part of the tusk, and a linear tract is continued along the centre of the solid part of the tusk.

The enamel is thinner than in the teeth of the Crocodile. There is a trace of cement on the exterior of the sections of the implanted base of the tusks. In the lower jaw, *ib.* 25, 23, the alveolar border of the dentary element presents a smooth and even edge, which seems to have played like a scissor-blade upon the inner side of the corresponding edentulous border of the upper jaw. In some Dicynodonts (*Ptychognathus*) the symphysis was singularly produced upward.

Until the discovery of the *Rhynchosaurus*<sup>1</sup> and *Oudenodon*, this edentulous and horn-sheathed condition of the jaws was supposed to be peculiar to the Chelonian order among reptiles.<sup>2</sup> In the Saurian Dicynodon we find, superadded to the horn-clad mandibles of the Tortoise, a pair of tusks, borrowed as it were from the mammalian class, or rather foreshadowing a structure which, in the actual creation, is peculiar to certain members of the highest-organised warm-blooded animals.

In the other Reptilia, recent or extinct, which most nearly approach the Mammalia in the structure of their teeth, the difference characteristic of the inferior and cold-blooded class is manifested in the shape, and in the system of shedding and succession, of the teeth: the base of the implanted tooth seldom becomes consolidated, never contracted to a point, as in the fangs of most mammalian teeth; and at all periods of growth one or more germs of teeth are formed within or near the base of the tooth in use, prepared to succeed it, and progressing towards its displacement. The dental armature of the jaws is kept in serviceable order by uninterrupted change and succession; but the matrix of the individual tooth is soon exhausted, and the life of the tooth itself may be said to be comparatively short.

The Dicynodonts not only manifest the higher type of free implantation of the base of the tooth in a deep and complete socket, common to Crocodilians, Megalosaurus, and Thecodonts, but make an additional step towards the mammalian type of

<sup>1</sup> Transactions of the Cambridge Philosophical Society, vol. vii. part iii.

<sup>2</sup> CLVIII.

dentition, by maintaining the serviceable state of the tusk by virtue of constant renovation of the substance of one and the same matrix, according to the principle manifested in the long-lived and ever-growing tusks of the Walrus, and the scalpriform incisors of the Rodentia.

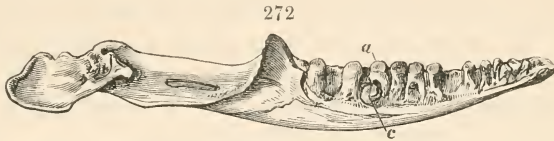
Naturalists have availed themselves of characteristics of the dental system to arrange the genera of the squamate Lacertians. In the first group, the teeth are solid, or without any permanent internal cavity, and are ankylosed by their base to the alveolar groove. The species which present this character are called 'Pleodonts.' In the second group, the teeth are excavated, or retain the pulp-cavity, and are less firmly fixed to the jaws, being applied vertically, like piles or buttresses, against the outer alveolar parapet, but not adhering by their base. This group is called 'Cœlodonts.'

The Monitor of South America (*Tupinambis teguixin*) is an example of the Pleodont group, in which the premaxillary teeth are ten in number. The maxillary teeth vary from ten to fifteen on each side, and increase in size as they are placed farther back: the hindmost teeth are tricuspid in young individuals, and present the form of simple tubercles in the old Monitors. The mandibular teeth, fifteen to eighteen in number in each ramus, correspond in size and form with those above. In the Cœlodont group, the 'Swift lizards' (*Tachydromus*) have the pterygoid bones armed with minute teeth. The teeth on both upper and lower jaws are of larger size, and the hinder ones are tricuspid. The true Lizards (*Lacerta*) have two kinds of teeth *quoad* form; the anterior small, conical, and recurved: the posterior larger, and bi- or tri-cuspid. Some species have also pterygoid teeth; as the common *Lacerta agilis*.

In the gigantic fossil Sea-monitor of Maestricht (*Mosasaurus*) the teeth combine the 'Pleodont' with the 'Acrodont' characters. All the teeth are slightly recurved, and their peripheral surface is smooth: the crown is pyramidal, with the outer side nearly plane, or slightly convex, and separated by two sharp ridges from the remaining surface, which forms a half-cone. The larger teeth are implanted upon the premaxillary, maxillary, and premandibular bones; a series of similarly shaped but much smaller teeth are placed upon the pterygoid bones.

Most of the smooth-scaled Lizards have small mouths and slender sharp teeth, fitted best for insect food: they are usually confined to the upper and lower jaws; but the medicinal Scink of ancient pharmacy (*Scincus officinalis*) has four or five small obtuse

teeth upon each pterygoid bone. The chief exception to the typical dentition of the present family is made by the large scincoid lizards of Australia, which, on that account, have received the generic name of *Cyclodus*. The dentition of the *Cyclodus nigroluteus* is exemplified in the lower jaw, fig. 272. In the upper jaw, the single premaxillary bone has depressions for twelve teeth,



Lower jaw and teeth of *Cyclodus nigroluteus*. v.

of which only the alternate ones are usually in place; they are of very small size, with the fang compressed laterally, and the crown antero-posteriorly, so as to resemble a true incisor in form, the summit sloping to an edge from behind forwards, with the middle of the cutting surface a little produced. Each superior maxillary bone has depressions for fourteen teeth; they quickly increase in size, and exchange their conical for a sub-hemispherical crown; the eighth to the thirteenth inclusive are the largest teeth; they are set obliquely, and pretty close together. In the lower jaw there are two small incisors, at the anterior part of each pre-mandibular bone corresponding with those of the premaxillary; these are succeeded by five or six conical teeth, and the rest correspond in size and form with the tuberculate molars of the upper jaw. All the teeth are attached, after the Pleurodont type, by their base and outer margin to shallow depressions on the outer side of the external alveolar parapet. The germs of the successional teeth, *c*, fig. 272, are developed at the inner side of the base of their predecessors, *a*, which they excavate, undermine, and displace in the usual manner.

Certain genera of the *Iguanian* family of Lizards, e. g. *Istiurus*, *Lophyrus*, *Calotes*, and *Otocryptis*, have the teeth soldered, like those of *Mosasaurus*, to the summit of the alveolar ridge, and thence are called 'Acrodonts:' in all these lizards the maxillary and mandibular teeth may be divided into anterior laniary and posterior molar teeth. In other Iguanians the teeth are lodged in a common shallow oblique alveolar groove, and are soldered to excavations on the inner surface of the outer wall of the groove: these are called 'Pleurodents.' Most of them possess pterygoid as well as maxillary teeth: but the following genera,

*Hyperanodon*, *Tropidolepis*, *Phrynosoma*, and *Callisaurus*, are exceptions.

In the Pleurodont Iguanians, the teeth never present the true laniary form; and, if simply conical, as at the extremes of the maxillary series, the cone is more or less obtuse; but, in general, it is expanded, more or less trilobate, or dentated along the margin of the crown. The *Amblyrhynchus*, a genus remarkable for the marine habits of at least one of the species (*Amblyrhynchus ater*), whose diet is sea-weed, has the tricuspid structure well developed in the posterior teeth. The typical genus of the present family of Saurians (*Iguana tuberculata*) is characterised by the crenate or dentated margin of the crown of the maxillary and premandibular teeth, a few of the anterior small ones excepted. The pterygoid teeth are arranged in two or three irregular rows, resembling somewhat the 'dents en cartes' of Fishes. In the full-grown *Iguana tuberculata* there are from forty-seven to forty-nine teeth in both upper and lower jaws. The number is less in young subjects. The two rows of pterygoid teeth are in close order on each side. In the horned Iguana (*Metopoceros cornutus*) there is a single row of small teeth implanted in each pterygoid bone, fig. 98, D, 24.

The teeth of the *Iguanodon*, though resembling those of the Iguana, do not present an exact magnified image of them, but differ in the greater relative thickness of the crown, its more complicated external surface, and in a modification of the internal structure, by which this huge herbivorous extinct lizard deviates from every other known reptile.

As in the Iguana, the base of the tooth is elongated, contracted, and subcylindrical; the crown expanded, and smoothly convex on the inner side. When first formed, it is acuminate, compressed, its sloping sides serrate, and its external surface traversed by a median longitudinal ridge, and coated by a layer of enamel; but, beyond this point, the description of the tooth of the *Iguanodon* indicates characters peculiar to that genus. Three longitudinal ridges, fig. 273, traverse the outer surface of the crown, one on each side of the median primitive ridge; these are separated from each other, and from the serrated margins of the crown, by four wide and smooth longitudinal grooves. In the upper jaw the teeth are less curved, and are thicker transversely to the jaw: the primary ridge is much more prominent. The marginal serrations present, under a low magnifying power, the form of





transverse ridges, themselves notched, so as to resemble the mammillated margins of the unworn plates of the elephant's grinder. These ridges or dentations do not extend beyond the expanded part of the crown: the longitudinal ridges are continued farther down, especially the median ones, which do not subside till the fang of the tooth begins to assume its subcylindrical form.

At the earlier stages of abrasion, a sharp edge is maintained at the external part of the tooth by means of the enamel which covers, and is restricted to, that surface of the crown. The prominent ridges upon that surface give a sinuous contour to the middle of the cutting edge, whilst its sides are jagged by the lateral serrations. The dentine next the enamel is harder than the vaso-dentine of the opposite half of the crown. When the crown is worn away beyond the enamel, it presents a broad and nearly horizontal grinding surface, and another dental substance is brought into use to give an inequality to that surface; this is the ossified remnant of the pulp, which, being firmer than the surrounding dentine, forms a slight transverse ridge in the middle of the grinding surface. The tooth in this stage has exchanged the functions of an incisor for that of a molar, and is prepared to give the final compression, or comminution, to the coarsely divided vegetable matters, such as might be afforded by the *Clathrariæ* and similar fossil plants, which are found buried with the Iguanodon.

In the Crocodilian Monitor (*Varanus bivittatus*) the large fixed compressed teeth, of which there may be about seven in each upper maxillary bone and six in each premandibular, are ankylosed by the whole of their base and by an oblique surface leading upwards on the outer side of the tooth to a slight depression on the alveolar surface. The base of the tooth is finely striated, the lines being produced by inflected folds of the external cement, as in the Ichthyosaur and Labyrinthodon, but they are short and straight, as in those of the former genus. The great *Varanus*, like the variegated species, manifests its affinity to the Crocodilians in the number of successive teeth which are in progress of growth to replace each other; but, from the position in which the germs of the successional teeth are developed, the more advanced teeth in this species, as in the *Varanus variegatus*, do not exhibit the excavations that characterise the same parts of the teeth of the Enaliosaurs and Crocodiles.

In some extinct Saurians, which, in other parts of their organisation, adhere to the Lacertine division of the order, the teeth were implanted in sockets, either loosely or confluent with the bony walls

of the cavity : these are termed the 'Thecodont' Lacertians : their dental character is seen in the oldest known of all Saurians, viz. the (*Protosaurus* of the Thuringian copper-slates), and the *Palæosaurus* of the dolomitic conglomerates near Bristol. The compressed Varanian form of tooth, with trenchant and finely dentated margins, which characterised these ancient Lizards, is continued in the comparatively more recent and gigantic species called *Megalosaurus*. In this terrestrial carnivorous Reptile the teeth, when first protruded above the gum, presented a double cutting edge of serrated enamel ; the position and line of action were nearly vertical, and, like the two-edged point of a sabre, the teeth cut equally on each side. As the tooth advanced in growth it became curved backward, in the form of a pruning-knife, and the edge of serrated enamel was continued downward to the base of the inner and cutting side of the tooth, whilst on the outer side a similar edge descended but a short distance from the point, and the convex portion of the tooth became blunt and thick, as the back of a knife is made thick for the purpose of producing strength. The strength of the tooth was further increased by the expansion of its side. 'In a tooth thus formed for cutting along its concave edge, each movement of the jaw combined the power of the knife and saw : whilst the apex, in making the first incision, acted like the two-edged point of a sabre. The backward curvature of the full-grown teeth enabled them to retain, like barbs, the prey which they had penetrated. In these adaptations we see contrivances which human ingenuity has also adopted in the preparation of various instruments of art.'<sup>1</sup>

The teeth of the *Megalosaur* consist of a central body of dentine, with an investment of enamel upon the crown, and of cement over all, but thickest upon the fang. The marginal serrations are formed almost entirely by the enamel. The remains of the dentinal pulp are converted into a coarse bone in the completely formed tooth.

In most Pterodactyles the teeth are of one kind, few and far apart, fig. 111, with long, slender, compressed, slightly recurved, pointed crowns ; but some, from the more ancient secondary deposits, show, behind a few teeth of the above prehensile character, a close-set row of small lancet-shaped teeth : such modification characterises the genus *Dimorphodon*.

The teeth of the Ichthyosaur have a simple more or less acutely conical form, with a long and, usually, expanded or

<sup>1</sup> Buckland, Bridgewater Treatise, vol. i. p. 237.

ventricose base, or implanted fang. They are confined to the premaxillary, maxillary, and premandibular bones, in which they are arranged in close series, and of nearly equal size. They consist of a body of unvascular dentine, invested at the base by a thick layer of cement, and at the crown by a layer of enamel, which is itself covered by a very thin coat of cement; the pulp-cavity is more or less occupied in fully formed teeth by a coarse bone. The external surface of the tooth is marked by the longitudinal impressions and ridges, but the teeth vary both as to outward sculpturing and general form in the different species.<sup>1</sup> The chief peculiarity of the dental system of the Ichthyosaur is the mode of the implantation of the teeth: instead of being ankylosed to the bottom and side of a continuous shallow groove, as in most Lacertians, or implanted in distinct sockets, as in the Thecodon, Megalosaur, or Pterodactyle, they are lodged loosely in a long and deep continuous furrow, and retained by slight ridges between the teeth, along the sides and bottom of the furrow, and by the gum and organised membranes continued into the groove and upon the base of the teeth. The germs of the new teeth are developed at the inner side of the base of the old ones.

The best and most readily recognisable characters by which the existing Crocodilians are grouped in appropriate genera are derived from modifications of the dental system.

In the Caimans (genus *Alligator*) the teeth vary in number from  $\frac{18-18}{18-18}$  to  $\frac{22-22}{22-22}$ : the fourth tooth of the lower jaw, or canine, is *received into a cavity* of the palatal surface of the upper jaw, where it is concealed when the mouth is shut. In old individuals the upper jaw is perforated by these large inferior canines, and the fossæ are converted into foramina.

In the Crocodiles (genus *Crocodylus*) the first tooth in the lower jaw perforates the palatal process of the premaxillary bone when the mouth is closed; the fourth tooth in the lower jaw is *received into a notch* excavated in the side of the alveolar border of the upper jaw, and is visible externally when the mouth is closed.

In the two preceding genera the alveolar borders of the jaw have an uneven or wavy contour, and the teeth are of an unequal size.

In the Gavials (genus *Gavialis*) the teeth are nearly equal in size and similar in form in both jaws, and the first as well as the

<sup>1</sup> v. pl. 73.

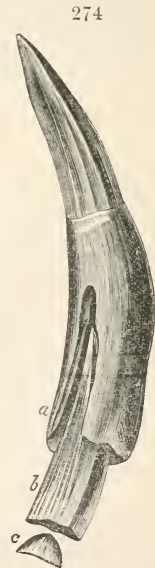
fourth tooth in the lower jaw passes into a groove in the margin of the upper jaw when the mouth is closed.

In the Alligators and Crocodiles the teeth are more unequal in size, and less regular in arrangement, and more diversified in form, than in the Gavials: witness the strong thick conical laniary teeth as contrasted with the blunt mammillate summits of the posterior teeth in the Alligator, fig. 275. The teeth of the Gavial are subequal, most of them present the form of a crown, shown in fig. 274, long, slender, pointed, subcompressed from before backward, with a trenchant edge on the right and left sides, between which a few faint longitudinal ridges traverse the basal part of the enamelled crown.

In the black Alligator of Guiana the first fourteen teeth of the lower jaw are implanted in distinct sockets, the remaining posterior teeth are lodged close together in a continuous groove, in which the divisions for sockets are faintly indicated by vertical ridges, as in the jaws of the Ichthyosaurs. A thin compact floor of bone separates this groove, and the sockets anterior to it, from the large cavity of the ramus of the jaw; it is pierced by bloodvessels for the supply of the pulps of the growing teeth and the vascular dentiparous membrane which lines the alveolar cavities.

The tooth-germ is developed from the membrane covering the angle between the floor and the inner wall of the socket. It becomes in this situation completely enveloped by its capsule, and an enamel-organ is formed at the inner surface of the capsule before the young tooth penetrates the interior of the pulp-cavity of its predecessor.

The matrix of the young growing tooth affects, by its pressure, the inner wall of the socket, as shown in fig. 275, and forms for itself a shallow recess: at the same time it attacks the side of the base of the contained tooth; then, gaining a more extensive attachment by its basis and increased size, it penetrates the large pulp-cavity of the previously formed tooth, either by a circular or semi-circular perforation. The size of the calcified part of the tooth-matrix which has produced the corresponding absorption of



Teeth in different stages of formation from one alveolus of the Gavial: *a* is the base partly absorbed by the pressure of *b*, the successional tooth; below which is figured *c*, the germ of the next tooth to follow. v.



the previously formed tooth on the one side, and of the alveolar process on the other, is represented in the exposed alveolus of fig. 275, the tooth *a* having been displaced and turned round to show the effects of the stimulus of the pressure. The size of the perforation in the tooth, and of the depression in the jaw, proves them to have been, in great part, caused by the soft matrix, which must have produced its effect not by mere mechanical force. The resistance of the wall of the pulp-cavity having been thus overcome, the growing tooth and its matrix recede from the temporary alveolar depression, and sink into the substance of the pulp contained in the cavity of the fully formed tooth. As the new tooth, *ib. c*, grows, the pulp of the old one is removed; the old tooth itself is next attacked, and, the crown being undermined by the absorption of the inner surface of its base, may be broken off by a slight external force, when the point of the new tooth is exposed. The frail remains of the old tooth are sometimes lifted off the socket upon the crown of the new one, as in fig. 275, *b*, when they are speedily removed by the action of the jaws.



Section of lower jaw, with four alveoli and teeth, of the black Alligator. v.

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No sooner has the young tooth penetrated the interior of the old one than another germ begins to be developed from the angle between the base of the young tooth and the inner alveolar process, or in the same relative position as that in which its immediate predecessor began to rise, and the processes of succession and displacement are carried on, uninterruptedly, throughout the long life of these cold-blooded carnivorous Reptiles.

From the period of exclusion from the egg, the teeth of the Crocodile succeed each other in the vertical direction; none are added from behind forward, like the true molars in Mammalia. It follows, therefore, that the number of the teeth of the Crocodile is as great when it first sees the light as when it has acquired

its full size; and, owing to the rapidity of the succession, the cavity at the base of the fully formed tooth is never consolidated.

The fossil jaws of the extinct Crocodylians demonstrate that the same law regulated the succession of the teeth at the ancient epochs when those highly organised Reptiles prevailed in greatest numbers, and under the most varied generic and specific modifications. Of these the most remarkable, in reference to the dental system, is the *Galeosaurus*, in which the well-marked differences of size and shape permit the division of the teeth, in both upper and lower jaws, into incisors, canines, and molars. This is the nearest approach to a mammalian type of dentition hitherto observed in the Reptilian class.<sup>1</sup>

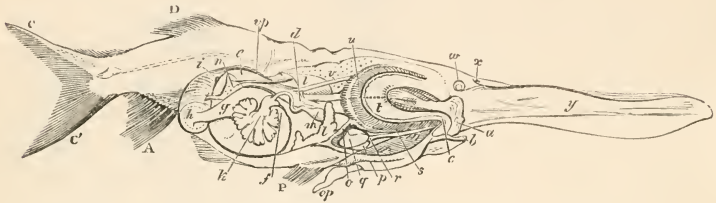
§ 72. *Alimentary canal of Fishes.*—The cavity, commonly termed ‘abdominal,’ which lodges the main part of the alimentary canal and its appendages, seems to occupy a smaller proportion of the trunk in Fishes, fig. 276, *l, h, i*, than in Reptiles, fig. 292, *d, w*, by reason of the slight and gradual contraction of the body beyond the vent to form the muscular organ of the tail-fin: the greater and more abrupt contraction of the answerable part in Reptiles distinguishes it more plainly as the ‘tail’; the ‘trunk’ is usually a longer segment of the body than in Fishes. In these, however, the abdominal cavity commences immediately behind the head: in most Reptiles a ‘neck’ intervenes. In Fishes a thoracic or pericardial cavity, fig. 276, *o*, is partitioned off from the fore-part of the proper abdominal one: and there are in this class exceptional examples of the shortest abdominal cavity in proportion to the length of the body known in the Vertebrate province, as e. g. in *Gymnotus*, fig. 232, in which the abdomen does not extend into the compartment, *b*, much beyond the vent, which is seen near the angle of the cut integument, beneath the mandible.

The cavity containing the beginning of the alimentary canal is called the ‘mouth.’ This, in Fishes, is the common entry and vestibule to both the digestive, fig. 276, *d* to *g*, and the respiratory, *ib. t, u*, organs; it is, therefore, of great capacity: and, as the transmission of the food to the stomach and of the respiratory currents to the gills is performed by similar acts of deglutition, the bony arches which surround the mouth are not only large, but are complicated by a mechanism for regulating the transit of the nutritious and oxygenating media, each to its respective locality. The branchial slits, in most Fishes, are provided with

<sup>1</sup> CCXXIII. p. 58, pl. II.

denticles and sieve-like plates or processes, fig. 85, 63, to prevent the entry of food into the interspaces of the gills, and the branchial

276



Digestive organs *in situ*, Planirostra.

outlets are guarded by valves which reciprocally prevent the regurgitation of the respiratory streams back into the mouth.

The necessary cooperation of the jaws with the hyoid arch in the rhythmical movements of respiration is incompatible with protracted maxillary mastication; and, accordingly, the branchial apparatus renders a compensatory return by giving up, as it were, the last pair of its arches to the completion of the work which the proper or anterior jaws were compelled by their services to respiration to leave unfinished: and thus the mouth of typical Fishes is closed at both ends by dentigerous jaws.<sup>1</sup>

The first portal to the alimentary tract is usually formed by the upper and lower jaws, fig. 276, *a, b*, and their teeth: the Gymnodonts are so called on account of their conspicuous manifestation of this character, fig. 258. In most Fishes the jaws are covered by the skin, which, in passing into the mouth, takes on the character of the mucous membrane. In some Fishes the integument is folded before passing over the jaws, and the arched and fortified barrier is preceded by a fosse inclosed by fleshy lips. The Wrasses (*Labridæ*), Mulletts (*Mugilidæ*), and the Carp-tribe (*Cyprinidæ*) exemplify this character. In *Crenilabrus*, *Chærops*, and *Julis*, the lips are plicated. In *Mugil labeosus* the thick upper lip has a transverse fold. In some *Cyprinidæ* the labial organs are developed to excess, as, for example, in the genus thence termed *Labeobarbus*, in which the lips are not only unusually thick and fleshy, but the lower one is produced downward like a pointed beard: it forms a long cone in *Mormyrus Petersii*. The labiated Fishes have not, however, so distinct a 'sphincter oris' as

<sup>1</sup> The Mulletts 'take in a quantity of sand and mud, and after having worked it for some time between the pharyngeal bones, they eject the roughest and indigestible portion of it.' CLXXIV. iii. p. 411.

Mammals: nor does the skin, continued from the lip over the jaw, show so well the character of the 'gun.' Many Fishes, especially those of the Cyprinoid, Mugiloid, and Siluroid families, have fleshy and sensitive labial barbs or cirri; those of the Siluroids being supported by bony or gristly stems. Tentacles depend from the rostral prolongation of the Sturgeon, and from the mandibular symphysis of the Cod. The Lepidosiren and Cod have fringed processes or filaments between the teeth and lips, which seem designed to assist in testing and selecting the food.<sup>1</sup> The lips of most Sharks and Rays are partially supported by labial cartilages.

The edentulous Sturgeon is compensated by a produced cartilaginous snout, with which it upturns the mud in quest of food at the bottom of the rivers it frequents. The allied *Spatularia*, in which a minutely shagreened surface on the jaws represents the whole dental system, has had the force of development of subsidiary organs of alimentation expended in the production of the still more remarkable rostrum, fig. 276, *y*, which is broad and flat, like the mandible of a spoonbill, and is more than half the length of the entire body. Other modifications and actions of the mouth have been noticed in the description of the jaws.

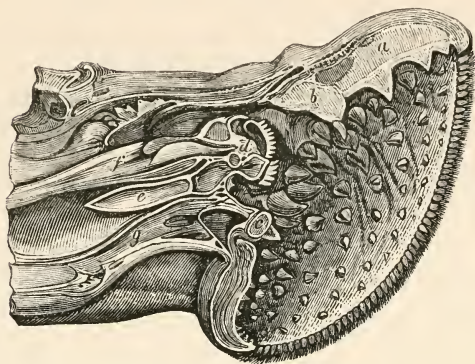
The conical lip of the suctorial Myxinoids, fig. 248, sends off from its anterior expanded border six or eight long tentacula: this border is fringed by numerous cirri in the Lamprey, fig. 277, the inner surface of the lips is beset with short branched tentacles in the Ammocete: the Lancelet has more simple, but highly vascular intra-buccal processes, fig. 169, *g, g*, and the vertically fissured aperture of its mouth is provided on each side with a series of long slender jointed and ciliated tentacula, *ib. f, f*, which mainly tend, by the perpetual vortex they cause in the surrounding water, to bring the animalcular nutriment within the grasp of the pharynx, *ph*, the orifice of which is also surrounded by vibratile cilia. There is no tongue in this rudimentary fish: that organ is often absent or very small in the typical members of the Class; its basis, the glossohyal, when it projects at all into the mouth, as in fig. 276, *c*, is rarely covered by integuments so organised as to suggest their being endowed with the sense of taste. In *Anguillidæ* the lingual membrane is raised by some adipose and muscular

<sup>1</sup> Mr. Couch narrates an instance of a large Cod, in good condition, taken on a line at Polperro, Cornwall, in which the orbits contained no eyeballs, but were covered with an opaque reticulated skin. So that he felt convinced that 'eyes never had existed;' yet the fish was in good condition, and must have depended on the tactile organs about the mouth for the discovery of its food. xcviil. p. 72.



tissue. But the surface of the prominent tongue is generally callous, and either smooth and devoid of papillæ, or, if the repre-

277



Vertical section of mouth, Lamprey. v.

sentatives of these be present, they are calcified and the tongue is beset with teeth. It, then, seizes and passes the food on to the gullet; but the supporting arch of the tongue, fig. 85, 38-40, works chiefly for respiratory purposes. In the Lamprey, the tongue, fig. 277, *d*, is more exclusively related to the digestive function than in higher Fishes: it can be protruded and retracted, like a piston, when the sucker is attached to the prey; and it is armed by small serrate teeth for tearing the flesh. In a few Fishes the integument of the palate presents that degree of vascularity and supply of nerves which indicates some selective sense, analogous to taste. In the Cyprinoids the palate is cushioned with a thick soft vascular substance, exuding mucus by numerous minute pores, but more remarkable for its irritable erectile or contractile property:<sup>1</sup> if any part of this be pricked in a live Carp, the part rises immediately into a cone, which slowly subsides; this peculiar tissue is richly supplied by branches of the glosso-pharyngeal nerves: it may assist in the requisite movements of the vegetable food, as well as add to it an animalising and solvent mucus, whilst it is undergoing mastication by the pharyngeal teeth. In the *Gymnotus* there are four series of branched fleshy processes in the mouth, one upon the dorsum of the tongue, a second depending from the palate, and one along each side of the mouth.

The only representatives of a salivary system in Fishes are the mucous follicles that communicate with the mouth.<sup>2</sup> The chief of

<sup>1</sup> XCIX.

<sup>2</sup> The reddish vascular body, discovered by Retzius (CXXI.) between the basi-

these, in the Lamprey, open into a pair of membranous pouches, which discharge the secretion each by a small orifice below the side of the tongue.<sup>1</sup>

There are neither tonsils nor velum palati in Fishes: the folds of membrane behind the upper and lower jaws, of which 'internal lips' the Sword-fish and Dory afford good examples, seem intended to prevent the reflux of the respiratory streams of water rather than the escape of food from the mouth. In the *Lepidosiren* these folds or inner lips are papillose and glandular. That of the upper jaw in the Ray has a marginal fringe.

In the aberrant *Dermopteri* and *Plagiostomi*, at the two extremes of the class, in which there are numerous branchial apertures on each side, and the respiratory streams do not necessarily enter by the mouth, the last pair of branchial arches are not metamorphosed into pharyngeal jaws, and the entry to the gullet is simply constricted by a sphincter; in the *Lepidosiren* it is further defended by a soft valvular fold like an epiglottis.<sup>2</sup>

The alimentary canal is usually short, simple, but capacious, in Fishes; in a few instances, e.g. *Branchiostoma* (fig. 169, *ph, as*), *Myxinoids*,<sup>3</sup> *Exocetus*, *Lepidosiren*,<sup>4</sup> it extends in almost a straight line from the pharynx to the anus: but it is generally disposed in folds and sometimes in numerous convolutions. In *Dermopteri* the stomach is hardly defined: in the rest of the class the alimentary canal is primarily divided into a gastric and an intestinal portion by the constriction called 'pylorus,' fig. 281, *c*. The gastric portion is subdivided into 'œsophagus,' *ib. a*, and stomach, *ib. b*, the boundary line being more commonly indicated by a change of structure of the lining membrane than by a cardiac constriction: the intestinal portion is subdivided into a 'small' and a 'large intestine;' the latter usually answering to the 'intestinum rectum,' and the boundary, when well defined, being a constriction and an internal valvular fold; but very rarely marked by an external cæcum. From the œsophagus the alimentary canal is situated wholly or in part in the abdominal cavity, to the walls of which it is usually suspended by mesogastric and mesenteric duplicatures of the peritoneal lining membrane of the abdomen. When not wholly so situated, the part extends beyond the peritoneal region into the muscular mass of the tail; a portion of the

branchials and the sterno-hyoid muscles in Cartilaginous Fishes, and which exists also in *Gadus*, *Salmo*, and some other Osseous Fishes, has been compared to a sublingual salivary gland: but it is a "vaso-ganglion" like the thyroid.

<sup>1</sup> CCXXIV.

<sup>2</sup> XXXIII. p. 342, fig. *j, d*.

<sup>3</sup> XXI. Neurologie, tab. iii. fig. 6.

<sup>4</sup> XXXIII. pl. 25.

intestine, for example, lies between the right myocommata and the hæmal spines in the Sole. The peritoneal serous membrane, which defines the abdominal cavity, extends anteriorly to the pericardium, from which it is separated by a double aponeurotic septum, fig. 276, *o*: it is continued along the back over the ventral surface of the kidneys and the air-bladder, when this exists, a little way beyond the anus, and is reflected upon the alimentary canal, *ib. d, i*, the liver, *l, l*, the spleen, *n*, the pancreas, *h*, or its cæcal substitutes, the ovaria or testes, and the urinary bladder, if this be present. In many Fishes the peritoneum does not form a shut sac, but communicates with the external surface, by one orifice (*Branchiostoma*, fig. 169, *od*, *Lepidosiren*, XXXIII. pl. 25, fig. 1, *a*), or two (Lamprey, Eel, Salmon, Sturgeon, Planirostra, Chimæra, and Plagiostomes, fig. 352, *p, p*), situated, except in the Lancelet, in or near the cloaca: the membrane in the neighbourhood of these orifices is beset with vibratile cilia.<sup>1</sup> The peritoneal orifices give exit to the generative products (milt or roe) in the Lancelet, Myxinoids, Lampreys, Murænida, and Salmonida, but not in the *Lepidosiren* and *Plagiostomes*. In the *Myxinoids*, *Ammocetes*, *Sturgeons*, *Chimæra* and *Plagiostomes*, the peritoneum communicates also with the pericardium.<sup>2</sup>

The jaws and mouth are subservient in most Fishes to the respiratory as well as the digestive functions: in the Lancelet, this community of offices extends through a great part of the alimentary canal, which is dilated into a capacious sac, and is richly provided with branchial vessels and vibratile cilia arranged along transverse linear clefts, by which the water escapes into a surrounding cavity: (the arrow *a* extends from the pharynx into the intestine in fig. 169:) the œsophageal portion of the alimentary canal is here seen to be longer than the whole gastric and intestinal portions. In the *Cyclostomes* lateral diverticula are derived from the œsophagus and metamorphosed into special respiratory sacs, communicating by narrow canals both with the œsophagus and with the external surface, fig. 315, *f, m, h*: in other Fishes the respiratory apparatus is more concentrated and brought more forward, so as to communicate with the pharynx, and to leave the œsophagus free for the exclusive transmission of food to the stomach.

The œsophagus, fig. 279, *d*, is usually a short and wide funnel-shaped canal with a thick muscular coat and a smooth epithelial

<sup>1</sup> CCXXXIV. p. 360.

<sup>2</sup> LXIX. pl. 8.

lining, more or less longitudinally folded to admit of increased capacity for the deglutition of the often unmasticated or undivided food. The muscular fibres are arranged in different fasciculi, the outer ones being usually circular, the inner ones longitudinal. Some fasciculi from the abdominal vertebræ are attached to the œsophagus in the *Cottus scorpius*.<sup>1</sup> The cardiac half of the œsophagus is characterised by increasing width in most *Cyprinidæ*, and by a more vascular or otherwise modified texture in the *Pharyngognathi*, *Lophobranchii*, the Gobioids, Blennies, Flying-fish, Garfish, and some others. The inner surface of the œsophagus sends off short processes, papilliform in *Box* and *Cæcio*, obtuse in *Acipenser*,<sup>2</sup> hard and almost tooth-like in *Rhombus xanthurus*, *Stromatæus fiatola*, and *Tetragonurus*. The inner surface of the gullet presents longitudinal papillose ridges in *Planirostra*. But the most striking peculiarities of the œsophagus are met with in the Plagiostomes. A layer of grey parenchymatous substance is interposed between the muscular and inner coats at the cardiac half of the œsophagus in the *Torpedo*. Numerous pyramidal retroverted processes, jagged or fringed at their extremity, project from the inner surface of the œsophagus in the Dog-fish (*Spinax acanthias*),<sup>3</sup> and some other Sharks, fig. 278, *a*. In the great Basking Shark (*Selache*) the homologous processes near the cardia acquire unusual length, dividing and subdividing as they extend inwards, so that the cardiac opening is surrounded by ramified tufts directed towards the stomach.<sup>4</sup> This valvular mechanism, fig. 278, *b*, would prevent the return of such fishes or mollusks as may have been swallowed alive and uninjured by the small obtuse teeth of this great Shark. In many Osseous Fishes we may, finally, notice the communication of the 'ductus pneumaticus' with the œsophagus, usually by a small simple foramen; but provided with special muscles in the *Lepidosteus*, where it opens upon the dorsal aspect of the œsophagus, and with a sphincter and cartilage in the *Polypterus*, and *Lepidosiren*, where it communicates like a true glottis with the ventral surface of the beginning of the œsophagus. In the Globe-fishes (*Diodon*, *Tetrodon*) the great air-sac seems to be a more direct developement, as a cul de sac, of the œsophagus.<sup>5</sup> These singular fishes blow themselves up by swallowing the air, which escapes through a large anterior oblique orifice into the sac: and this again communicates with

<sup>1</sup> XCIX.<sup>2</sup> XX. vol. i. p. 126, prep. no. 463.<sup>3</sup> Ib. prep. no. 664.<sup>4</sup> Ib. prep. no. 464. A.<sup>5</sup> Ib. vol. iii. p. 271, pl. 47, preps. nos. 2093—2095.

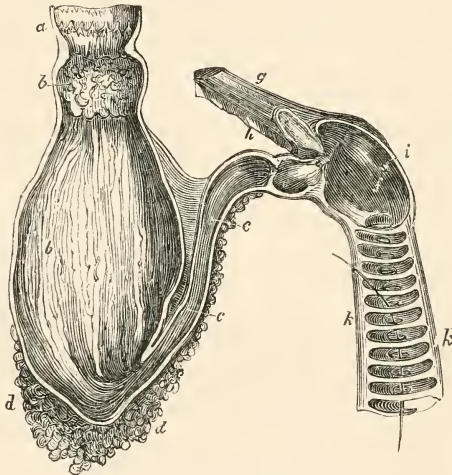


the forepart of the œsophagus by a second orifice much smaller than the first, and having a tumid valvular margin.

The cardiac orifice of the stomach is occasionally defined by a constriction, as in the Planirostra and Mormyrus, fig. 280: but an increased expansion with increased vascularity and a more delicate epithelial lining of the mucous membrane more usually indicate, in Fishes, the beginning of the digestive cavity. The stomach is a simple and commonly an ample cavity, with a great disproportion in the diameters of the cardiac and pyloric orifices; in the Cornish Porbeagle-Shark, for example, the cardiac entry will readily admit a child's head, whilst the pyloric outlet will barely allow of the passage of a crow-quill.

There are two predominant forms of the stomach in Fishes, viz. the 'siphonal' and the 'cæcal.' In the first it presents the form of a bent tube or canal, as in the Turbot, fig. 287, *a, b*, Flounder, Sole, Cod, Haddock, Salmon, fig. 286, *a, b*, Carp, Tench, Ide, Lumpfish, File-fish, Lepidosteus, Sturgeon, Paddle-fish, and most Plagio-

278

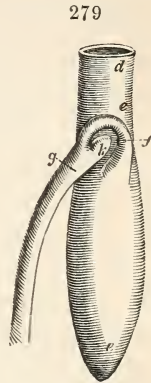


Alimentary canal of Shark. CCLXVI.

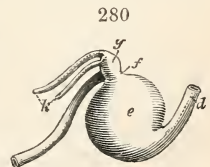
stomes, fig. 278: in the second form the cardiac division of the stomach terminates in a blind sac, and the short pyloric portion is continued from its right side, as in the Perch, the Scorpenæ, the Gurnards, the Bull-heads, the Smelts, the Whiting, fig. 285, the Angler, the Pike, the Lucioperca, the Sword-fish, fig. 282, the Silurus, the Herring, the Sprat, fig. 288, the Pilchard, the Conger, the Muræna, and the Polypterus, fig. 279. A transitional form, in which the pyloric end is bent so abruptly upon

the cardiac as to make the cæcal character of the latter doubtful, is presented by the short and capacious stomach of the Burbot, the Blenny, and the Gymnotus. In the *Mormyrus* the stomach presents the rare form of a globular sac, fig. 280, *e*. In the siphonal stomach of the *Cyprinidæ* and *Balistidæ* the pylorus is little if at all discernible, and the transition into intestine is gradual. In the Salmon the intestine is indicated by the pyloric appendages, fig. 286, *c*: in the Sharks there is a true pylorus, and in *Selache*, fig. 278, an interposed pouch. Where the cæcal character of the stomach is well marked, the length of the blind end of the cardia varies considerably. In the Turbot it is wide and short, fig. 287, *b*: in the Sand-lance (*Ammodytes*) it is very large: in the Polypterus, fig. 279, *e*, Conger, and Swordfish, fig. 282, it forms almost the whole of the elongated stomach, the short pyloric portion, fig. 279, *f*, being continued from near its commencement: in the equally elongated stomach of the Pike, the pyloric portion is continued from the cardiac sac at a little distance from its blind end; the Herring, Sprat, fig. 288, Whiting, fig. 285, Gurnard, and Scorpena show an intermediate position of the pyloric portion, and this is usually attended with a shorter and wider form of the cardiac cæcum. The pyloric portion is usually slender, fig. 278, *c*, or conical, figs. 285, 287; but it dilates into a wide sac in *Sargus* and *Lophius*; and forms a small oval pouch in *Trachypterus*.

In certain Fishes the stomach deviates from the typical forms either into the extreme of simplicity or the converse, without, however, attaining in any species that degree of complexity which characterises some of the higher-organised Vertebrates. A proper gastric compartment of the alimentary canal cannot be said to exist in the Lancelet: the long cæcum, fig. 169, *hd*, *l*, continued from it just beyond the cardia, appears to be a simple form of liver. In the higher *Dermopteri*, as the Sand-prides, the Myxines, and the Lampreys, as also in *Cobitis* and *Lepidosiren*, the stomach is continued straight from the œsophagus to the intestine. I have found the capacious cardiac division of the stomach of the *Lophius* partially divided into two sacs; the unusually wide and short pyloric portion forming a third sac: there may also be observed a few



Stomach and pancreas, *Polypterus*.



Stomach and pancreas, *Mormyrus*.

obtuse processes from the inner side of the cardia in this fish. In the Gillaroo Trout the ascending or pyloric half of the bent or siphonal stomach has its muscular parietes unusually thickened, by which it is enabled to bruise the shells of the small fluviatile testaceans that abound in the streams to which this variety of trout is peculiar.<sup>1</sup> The pyloric portion of the stomach is very muscular in the Indian Whiting (*Johnius*), and in some species of *Scomber*: but the modification which gives the stomach the true character of a gizzard is best seen in the Mulletts (*Mugil*). The cardiac portion here forms a long cul de sac; the pyloric part is continued from the cardiac end of this at right angles, and is of a conical figure externally; but the cavity within is reduced almost to a linear fissure by the great development of the muscular parietes, which are an inch thick at the base of the cone; and this part is lined by a thick horny epithelium.<sup>2</sup> In the Herring the ductus pneumaticus of the swim-bladder is continued from the attenuated extremity of the cardiac end of the stomach, fig. 281, *b*. In the Basking-shark the contracted pyloric division of the stomach, figs. 278, *c*, and 284, *f*, communicates by a narrow aperture with a second small rounded cavity, fig. 284, *f'*, which opens by a narrow pylorus into the short and capacious duodenum, fig. 278, *f*, 284, *g*.

Such are the observed extremes of the modifications of the stomach in Fishes, which it will be seen, therefore, are far from according with or paralleling those of the dental system. There is often, indeed, no essential difference of form in the stomach of a fish with exclusively laniary teeth, e. g. the carnivorous Salmon, and in that of one with exclusively molar teeth, e. g. the herbivorous Carp. The *Ætobates*, whose teeth form a crushing pavement, has a stomach similar in shape and size to that in the common Ray, in which every tooth is conical and sharp-pointed.

The inner surface of the stomach presents few modifications in Fishes: it is usually smooth; rarely reticulate, as in the *Gymnotus*; still more rarely papillose. The lining membrane is thrown into wavy longitudinal rugæ in the cardiac portion of the stomach of most Sharks, fig. 278. The gastric follicles are conspicuous, especially in the pyloric portion of the stomach in many Fishes, as, e. g., the Gurnards, Blennies, and Lump-suckers. The circular pyloric valve is commonly well developed, and has sometimes a fimbriated margin. The solvent power of the gastric secretion is conspicuously exemplified in Fishes: if a voracious species be captured after having swallowed its prey, the part lodged in the stomach is usually found more or less dissolved, whilst

<sup>1</sup> XCII. p. 126.

<sup>2</sup> xx. vol. i. p. 141. prep. no. 502.

that which is in the œsophagus may be entire; and, in specimens dissected some hours after death, one may observe what Hunter so well describes, 'the digesting part of the stomach itself reduced to the same dissolved state as the digested part of the food.'<sup>1</sup>

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, other portions are returning towards the cardia. More direct constrictive and dilative movements occur, with intervals of repose, at both the orifices, the vital contraction being antagonised by pressure from within. The pylorus has the power, very evidently, of controlling that pressure, and only portions of completely comminuted and digested food (chyme) are permitted to pass into the intestine. The cardiac orifice appears to have less control over the contents of the stomach; coarser portions of the food from time to time return into the œsophagus, and are brought again within the sphere of the pharyngeal jaws, and subjected to their masticatory and comminuting operations. The Fishes which afford the best evidence of this ruminating action are the Cyprinoids, (Carp, Tench, Bream,) caught after they have fed voraciously on the ground-bait previously laid in their feeding haunts to insure the angler good sport. A Carp in this predicament, laid open, shows well and long the peristaltic movements of the alimentary canal; and the successive regurgitations of the gastric contents produce actions of the pharyngeal jaws as the half-bruised grains come into contact with them, and excite the singular tumefaction and subsidence of the irritable palate, as portions of the regurgitated food are pressed upon it. The shortness and width of the œsophagus, the masticatory mechanism at its commencement, and its direct terminal continuation with the cardiac portion of the stomach, relate to the combination of an act analogous to rumination, with the ordinary processes of digestion, in all Fishes possessing those concatenated and peculiar structures. Sometimes the Fishes, as, for example, the Sturgeon, the Paddle-fish, the Dog-fish, and the Selache, whose œsophagus is best organised to prevent regurgitation from the stomach, are devoid of the pharyngeal jaws and teeth.

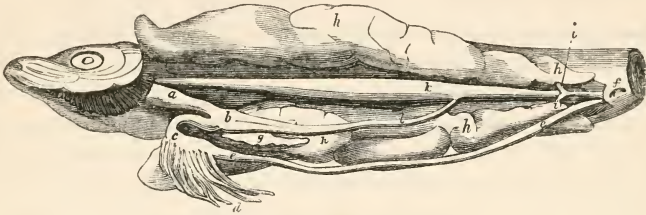
Fishes disgorge the shells and other indigestible parts of their food: and when hooked or netted, sometimes empty their stomach by an instinctive act of fear, or to facilitate escape by lightening their load.

<sup>1</sup> XCII. p. 120.



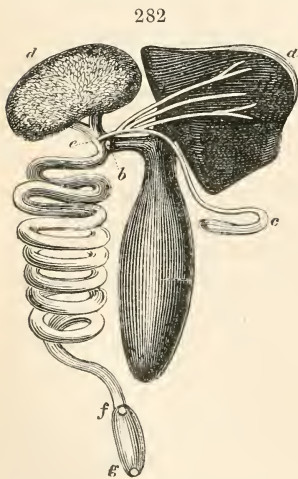
The intestinal canal is shorter in Fishes generally than in the higher Vertebrates: in the Dermopteri, Plagiostomes, Holocephali, Sturionidæ, Paddle-fish, fig. 276, *f* to *i*, the Lepidosiren,<sup>1</sup> the Flying-fish, the Loach, the Garpike, the Wolf-fish, the Salmon,

281



Abdominal viscera, Herring. cxvi.

the Herring, fig. 281, and the apodal fishes, it is shorter than the body itself: in some of the above-cited examples the intestine extends in a straight line from the pylorus to the anus, fig. 281, *e, e, f*; in most fishes it presents two or three folds; the Sun-fish (*Orthogoriscus*) shows about six longitudinal ones: the intestine is sinuous in the Sword-fish, fig. 282, *e, f*; concentrically and subspirally wound in the Mullet, in which the convolutions are numerous and form a triangular mass; and it is in this fucivorous fish, in the Chætodonts, and the Carp-tribe, that the intestinal canal attains its greatest length in the present class.

Diagram of digestive organs, *Xiphias*.  
xxviii.

With a few exceptions, of which the Dermopteri and the Lepidosiren are examples, the intestines are divided into 'small,' and 'large.' The beginning of the small intestine, to which is arbitrarily given the name of 'duodenum,' fig. 278, *i*, fig. 281, *e, e*, is usually wider than the rest of that division of the canal: it receives the ducts of the liver and pancreas; and, in most Osseous Fishes, that of the cæca, fig. 281, *d*, which are usually termed, from their communication with, or development from, the commencement of the small intestine, 'appendices pyloricæ.' The termination of the small intestine is commonly marked by a circular valve. In the Bogue-bream (*Box*

<sup>1</sup> xxxiii. pl. 25, figs. 1 and 2.

*vulgaris*) and the Flounder, there is a small cæcal process at the commencement of the large intestine; there are two short cæca at the same part in *Box Salpa*.<sup>1</sup> The large intestine is usually short and straight in Fishes, answering to the rectum of higher animals, fig. 282, *f, g*. In some Fishes, e. g., *Salmo*, *Clupea*, *Esox*, *Anableps*, *Anarrhichas*, and the Gymnodonts, it preserves the same diameter as the small intestine, and the term 'large' becomes arbitrary: in *Gasterosteus*, *Centriscus*, *Ostracion*, *Balistes*, and *Syngnathus*, it is even narrower than the 'small intestine;' but most commonly it is wider, as in the Percoid family, the Gurnards (*Triglidae*), the Breams (*Sparidae*), *Sciæna*, *Scomber*, *Cottus*, *Labrus*, *Pleuronectes*, *Gadus*, *Lophius*, *Cyclopterus*, the *Siluridae*, the *Plagiostomi*, and the *Planirostra*, fig. 276, *h*.

The tunics of the intestinal canal consist in Fishes, as in other Vertebrates, of the peritoneal or serous, the muscular, and the mucous coats, with their intervening cellular connecting layers, and the epithelial lining; the muscular and mucous coats are commonly thicker and of a coarser character than in the warm-blooded classes; pigmental cells are not unfrequently developed in the serous coat; the epithelial scales of the intestine of the Lancelet support vibratile cilia.

The muscular fibres are arranged in a thin outer longitudinal and a thick inner circular stratum (Sturgeon);<sup>2</sup> the elementary fibres in general present the smooth character of those of the involuntary system; but Reichert<sup>3</sup> has detected the transversely striated fibre in the muscular tunic of the whole tract of the intestine in the Tench.

The mucous membrane presents numerous modifications, some of them more complex and remarkable than in any of the higher Vertebrates. It is commonly thick and glandular, and always highly vascular. In the small intestines it presents, in some Fishes (Cod),<sup>4</sup> a smooth and even surface; in some it is produced into obliquely longitudinal or wavy folds;<sup>5</sup> in the Herring it presents feeble transverse rugæ; in many Fishes it is reticulate, as in the Wolf-fish<sup>6</sup> and *Muræna*;<sup>7</sup> this character is present in the peculiarly thick and parenchymatoid mucous tunic of the small intestine of the Sturgeon, where the larger meshes include irregular spaces, subdivided into smaller cells.<sup>8</sup> In a few Fishes the mucous membrane is coarsely villose or papillose. In

<sup>1</sup> xxxiii. t. vi. pp. 624, 270.    <sup>2</sup> xx. vol. i. p. 200, preps. nos. 637, 639.    <sup>3</sup> xciii. p. 26.

<sup>4</sup> xx. vol. i. p. 199, prep. no. 633.    <sup>5</sup> Ib. Turbot, prep. no. 634, Salmon, prep. no. 635.

<sup>6</sup> Ib. prep. no. 630.

<sup>7</sup> Ib. prep. no. 631.

<sup>8</sup> Ib. prep. no. 638.

Orthogoriscus it is both reticulate and villous, the villi being longest at the beginning of the canal. There is often a well-marked difference in the character of the lining membrane of the small and large intestines : thus, in the Salmon, the rugæ become fewer, larger, and less oblique as they approach the rectum ; the commencement of this intestine is marked by a large transverse fold or circular valve, which is succeeded by several others less produced, and resembling the valvulæ conniventes in the human jejunum.<sup>1</sup> The straight 'large intestine,' which is relatively longer in the *Amia*, *Polypterus*, *Paddle-fish*, fig. 276, *h, i*, *Sturgeon*, and *Chimæra*, is characterised by the continuity of such transverse folds as those in the Salmon, producing an uninterrupted spiral valve of the mucous membrane. In the *Lepidosiren* the entire tract of the straight and short intestine is traversed by this peculiarly piscine extension of the inner coat.<sup>2</sup> The spiral valve characterises the large intestine, fig. 278, *h*, in all the *Plagiostomes*, and establishes the essential difference between the short and apparently simple intestinal canal of these cartilaginous fishes, and that of the low-organised *Myxinoid* species.

The true homologue of the small intestine is extremely short in the *Plagiostomes* ; it is narrow in the *Rays*, expanded and sometimes sacciform, fig. 284, *g*, in the *Sharks*, where it seems to form the commencement of the suddenly expanded large intestine : this is straight, and though constituting the chief extent of the intestinal canal, it is very short in proportion to the body ; not exceeding, for example, one eighth of the entire length of the body in the *Alopias* or *Fox-shark*. The economy of space in the abdominal cavity is, however, effected at the expense of the serous and muscular coats, not of the mucous membrane. The required extent of secreting and absorbing superficies is gained by raising or drawing inwards, from the intestinal parietes, the mucous membrane in a broad fold at the beginning of the large intestine, and continuing it in spiral volutions to near the anus. The coils may be either longitudinal and wound vertically about the axis of the intestinal cylinder, or they may be transverse to that axis. In the first case, when the gut is slit open lengthwise, the whole extent of the fold may be uncoiled and spread out as a broad sheet ; and, if the gut be divided transversely, the cut edges of the valve present a spiral disposition, as in fig. 283. The longitudinal form of the spiral valve may be seen in the squaloid genera *Carcharias*, *Scoliodon*, *Galeocerdo*, *Thalassorhinus*,

<sup>1</sup> xx. vol. i. p. 199, prep. no. 635.

<sup>2</sup> xxxiii. p. 343, pl. 25, fig. 2.

and *Zygæna*.<sup>1</sup> In the second and more common modification, the fold of mucous membrane is disposed in close transverse coils, as shown in the longitudinal section of the *Selache*'s gut, fig. 284, *h*; and a transverse section exposes only the flat surface of one of the coils. In the Fox-shark (*Alopias Vulpes*); the valve describes thirty-four circumgyrations within seven inches' extent of the intestine; the mucous membrane is minutely honeycombed: a few scattered fibres of elastic or involuntary muscular tissue may be traced in the vasculo-cellular layer included within the mucous fold, and they form a slender band within the free border of the valve, retaining much elasticity in the dead intestine, and drawing that border into festoons. Besides *Selache*, fig. 284, *h*, and *Alopias*, the spiral valve is transverse in *Galeus*, *Lamna*, and all the Dog-fishes (*Scylliidae* and *Spinacidae*). The trunk of the 'arteria meseraica intestinalis,' and that of the corresponding veins of the longitudinally convoluted valve, run along its free thickened border, and the vein quits its commencement to join the vena portæ:<sup>2</sup> the arterial and venous trunks of the transversely spiral valve are external to the gut.

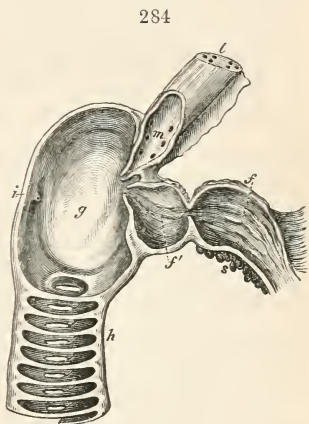
One may connect the peculiarity of the spiral valve with the necessity for reducing the mass and weight of the abdominal contents in the active high-swimming Sharks, which have no swim-bladder: the essential part of an intestine being its discerning and absorbing surface, we see in them the requisite extent of the vasculo-mucous membrane packed in the smallest compass, and associated with the least possible quantity of accessory muscular and serous tunics, by the modifications above described. Analogous ones exist, however, in other Plagiostomes, and in the Lamprey, to which the above physiological explanation will not apply; and the spiral valve is associated with the air-bladder in some of the highly organised Ganoids, and in the Lepidosiren. Nevertheless,

<sup>1</sup> XLVI. t. iv. p. 314; t. xvi. p. 277, pl. 2 and 3. See also, xx. prep. no. 645; probably from *Scoliodon*.

<sup>2</sup> Duvernoy, xcvi. p. 274, pl. 10.



Spiral valve, *Zygæna*.  
XCVIII.



Spiral valve, *Selache*. CCLXVI.



it is to be remarked that the intestinal canal is shortest, and the spiral valve most complex and extensive, in the Sharks. In both these and the Rays, the valve subsides at a short distance from the anus; and into the back part of this terminal portion of the rectum an elongated cæcal process with a glandular inner surface opens fig. 352, *i*. The anus itself communicates with the fore part of a large cloacal cavity in the Plagiostomes. In other Fishes, where it opens distinctly upon or near the external surface, it is anterior in position to the orifices of oviducts, or spermducts, fig. 281, *f*, and of the uterus or urinary bladder; the Lepidosiren has the peculiarly ichthyic arrangement of the anal, genital, and urinal outlets.<sup>1</sup>

In the Dermopteri the intestinal canal is rather closely attached to the back of the abdomen, though the primitively continuous mesenteric fold becomes reduced in the Lampreys to filamentary processes accompanying the mesenteric vessels. A similar reduction of the mesentery to detached membranous bands occurs in the Syngnathi and Cyprinidæ. The mesentery is entire in the Lepidosiren, the Plagiostomes, and many other Fishes: it is usually single and continuous from the stomach to the end of the intestine: there are two parallel mesogastrics in the Eel, and a kind of omental accumulation of adipose matter is sometimes found along the ventral surface of the intestines: a second mesentery is continued from this part of the intestine to the ventral parietes of the abdomen in the Muræna.

The position of the cloacal outlet varies much in Fishes: in some of the jugular species it follows the ventral fins to the region of the throat; and in the apodal Gymnotus, fig. 232, it is placed so far forward as to remind us of the position of the excretory outlet in the Cephalopods. It is beneath the pectorals in the *Amblyopsis spelæus*: but the more normal posterior position of the vent obtains in most abdominal and all cartilaginous Fishes.

Petrified fæces or 'coprolites' give some insight into the structure of the intestinal canal in extinct species of Fishes: some that have been found in the skeleton of the abdomen of the great *Macropoma* of the Kentish Chalk, and detached coprolites associated with the scales and bones of the more ancient *Megalichthys*, indicate by their exterior spiral grooves that these

<sup>1</sup> xxxiii. pl. 25, fig. 1, *m*, *n*, *o*, *l*. The Branchiostoma offers no exception to this rule; the opening by which the ova and semen are expelled is a common peritoneal outlet.

ancient Ganoids, like their modern representative, the *Polypterus*, possessed the spiral valve.

§ 73. *Liver of Fishes.*—The liver makes its first appearance in the lowest vertebrated, as in the lowest articulated, species, under the form of a simple cæcal production from the common alimentary canal. Commencing in the Lancelet, fig. 169, *hd*, a little beyond the orifice *py*, the hepatic cæcum, *l*, extends forward from its place of communication with the canal *ii*, and terminates in a blind end. In the Myxinoids the liver, as in all higher Fishes, fig. 282, *a*, is a well-defined conglomerate, or acinous, parenchymatoid organ, with a portal and an arterial circulation, with hepatic ducts, and generally a gall-bladder and cystic duct, *ib. c*, by which the bile is conveyed to the duodenum, from which the stomach is divided by a pyloric valvular orifice.<sup>1</sup>

The texture of the liver is soft and lacerable; its colour usually lighter than in higher Vertebrates, being whitish in the *Lophius*, and in many other Fishes of a yellowish grey or yellowish brown: it is, however, reddish in the Bream, of a bright red in the *Holocentrum orientale*, orange in *Holocentrum hastatum*, yellow in *Atherina presbyter*, green in *Petromyzon marinus*, reddish brown in the Tunny, dark brown in the *Lepidosiren*, almost black in the Paddle-fish. In the *Siluridæ* a portion of the liver, usually forming a middle lobe, thinner than the rest and of a lighter colour, has been described as the ‘pancreas:’ it has a distinct duct, opening near that of the ductus choledochus. In most Fishes the liver is remarkable for the quantity of fine oil in its substance, under which form almost the whole of the adipose matter is there concentrated in the Cod tribe, the Rays, and the Sharks.<sup>2</sup> Fishes which, like the Salmon and Wolf-fish, have oil more diffused through the body, have comparatively little oil in the liver.

The liver is generally of large proportional size: it is attached at the fore-part of the abdomen to the aponeurotic wall partitioning off the pericardium, fig. 276, *l o*, and extends backward, with a few exceptions, further on the left than on the right side: in the Carp, the Bream, and the Stickleback, the right lobe is longest. Its shape varies with that of the body or of the abdominal cavity; it is broadest, for example, in the Rays, longest in the Eels; not,

<sup>1</sup> The Bream is the only fish in which I have found the cystic duct terminating directly in the stomach.

The myriads of Dog-fish captured and commonly rejected on our coasts show that the fishermen have not yet taken full advantage of this anatomical fact, which exposes to them an abundant source of a pure and valuable oil.

however, elongated in the Gymnotus, in which apodal fish, by reason of the peculiar aggregation of the organs of vegetative life in the region of the head, the liver is divided into two short and broad lobes connected by a transverse lobule. The liver consists of one lobe in most Salmonoid and Lucioid Fishes, in the Gymnodonts and Lophobranchs, in the Mulletts, Loaches, and Bullheads. It is long and simple in the Lamprey and Lepidosiren; long and bilobed in the Conger. The Lump-fish has a lobulus besides the chief lobe, which is round and flat. There is a short thick convex lobe to the right of the long left lobe in the Lophius. In many Fishes the two lobes are subequal: they are rarely quite distinct, as in the Myxinoids; but commonly confluent at their base, as in the Wolf-fish, or connected by a short transverse portion, as in most Sharks, the Siluroids, the Polypterus, the Dory, the Coryphene, the Chætodonts, and the Cod tribe. In the Whiting the two chief lobes extend the whole length of the abdomen; in the Shark about half the length, fig. 352, *b* (in which the left lobe is cut away). The liver is trilobed in the Corvina, the Clupeoid, and the Cyprinoid Fishes: in many of the latter family it almost conceals the convoluted intestinal canal. The broad and flat liver of the Raiidæ is trilobed. The liver is much subdivided in the Sandlance and in the Tunny, in which latter fish it presents remarkable modifications of the vascular system.<sup>1</sup> There are few well-established exceptions to the general rule of the presence of a gall-bladder in the class of Fishes. My dissections confirm the statement of its absence in the Lump-fish by Cuvier<sup>2</sup> and Wagner.<sup>3</sup> Cuvier did not detect a gall-bladder in *Lates niloticus*, *Holocentrum Sogho*, *Sphyræna Barracuda*, *Trigla lyra*, *Trigla cuculus*, *Corvina dentex*, *Glyphisodon saxatilis*, *Lepidopus argenteus*, *Labrus turdus*, *Ammodytes*, and *Echineis remora*. The gall-bladder is wanting in the Ammocete and Lamprey, but exists in the Myxinoids; it is absent in *Pristis*, *Zygæna*, and *Selache*, but is present in *Galeus*, and others of the Shark tribe. The rich series of observations recorded by Cuvier<sup>4</sup> and his able Editors<sup>5</sup> on the gall-bladder and gall-ducts in Fishes have not afforded a clue to the law of the development of the special receptacle of the biliary secretion in Fishes. The pouch in which the aggregated hepatic ducts terminate in the *Selache maxima* may compensate for the absence of the gall-bladder in that Shark; these ducts are enclosed in a broad flat band of dense cellular tissue, fig. 284, *l*, which passes

<sup>1</sup> CIII.<sup>2</sup> XII. t. iv. p. 551.<sup>3</sup> XLVII.<sup>4</sup> XXIII. passim.<sup>5</sup> XII. t. iv. pt. ii. p. 559-569.

obliquely down in front of the stomach as far as the duodenum, when each of the ducts opens by a separate oblique orifice into a common cavity, *ib. m*, of an oval form, communicating with the duodenum by a single opening.

The gall-bladder is usually situated towards the fore-part of the liver, and attached to the right lobe when this exists, as in *fig. 276, m*. In some Cyprinoids and Rays, and in the Sturgeon, it is imbedded in the substance of the liver. In many Chætodonts and Salmonoids, in the Sword-fish, *fig. 282, c*, in the Eel and the *Muræna*, it hangs freely at some distance from the liver. I found the gall-bladder three inches from the liver in a *Lophius* of two feet in length. The size of the gall-bladder varies in different Fishes; it is very small in most Rays: in Osseous Fishes it usually bears a direct relation to that of the liver itself. It is pyriform in the *Lophius*, Mullet, Sea-perch (*Sebastes*), Pike, Sturgeon, Planirostra, and most other Fishes: it is subspherical in the Grey-shark (*Galeus*), and in the Wolf-fish: it is like a long-necked flask in *Polypterus*; is bent like a retort in *Xiphias*, *ib. c*: and is remarkably long and slender in *Sciæna*, *Upeneus*, *Lates nobilis*, and in the Bonito, the Tunny, and other *Scombridæ*. The bile is sometimes conveyed to the gall-bladder, *fig. 291, c*, by hepato-cystic ducts, *ib. d, d*, and thence by a cystic duct, *ib. e*, into the duodenum (Wolf-fish, Erythrinus, Lepidosiren): or it passes at once to the intestine by a single hepatic duct, formed by the union of several branches from the liver (*Zygæna*, where the duct is very long): or by two hepatic ducts opening separately into the intestine, as in *Pristis*: or an hepatic duct from the left lobe joins a cystic duct from the bladder, receiving the gall from the right lobe, and the secretion is conveyed by a 'ductus communis choledochus' into the duodenum, as in *Pimelodus*: or the bile is conveyed to the duodenum partly by a cystic duct and partly by a distinct hepatic duct, as in the Salmon, in which the latter dilates before it terminates. In the *Lophius* three hepatic ducts join the very long cystic, which duct sometimes dilates where it receives them. In the Sword-fish three or four hepatic ducts communicate with the cystic, to form the ductus communis, *fig. 282, b*. In the Turbot there are more numerous hepatic ducts, some of which communicate with different parts of the cystic duct, and four open into the dilated termination of the ductus communis.<sup>1</sup> In the *Galeus* the cystic duct runs some way through the substance of the liver, and sometimes between the tunics of the pyloric canal of the stomach,

<sup>1</sup> xx. vol. i. prep. no. 811 A.



before it enters the commencement of the wide intestine, near the beginning of the spiral valve. The gall-duct in the Sturgeon and Planirostra terminates at a greater distance above the valvular intestine. The ordinary position of the entry of the bile into the alimentary canal in Osseous Fishes is at the commencement of the small intestine near the pylorus. The terminal part of the gall-duct is usually slightly expanded, fig. 291, *e*, and its orifice is often supported on a papilla, as in the Sturgeon, the Skate, and the *Labrax lupus*.

§ 74. *Pyloric Appendages and Pancreas of Fishes.*—In most



Alimentary canal of the Whiting (*Merlangus vulgaris*), showing the pile of caeca around the pylorus. CCXXXI.

Osseous Fishes the intestine buds out at its commencement into long and slender pouches, or caeca, fig. 281, *d*, into which it appears that the food does not enter, and which, therefore, increase the direct secreting surface of the alimentary tract, over and above the extent of the mechanism for pounding and propelling the chyme, or of the vascular surface which selects and absorbs the chyle. By a very gradual series of changes of these caecal processes, within the limits of the class of Fishes, they become massed into a body, fig. 282, *d*, like the conglomerate gland, called 'pancreas' in Man. The secretion of the rudimental representatives of this gland is so like the fluid which the ordinary mucous surface of the intestine eliminates and sets free from its capillary system, that conditions of the ordinary alimentary tract exist in some Fishes which render needless the development of the special accessory surfaces. The

*Dermopteri* show no trace of pancreas; their whole digestive canal is simple: the organisation for which that canal is the

commissariat is the most simple in the Piscine class. The Lamprey, at the head of the Dermopterous order, derives from the slight spiral extension of its intestinal mucous coat the

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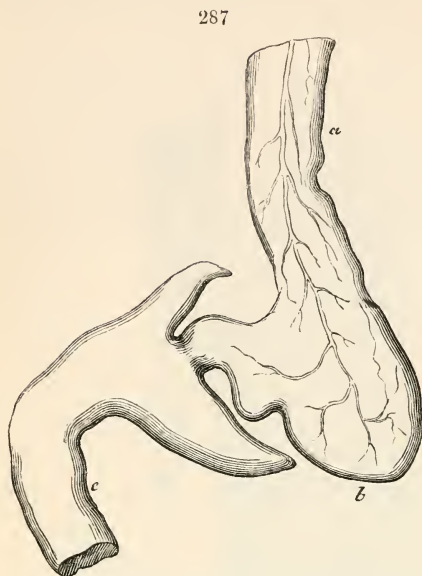


Portion of the alimentary canal of the Salmon (*Salmo salar*), showing one double row of caecal appendages and portions of the other. CCXXXI.

required concomitant complexity of the digestive canal. In several Osseous Fishes, either the inactive nature of the species, or the extent or special modifications (the long intestine and glandular palate of the Carp, the thickened mucous membrane

of the duodenum of the Eel, for example) of the ordinary tract of the alimentary canal, render unnecessary the presence of a pancreas. Thus there is no cæcal production of the duodenum in the Ambassis, Wolf-fish, Warty Agriope, nor in most Labroids, Cyprinoids, Lucioids, Siluroids, nor in the apodal *Malacopteri*, nor in the Lophobranchs and Plectognats; nor in the genera *Antennarius*, *Malthæus*, and *Batrachus*.

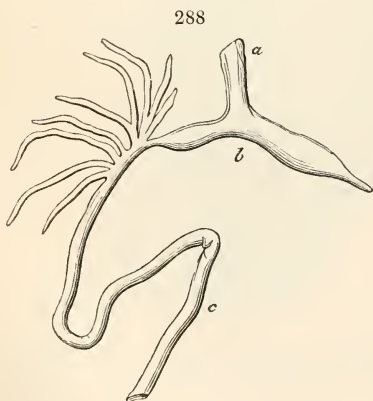
The pancreas is represented by a single pyloric cæcum in the Sandlance and Polypterus, fig. 279, *k*: by two cæca in most Labyrinthibranchs, in many species of Amphiprion, in the Lophius, the Turbot, fig. 287, and the Mormyrus, fig. 280, *k*: by three cæca in the Perch,



Pyloric cæca of the Turbot (*Rhombus maximus*). CCXXXI.

the percoid Popes (*Acerina*), the Asprodes, and Diploprions: of from four to nine cæca in the genus *Cottus*: of from five to nine cæca in the genus *Trigla*:

of six cæca and upwards in *Scorpena* and *Holocentrum*: of nine cæca in the Sprat, fig. 288: and so on, increasing to a numerous group of pendent pyloric pouches, as we find in the Scomberoids, Chætodonts, Gadoids, fig. 285, Halecoids, fig. 286, Cyclopterus, and Lepidosteus. There is a difference, however, worthy of note, in the mode and extent of attachment of these numerous



Pyloric cæca of the Sprat (*Clupea sprattus*)

cæca: in the Salmon, fig. 286, Herring, fig. 281, *d*, Sprat, fig. 288, and Haddock, they rank almost in a line along the whole duodenum: in the Gymnotus, Lump-fish, and Whiting, fig.

285, they form a circular cluster around the distal side of the pylorus. Even in the longitudinally arranged cæca the principle of concentration dawns; thus the fifty pancreatic cæca of the Pilchard communicate with the duodenum by thirty orifices: but the fifty attenuated terminal blind sacs in the pancreas of the Lump-fish unite, reunite, and discharge their secretion by a circle of six orifices around the duodenal side of the pyloric valve. In the Tunny a more subdivided bunch of pancreatic cæca empty themselves by five orifices: in the Whiting about one hundred and twenty peripheral cæca progressively unite into four groups or bunches, fig. 289, communicating, each by a single duct, with the duodenum: in the Sword-fish, fig. 282, *d*, a more compact gland-like mass pours its secretion into the gut by two orifices, *e*: and, finally, in the Sturgeon and Paddle-fish, fig. 276, *k*, by a single opening of what now becomes the short and wide duct of the gland. The interposition of cellular tissue binding together longer, more slender, and more ramified cæca, with a concomitant increase of the vascular supply, and a common covering or capsule, finally converts the accessory intestinal growths into a parenchymatous conglomerate gland, as we see in the Sword-fish, Sturgeon, Holocephali, and Plagiostomes; the papilliform termination of the duct of such a pancreas is shown in the Selache, at fig. 284, *i*. It sometimes exceeds the liver in weight.

The existence of this developed form of secreting organ, over and above the spiral intestinal valve, may relate to the high organisation of these Cartilaginous Fishes, and to the great developement of the organs of locomotion, occasioning the necessity for rapid and complete digestion. But if we compare the few existing species of heavily laden Ganoid fishes, we shall again find good evidence of the compensation for a pancreas by the extension of the intestinal mucous membrane within the canal, the circumstances calling for a more complete developement of the digestive system in the predatory Sharks and large-finned Rays not being present. Thus the Polypterus, which has a spiral intestinal valve, has only one short pyloric cæcum, fig. 279, *k*; whilst the Lepidosteus, which has no spiral valve, has a compact group of above a hundred small cæca, which unite and reunite to communicate by a few apertures with the commencement of the duodenum.

The inner or mucous surface of the pyloric cæca is laminated

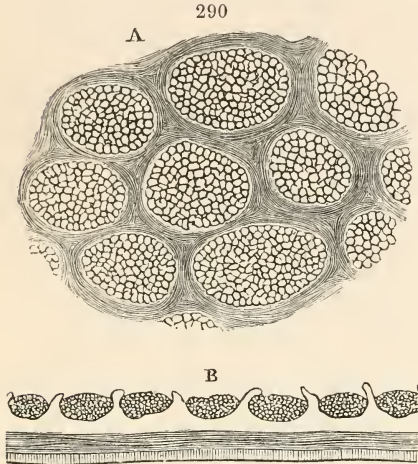
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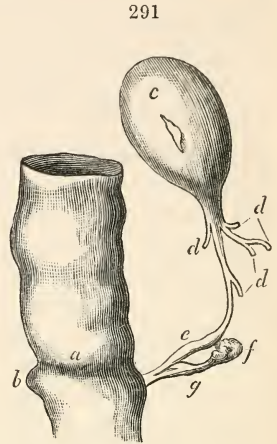
One of the four bunches of pyloric appendages of the Whiting, isolated; showing their union and reunion to form a single tube. CCXXXI.



in some Fishes: in others it is villous, with orifices of crypts at the basal intervals of the flattened villi: in the Herring, fig. 290, the surface is minutely honeycombed; the cells or crypts being about  $\frac{1}{150}$  of an inch in diameter, and each is filled with a mass of epithelial cells, as seen in the section B, fig. 290. The basis of



Crypts of pyloric caeca, Herring. CCXXXI.



Pancreas (f) of a Flounder. CCXXXII.

the crypts is fibrous and projects between and often beyond the level of their openings. The masses of epithelium resemble one of the stages of the contents of the ultimate follicles of the pancreatic acinus of a Mammal. The relation, however, of the pyloric appendages of the Fish to that of the pancreatic gland of the higher Vertebrates may be but one of analogy.

There is a minute, but more constant glandular body present both in fishes which possess (*Salmo*, *Gadus*, *Percia*) and those that do not possess (*Platessa*, *Belone*, *Brama*, e.g.) the pyloric caeca. It is too small, fig. 291, *f*, for the performance of the pancreatic function in digestion; but the contiguity of the terminal dilatation of the duct, *ib. g*, with that of the ductus choledochus, *ib. e*, and of their respective openings into the duodenum, suggests that this glandule may be the rudimental homologue of the pancreas of air-breathing Vertebrates.

In the *Lepidosiren* the body imbedded between the muscular and serous coats of the stomach, and referred to as probably 'splenic' in CXLV. p. 271, sends its secretion by ducts converging to one canal which opens beyond the pylorus, close to the orifice of the hepatic duct.<sup>1</sup>

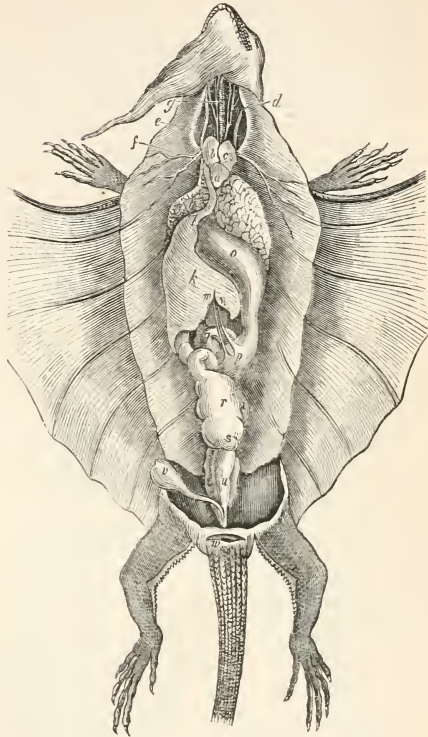
<sup>1</sup> According to CCXXXIII, p. 10.

§ 75. *Alimentary canal of Reptiles.*—The cavity containing, as in Fishes, the alimentary canal, with the kidneys and principal organs of generation, also lodges in Reptiles, fig. 292, the heart, *a*, *b*, *c*, and lungs, *h*, *i*. In most the whole cavity is lined by the peritoneum, which is reflected upon the several viscera. In the transverse section of the cavity, fig. 293, the thick line diagrammatically shows the peritoneum reflected from the vertebral centrum upon the aortal and caval trunks, *h*, the spleen, *b*, and stomach, *a*, whence it is continued to form the omental fold, *e*, *c*: from the ventral surface the peritoneum is reflected at one small part upon the remains of the umbilical vein, forming the so-called ‘falciform,’ *g*, and ‘round,’ *d*, ligaments of the liver. In the *Crocodylia* the peritoneum does not extend forward beyond the stomach and liver,

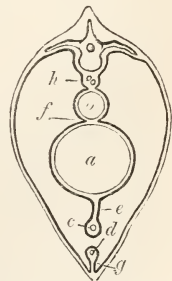
but is reflected upon the posterior (sacral) surface of both organs,<sup>1</sup> circumscribing a smaller ‘abdominal’ cavity, and including fewer viscera, than in Mammals.

In female Reptiles, the serous membrane of the abdomen is continuous with the mucous membrane of the oviducts; the subhexagonal or polygonal flattened cells of its epithelium giving place to the ciliated epithelial cells at the margin of the oviducal aperture. In both male and female *Chelonia*, the peritoneum is continued, as an infundibular canal, into the ‘corpus cavernosum’

292

Abdominal cavity and viscera, *Draco volans*. CCL.

293

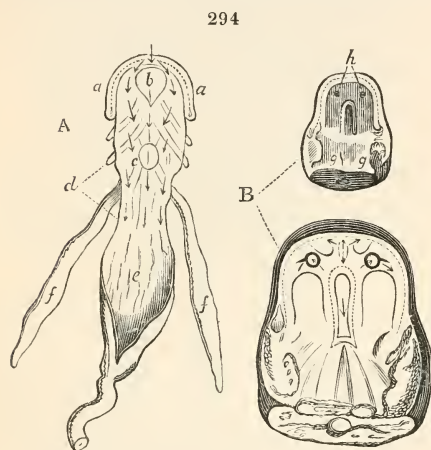


Transverse section of the abdominal cavity, Lizard. CCXXXV.

<sup>1</sup> CCXXXVI. vol. ii. p. 336.

of the penis<sup>1</sup> and clitoris: in the *Crocodylia*, besides communicating with that structure, the peritoneal canals open outwardly upon papillæ, situated on each side of the base of the penis<sup>2</sup> and clitoris. These are the exceptions, in the reptilian class, to the typical character of the peritoneum as a closed 'serous' sac. In most Reptiles pigmental cells are blended with or supersede the ordinary tessellated lining of epithelial cells in certain parts of the peritoneal surface.

The mouth in Reptiles gives passage to respiratory currents as well as to the food in the Perennibranchiates, and in all the air-breathers along that extent of the cavity which is posterior to the palato-nares, fig. 294, B, *h*: the *Crocodylia* alone having the nasal distinct from the oral passage.



Ciliated surface of the mouth and gullet, *Triton*.  
CCXXXVIII.

In *Chelonia*, the jaws with their horny covering form, as in Gymnodont fishes, the first portal to the alimentary canal: in many *Batrachia* the integument passes evenly over the alveolar margins of the jaws, as in fig. 294, *a, a*: in *Ophidia*, *Sauria*, and *Crocodylia*, a narrow tract of soft and vascular integument intervenes between the scale-clad border of the mouth and the jaws; sinking into a more or less shallow groove, which defines the lips and receives the secretion of a row of mucous crypts: but such lips are hard and inflexible: in certain Frogs and Toads they are of softer texture: but in none are produced or prehensile.

The walls of the mouth expand into pouches in certain Reptiles, as e.g. at the sides of the face in male Frogs, below the tongue in *Hyla*, and produced from the same part into a conspicuous gular bag, as in the *Draco volans*, fig. 303, *d*. But these pouches receive air, not, as in some higher Vertebrates, food; and usually relate to the powers of voice.

The bony walls of the mouth have been already described; the

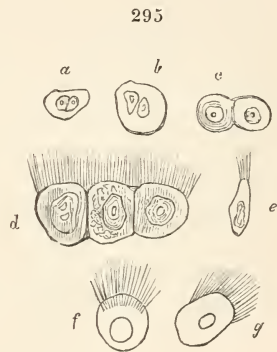
<sup>1</sup> xx. vol. iv. p. 62, preps. nos. 2448—2451.

<sup>2</sup> Ib. vol. iv. p. 60, prep. no. 2439; and CCXXXVII. p. 153.

lining membrane retains the ciliated epithelium in most *Batrachia*. In fig. 294, B shows the roof of the mouth of a Newt, of the natural size and magnified: A shows the floor of the mouth with the œsophagus, *d*, laid open from above, the stomach, *e*, and lungs, *f, f*. *a* is the lower jaw, *b* the tongue, *c* the glottis. The currents produced by the vibratile cilia are made visible by powdered charcoal, and their course is indicated by the arrows, beginning at the symphysis and extending to the cardiac end of the œsophagus. The ciliary movement 'is remarkably vivid in the mouth of the Serpent; and in the Tortoise it endures for several days after death, not ceasing till the parts are destroyed by putrefaction.'<sup>1</sup> Fig. 295 gives a magnified view of some of the ordinary nucleated epithelial scales, *a, b, c*, and of some ciliated scales, *d, e, f, g*, from the mouth of the Frog.

The tongue, as an organ of taste in Reptiles, has been noticed, p. 327. In Newts it is usually small, as at *b*, fig. 294. In most tailless *Batrachians* it is large: attached to the floor of the mouth, a little behind the symphysis of the mandible, with its free border directed backward.<sup>2</sup> This part can be raised and thrown out of the mouth by a rotatory movement, as on a hinge, with a certain elongation, equaling in some Toads two thirds or more of the length of the body. A glutinous saliva is spread over the surface: both the protrusile and retractile movements are executed with extreme velocity, and thus the insect is seized and swallowed more quickly than the eye can follow, when the *Batrachian* has brought its mouth within the distance at which the tongue can reach the fly.

The hyoid being raised and the mandible depressed, the genio-glossi, having their fixed point at the symphysis, raise and jerk forward the free part of the tongue; at the same instant the tongue is narrowed and lengthened by the action of transverse fibres in its substance: the return movements are due to the hyoglossi, acting from the hyoid arch, while this is at the same time depressed and retracted. In most Frogs the back part of the tongue is bifurcate, fig. 350, *a*, or bilobed (*Polypedates*): in



Nucleated and ciliated epithelial scales  
mouth of Frog

<sup>1</sup> CCXXXVIII. vol. i. p. 631.

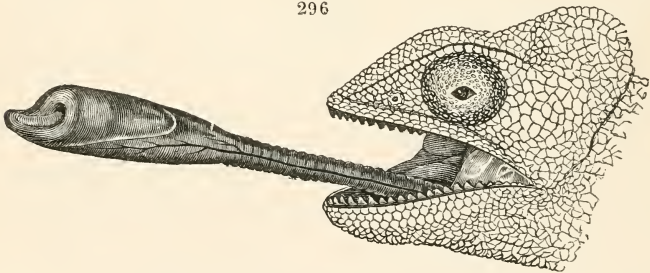
<sup>2</sup> In *Heteroglossus* the tongue is attached by a central pedicle.



*Oxyglossus* it is rounded, as in Toads and some *Hylidæ*, e. g. *Elosia*; but here the whole margin adheres: the rarest form, in anourous Batrachians, is that of *Rhinophrynus*, in which the fore part of the tongue is free.<sup>1</sup> In Serpents the tongue takes no other share in the prehension of food than by the degree in which it may assist in the act of drinking; it is very long, slender, cylindrical, protractile, consisting of a pair of muscular cylinders, in close connection along the basal two thirds, but liberated from each other, and tapering each to a point at the anterior third: these are in constant vibration when the tongue is protruded, and are in great part withdrawn, with the undivided body of the tongue, into a sheath when the organ is retracted. This act is performed by the 'glossohyoidei,' fig. 147,  $\Delta$ ; protrusion is effected by the geniohyoidei, ib.  $z, z'$ . The orifice of the sheath is strengthened by a pair of cartilaginous plates, on which other muscles act.<sup>2</sup> The ununited symphysis of the mandible leaves a passage for the tongue without the need of 'opening' the mouth: and the acts of protrusion and retraction are usually seen to be frequently repeated. The *Amphisbænidæ* and *Anguidæ* have short, thick, hardly protractile, and sub-bifurcate tongues.

The arboreal Chameleons, clinging on all fours to their tree branch, depend wholly on their singularly extensile tongue for the prehension of their volatile insect food. The movements of this organ are as instantaneous as in the Toad and Frog, and

296



Tongue of the Chameleon partially extended. ccl.

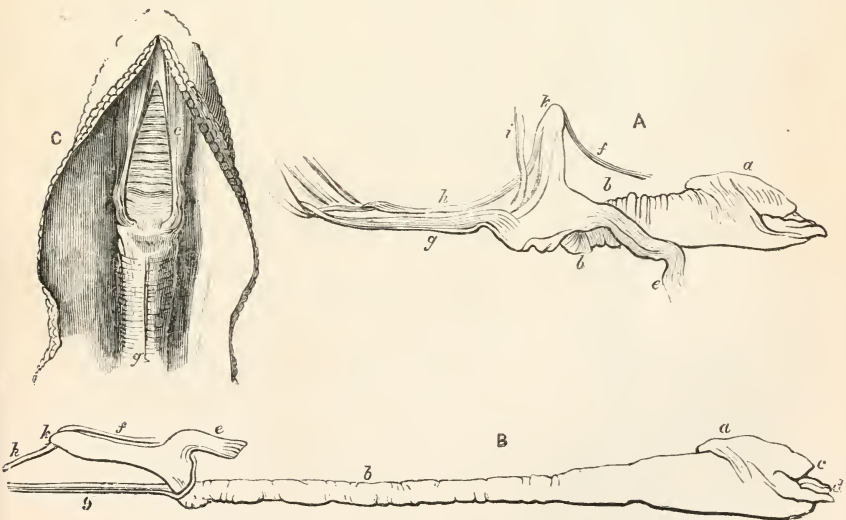
are due to combined muscular and elastic forces, acting within the tongue and upon its supporting bones, with concomitant modifications of the hyoid arch. The glosso-hyal is produced into a long and cylindrical, fibro-cartilaginous style; it penetrates a fibrous sheath in the substance of the tongue, which, when

<sup>1</sup> It affords the character of Dr. Günther's section *Proteroglossa*, CLXXV.

<sup>2</sup> CCXLI. p. 368, pl. 46, fig. 15.

retracted, fig. 297, A and C, is almost wholly supported thereby, and, when withdrawn, the cavity of the sheath is occupied by a ductile cellulosity. The bulbous end of the tongue, fig. 296, and fig. 297, A, B, is divided by a transverse curved groove into a shorter upper, *ib. a*, and a longer lower lobe, *ib. d*, resembling the prehensile part of the Elephant's proboscis; the surface is finely rugous, and bedewed by adhesive secretion. Between the bulb and the base the glossohyal sheath is immediately surrounded by fibrous, degenerating into lax elastic, tissue, covered by the lingual skin, which is thrown into circular rugæ or rings, in the contracted state (as in fig. 297, A, *b*, and in C, where this part of the tongue is exposed by divaricating the geniohyoid muscles, *c*). The tissue of the glossohyal sheath consists chiefly of unstriped muscular fibres, arranged transversely. The longitudinal fibres are those of a pair of 'glossohyoidei,' extending along the sides of the annular extensible part, and spreading out at the bulbous part, of the tongue. The circular fibres, strongly contracting, diminish the thickness, increase the length, and, squeezing the smooth supporting style, slip off the elongated part of the tongue from its fore part with a certain

297



Tongue of the Chameleon. CCXL.

jerk. But with this action is associated a more powerful propeller of the weighted bulbous end of the tongue, exercised by the muscles of its bony support. The geniohyoidei, fig. C, *e*, and A, *e*,

draw forward the basihyal upon the ends of the ceratohyals, *h*, which are steadied by the slender muscles ‘ceratomandibularis,’ *f*, and ‘ceratosternalis,’ *h*: so that the inverted bony arch, from being vertical, as at A, *h*, is made horizontal, as at B, *h*; the basihyal being brought forward about an inch, and with a force and precision, due to the fixation of the ceratohyal tips, by their guy-rope-like muscles, *f* and *h*, which adds greatly to the propelling force. This force, added to, and acting consentaneously with, the elongation of the annulose part of the tongue, *b*, A and B, jerks out the swollen prehensile end of the tongue to the full extent allowed by its elastic yielding tissue, which, on the cessation of the muscular actions and their momentum, retracts the bulb; and the drawing back of the tongue is effected by the contraction of the glossohyoidei, and of the elastic cellular tissue, readjusting the sheath upon the glossohyal: also by the retraction of the hyoid, through the sternohyoidei muscles, fig. 297, A, C, *g*. These are assisted by the omohyoidei, ib. A, *i*; and the actions of *e* and *g* are made more effective by the cooperation of *f* and *h*, in steadying the points of the inverted arch upon which the swinging movements to and fro of the basi- and glosso-hyals take place. The mechanism and forces of the extension and contraction of the Chameleon’s tongue are essentially the same as those of the tongue in Toads and Geckos, among which those species can most elongate the organ, when the hyoid muscles jerk it out of the mouth, which have the greatest proportion of ‘linguales’ fibres arranged so as to contract its breadth.<sup>1</sup>

The styliform glossohyal, besides supporting the retracted tongue and increasing the force of the constricting ‘linguales’ fibres, enables aim to be taken at the object to be reached. The Chameleon, having discerned its prey, brings its head into position, opens the mouth to the extent required for the tongue’s passage: then, steadying the apparatus ‘by a sort of tremulous rigid movement,’ shoots out the tongue, and retracts it with the fly, the velocity of the action being such as to ‘startle one afresh every time it is witnessed.’<sup>2</sup>

The tongue of the Crocodile, fig. 298, *c*, is slightly raised by its fleshy portion above the level of the membranous floor of the

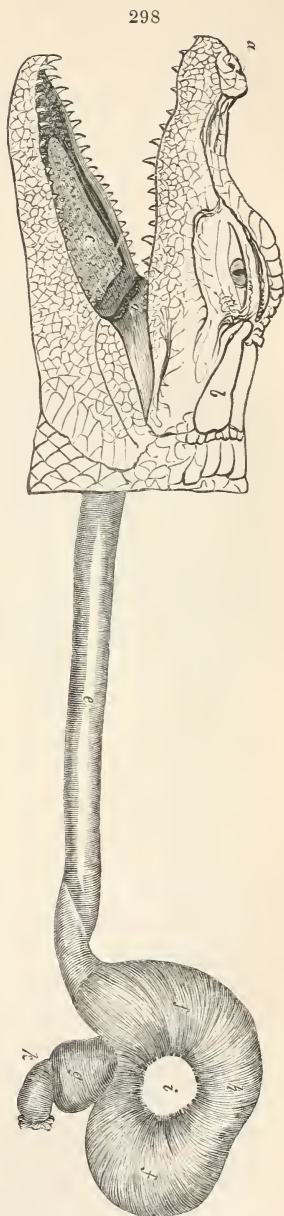
<sup>1</sup> The explanation above given agrees in essentials with that proposed by Hunter (xx. vol. iii. p. 68), and Cuvier (xii. ed. 1, tom. iii. p. 273); other hypotheses are cited in CCXXXIX. tom. vi. p. 76, and CCXL. vol. iv. p. 1147.

<sup>2</sup> CCXL. p. 1150. The whole of Dr. Salter’s excellent article is well worth careful study. A previous dissection of a Gecko’s tongue, after maceration, as the Chameleon’s ought to be, in alcohol, facilitates the recognition of the circular arrangement of non-striped ‘linguales’ fibres, described by Hunter and Cuvier.

mouth, but is not prolonged freely beyond it; its back part appears to rise, but this is due to the continuation of the membrane from the base of the tongue over a transverse cartilaginous plate, formed by the basihyal, which, abutting against the velum palati, *ib. d.*, can close the back part of the mouth. So that, when the Crocodile holds submerged a drowning prey, the water traversing the mouth has no access to the glottis.<sup>1</sup>

The membrane covering the dorsum of the tongue is beset by mucous crypts; the 'ceratoglossi' divide into fasciculi, which decussate across the median line.

A salivary apparatus is as little specialised in Batrachians as in Fishes. Mucous crypts upon the tongue or palate subserve the need of lubricating the quickly swallowed and unmasticated food. In Lizards a series of orifices of mucous crypts extend along the lip-groove of both jaws. In the Crocodile, besides the lingual follicles, there are groups of more complex ones on each side, behind the palato-nares, opening into the meshes of the plicated faucial membrane. In Chelonians there are groups of mucous follicles below the tongue, representing the sublingual glands of Mammals. The labial glands are abundantly developed in Ophidians. The secretion of the lacrymal glands is added to the lubricating fluid of the mouth. The poison-gland of venomous Serpents may be regarded as a specially developed parotid, but will be described in another section. In all Reptiles the secretions entering the mouth are rather mucous and mechanical in func-



Mouth, gullet, and stomach, Crocodile. CCL.

<sup>1</sup> xx. vol. iii. p. 72, prep. no. 1466.



tion than truly salivary, as exercising any alterant influence on the nature of the food.

A 'velum palati' is developed only in the *Crocodylia*: an epiglottis is not present in any Reptile: the basihyal valve of the Crocodiles is analogous to one, and some lizards show a rudiment of epiglottis. The sides of the pharynx are cleft by the gill-slits in the perennibranchiate *Batrachia*; and one slit on each side remains open in some of the caducibranchiate species, as, e. g., in *Menopoma*. In the Siren there are three clefts on each side, defended by interlocking pointed processes, closely resembling the narrower of the five lateral branchial clefts in the *Lepidosiren*, fig. 316, 1, 3, 4, 5.

The œsophagus is short and wide in *Batrachia*, fig. 294, *d*, *e*,

long and wide in *Ophidia*, fig. 300, *d*, *e*, *f*, of moderate length and width in *Chelonia*, narrower in *Crocodylia*, fig. 298, *e*, and still more so in insectivorous *Lacertilia*, fig. 303, *e*. It is remarkably dilatable and thin-coated

in Snakes, as at fig. 300, *f*, in which its intrinsic propelling power is supplemented by the constriction of the surrounding trunk-muscles during the deglutition of bulky prey. The other chief peculiarities in the structure of this part of the alimentary canal of Reptiles are, the perforation of its walls by certain elongated and



Retroverted processes in œsophagus of Turtle (*Chelone*). CCL.

enameled hypapophyses in *Deirodon*,<sup>1</sup> *ante*, p. 393, and the production of the lining membrane into pointed processes, directed to the stomach, and covered by thick epithelium in the Turtles (*Chelone*).<sup>2</sup> These aid in the deglutition of the long slippery seaweeds on which the Turtle feeds; in carnivorous *Chelonia* they are not present; the lining membrane in *Testudo indica*, e. g., is thrown into longitudinal rugæ when undistended, and presents a fine reticular and porous surface. The ciliated epithelium is continued along the gullet in *Triton*, fig. 294, *d*, and in the larvæ of Toads and Frogs.<sup>3</sup> The muscular tunic of the gullet is strongest in the Turtles.

The stomach presents, in Reptiles, its most simple form in the Ophidian and Batrachian orders, especially in the ichthyo- and

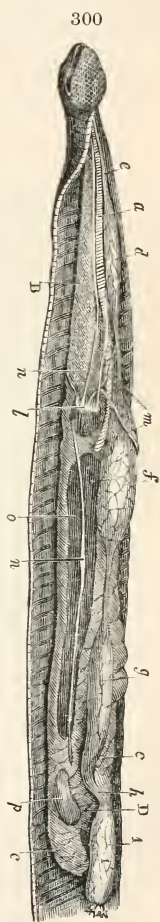
<sup>1</sup> Jourdan, in CCXLII. tom. vi. p. 160.

<sup>2</sup> xx. tom. i. p. 126, preps. nos. 460, 461; XLIII. pt. iv. pl. v. fig 7.

<sup>3</sup> CCXLIII. tom. i. p. 191.

ophio-morphous kinds of the latter. The transition from the gullet to the stomach is scarcely indicated externally. On the inner surface it is shown, in the Python, by the more vascular and rugous character of the longitudinal folds continued into it from the œsophagus, the interspaces of the folds being reticulate. The stomach, which is straight, as in the Rattlesnake, fig. 300, *g*, contracts at first gradually, then quickly, to the pylorus, whence a narrow canal, of about an inch in length in a Python of ten feet long,<sup>1</sup> conducts to the suddenly expanded intestine. In the Proteus, Siren, and Amphiuma the stomach is long, cylindrical, and nearly straight; there is no intervening canal between pylorus and intestine. The stomach is distinguished from the œsophagus by the thickness of its coats, and by the spongy and vascular character of the lining membrane. In the Siren and Triton, fig. 294, the pyloric end bends a little to the right; this bend is more marked in *Salamandra*. In the Frog, the stomach, fig. 305, *a, c*, is pyriform, placed on the left side of the abdomen, with a slight curve to the right side. In the Lizard the stomach, fig. 301, *a*, is fusiform, with a similar position: but, in curving to the right, it advances from behind forward. In the Flying Lizard (*Draco volans*), fig. 303, *f*, and the Iguana, the stomach is rather pyriform, but the shape varies with the state of the contents.

In the *Chelonia* the stomach so far accords with the broad and flattened form of trunk that it is placed more transversely, bending as it passes from the left to the right side. In fig. 302 the gradual passage from the œsophagus, *r*, to the stomach, *κ*, is shown in the fresh-water Tortoise, *Emys europæa*, in which the stomach is cylindrical and elongated, curving behind, and in a deep groove of the left lobe of the liver, *l*, to the right, where the pyloric portion of the stomach, *κ'*, becomes narrower and thicker in its coats. The muscular fibres of the layer radiate from an aponeurotic part on each side, at the chief bend. The mucous

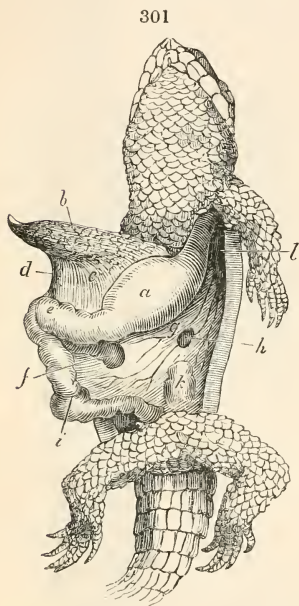


Viscera, in fore part of the abdomen, of the Rattlesnake. ccl.

<sup>1</sup> xx. vol. i. p. 143, no. 504 A.

membrane is disposed in longitudinal rugæ, most marked at the cardiac half; the orifices of gastric follicles are numerous at the pyloric portion. Here Hunter noticed 'a glandular part on one side, a little way from the pylorus, with many orifices.'<sup>1</sup> In the Turtle (*Chelone*) the muscular tunic of the stomach becomes, in the adult, remarkably thick, for due compression of the vegetable contents; in the young animal the coats are as thin as in *Emys*.<sup>2</sup> In this genus, and other carnivorous *Chelonia*, the cardiac orifice is very wide compared with the pyloric.

The *Crocodylia* present the most complex stomach known in



Abdominal viscera of a Lizard. CCXXXV.

existing members of the Reptilian class. The principal cavity is of a rather flattened sub-circular or full oval shape; there is a tendon, fig. 298, *i*, at the middle of each side, better defined than in *Chelonia*, and the muscular fibres radiate therefrom, ib. *f, f*. It communicates by a wide aperture with the œsophagus, and by a very narrow one with the pyloric portion, ib. *g*, which is a small sub-spherical pouch with a still smaller oblique aperture into the intestine, ib. *k*. The analogy to the gizzard of the bird is further shown by the frequent occurrence of stones in the stomach of the Crocodile.<sup>3</sup> In all carnivorous Reptiles the prey is swallowed whole, and its entry into the stomach is easy: but nothing is permitted to pass out into the intestine except the chyme and other fluids.

In herbivorous Reptiles the pylorus gives passage to vegetable matters whose digestion is completed in the colon.

In the disposition and attachment of the intestinal canal, the

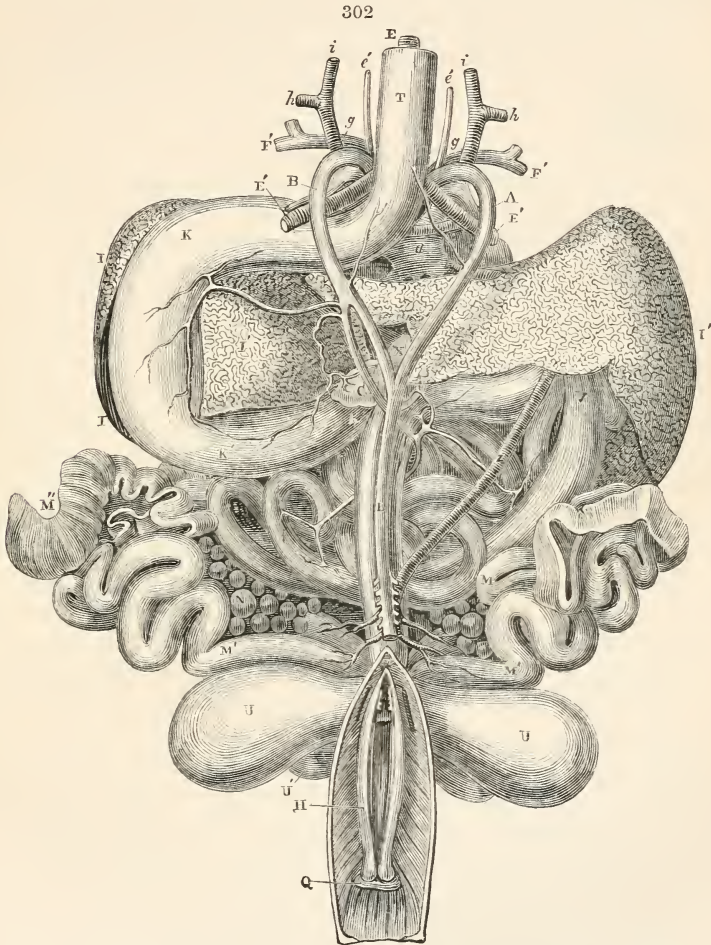
<sup>1</sup> CCXXXVI. vol. ii. p. 357.

<sup>2</sup> xx. tom. i. p. 146, preps. nos. 514-516.

<sup>3</sup> xx. vol. i. p. 146, prep. no. 518 A. In the stomach of a *Crocodylus acutus*, from Jamaica, Hunter 'found the whole of the feathers of a bird, with a few of the bones, which had lost all their earth, exactly similar to a bone which has been steeped in an acid....There were stones in the stomach of considerable size, larger, e. g. than the end of a man's thumb.' CCXXXVI. vol. ii. p. 337. Dr. Jones (CCXLV. p. 94) found in the stomach of an Alligator 'the bones, teeth, hoofs, and hair of a pig; the flesh had been entirely digested.'



*Crocodylia* again offer the chief exception to Reptiles in general; in these the mesogaster, fig. 301, *h*, is directly and broadly continued into the mesentery, as this is into a mesocolon; they are nominal distinctions of the same simple duplicature of the peritoneal membrane. In the Crocodile the intestine, after



Viscera of the Female Tortoise (*Emys europæa*) seen from behind; the lungs have been removed.  
XXXVIII.

forming the duodenal loops, passes back to cross the spine to the left, in close connection thereto: and, descending, again becomes loose, and defines a 'root' or beginning of a distinct 'mesentery'; in no Reptile is there a separate mesocolon. Thus, it is only in *Crocodylia* that a 'duodenal' portion of the intestine can be



distinctly defined; in other Reptiles it is indicated by its relation to the pancreas and to the ducts of this gland and the liver, as at *e, f*, fig. 301 (*Lacerta*), fig. 306, *c, d* (*Rana*), and fig. 305 (*Chelone*). The large intestine is definitely marked off in all Reptiles, but is short and, in most, simple, straight, and without caecal production at its beginning.

In no Reptile is the intestine so short and straight, or so long and convoluted, as in certain Fishes; as a general rule, it is shorter in proportion to the trunk than in warm-blooded Vertebrates.

In the Siren and Amphiume the intestine makes a few short turns in its longitudinal course, and expands into a straight and wide colon or rectum.<sup>1</sup> In the Menopome<sup>2</sup> the convolutions are more numerous, and the rectum is relatively wider. In *Cacilia* the intestine is continued in a slightly convoluted manner to the short rectum which opens near the hinder extremity of the snake-like body. The Newts and Salamanders have short intestines, with few coils; so likewise have the Toads and Frogs; but, in the larval state of the latter, the intestine is very long, and forms a double series of spiral coils, fig. 42, *i*; and the modification by absorption of this herbivorous type of gut to the carnivorous one is not among the least of the marvellous changes which the anurous Batrachian undergoes in passing to its adult condition. In most Serpents the short intestinal folds are packed closely together in a long mass by connecting cellular tissue. In Sea-snakes (*Hydrophis*) the convolutions are more free. In Lizards the intestinal convolutions are commonly few, fig. 301, *i*, fig. 303, *g*, and free. In the *Chelonia*, figs. 302 and 304, the convolutions of the small gut are larger and more numerous; they are also well marked in the *Crocodylia*.

The muscular tissue of the intestine shows an external layer of longitudinal fibres, and an internal layer of circular ones; the latter is remarkably thick in *Chelone*. In gilled and tailed *Batrachia* the mucous membrane presents fine undulatory longitudinal rugæ, not parallel, but often uniting. In Toads the rugæ are transverse at the jejunum: in Frogs the rugæ are zigzag. The mucous membrane of the intestine presents, in the Python, small, flattened, scale-like processes; in some Serpents they are longitudinally extended, and fringed at the margin; the appearance of circular or 'connivent' valves is due to the close coils of the gut within a common peritoneal sheath. In the Chamæleon the intestinal rugæ are rhomboidal, and their free border is minutely

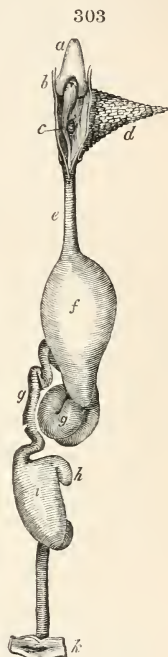
<sup>1</sup> xx. vol. i. p. 122, prep. no. 444.

<sup>2</sup> Ib. p. 203, prep. no. 654.

fimbriate. In a Tortoise (*Testudo indica*) the inner surface of the small intestine is reticulate: in *Testudo tabulata* and in the *Emys europæa* it is disposed in small and numerous longitudinal rugæ: in *Chelone imbricata* and *Chelone Midas* the principal rugæ have a wavy and slightly zigzag disposition. In the Crocodile the lining membrane of the jejunum is finely reticulate: in the ileum it rises into longitudinal folds: in the colon it again becomes minutely reticulate, and is thrown into irregular rugæ.

The intestinal tube usually somewhat diminishes in diameter as it approaches the colon. The *Batrachia* have no cæcum; the small intestine, in the Frog, makes a sudden bend, to terminate obliquely in the short and wide colon.<sup>1</sup> The more oblique entry of the ileum into the colon of the Crocodile gives the appearance of a short pouch on one side: some of the circular fibres of the muscular tunic enter the ileo-colic valve.<sup>2</sup>

In the Python the large intestine begins by a subelongate, pointed cæcum, marked off from the colon by a plaited valvular fold;<sup>3</sup> a succession of such folds occurs in the rest of the large gut. In some land and fresh-water Tortoises (*Testudo tabulata*, *Testudo græca*, *Emys europæa*) the ileum opens obliquely into the side of the beginning of the colon, leaving a short and simple 'caecal' summit of that gut;<sup>4</sup> the margins of the ileo-caecal orifice are puckered into folds, two of which, in *Testudo græca*, are continued into the colon, the intervening groove extending for a short distance along the curve of the colon. The colon is longer and wider in the herbivorous Tortoises, and usually contains grass, leaves, or other vegetable substances, the small intestines being empty. In some species of *Agama* (*Ardiscosoma*), *Galiotes*, *Stellio*, *Monitor*, and in the *Draco volans*, fig. 303, *k*, there is a small cæcum at the beginning of the colon, *ib. i*: and this gut, when distended, seems distinguishable from the narrower rectum. But the most complex large intestine has been met with in the herbivorous Iguanas.<sup>5</sup> The ileum terminates by a slit on a ridge



Alimentary canal,  
*Draco volans*. CCL.

<sup>1</sup> xx. vol. i. p. 204, no. 669.

<sup>2</sup> *Ib.* no. 670.

<sup>3</sup> *Ib.* no. 671 A.

<sup>4</sup> *Ib.* no. 671.

<sup>5</sup> xx. vol. i. p. 206, no. 671 B.

projecting into the cæcum, which is continued beyond, spirally, and contracting to open into the colon by a rounded puckered aperture, at the end of a conical valvular prominence. Valvular folds of the mucous membrane project into the colon from its concave side, decreasing in breadth as they descend. The coats of the intestine make smaller indentations from the convex side, opposite the intervals of the larger folds. Beyond these folds the colon diminishes in diameter, and makes a sudden turn upon itself before becoming the 'rectum.' The cæcum is, here, not a mere 'caput coli,' but a distinct segment of the alimentary canal, having an orifice for ingress, and a second for egress, of contents, analogous to the cardia and pylorus of the stomach, with parietes more muscular than either of the intestines with which it communicates.<sup>1</sup>

It would seem, from petrified contents or excretions of the intestine, that some part, probably the terminal one, of this canal had been provided, in the extinct Ichthyosaur, with a spiral valve, fig. 105 ('coprolite' figured below the pelvis).

The rectum does not open directly upon the exterior of the body in any Reptile, but into a cavity, or 'cloaca,' common to it

<sup>1</sup> The following Table (CCXLV. p. 92) gives the weight of the body, in grains, and the lengths of the alimentary canal, in inches, in various Reptiles.

	Length of body	Weight of the body	Length of the canal
	inches	grains	inches
<i>Menopoma alleghaniensis</i> . . . . .			24
<i>Rana Catesbiana</i> (Bullfrog) . . . . .		9, 800	34
<i>Heterodon niger</i> (Black viper) . . . . .	32	4, 620	26
<i>Psammodon flagelliformis</i> (Coachwhip snake) . . . . .	68	5, 141	42
<i>Coluber guttatus</i> (Corn snake) . . . . .	54	9, 600	54
<i>Coluber constrictor</i> (Black snake) . . . . .	54	5, 100	36
<i>Crotalus adamanteus</i> (Rattlesnake) . . . . .	48	6, 180	42
<i>Alligator mississippiensis</i> (Alligator) . . . . .		211, 940	147
<i>Chelone caretta</i> (Loggerhead turtle) . . . . .		36, 985	102
<i>Chelydra serpentina</i> (Snapping turtle) . . . . .		16, 235	46
<i>Emys reticulata</i> (Chicken terrapin) . . . . .		8, 400	38
<i>Emys serrata</i> (Yellow-bellied terrapin) . . . . .		27, 172	66
<i>Testudo Polyphemus</i> (Gopher) . . . . .		45, 500	78
<i>Trionyx ferox</i> (Soft turtle) . . . . .			48

	Length of the stomach	Length of small intestine	Length of large intestine
	inches	inches	inches
<i>Menopoma alleghaniensis</i> . . . . .	3½	16	6
<i>Rana Catesbiana</i> . . . . .	4	30	
<i>Chelydra serpentina</i> . . . . .	4	32	10
<i>Testudo Polyphemus</i> . . . . .	8	24	46

with the urinary, genital, and allantoic orifices, when the latter bladder persists in any degree.

In the *Batrachia*<sup>1</sup> the allantois opens into the fore part of the cloaca, or, as it seems, into that part of the rectum; behind the rectal outlet are the orifices of the two sperm-ducts or oviducts: behind these are the orifices of the ureters; the genital and urinary outlets are usually prominent. The rectal orifice is less distinct and constricted, and the cloaca seems more a continuation of the gut than in higher Reptiles. In the male Triton the rectum forms a valvular projection into the cloaca, after it has received the orifices of the vasa deferentia.

In true *Ophidia* there is no remnant of allantois opening into the fore part of the rectum or cloaca; in *Anguis* a small bladder remains in that connection,<sup>2</sup> which expands, in limbed Lizards, to larger proportions. In *Coleuber*, as in other Serpents, the terminal orifice of the rectum is well marked; behind it is a semilunar fissure, receiving the outlets of the oviducts, and behind that is the bilobed prominence on which the ureters open.<sup>3</sup> The cloaca in Lizards shows the valvular fold between the intestinal orifice and those of the genital and renal conduits, together with the orifice of the allantois at the fore part of the rectum. In the *Chelonia* the allantois, fig. 302, U', opens into the fore part of the cloaca, below or beyond the rectal orifice: this has a distinct sphincter;<sup>4</sup> the compartment of the cloaca receiving the terminal orifices of the genital and urinary canal, and of the allantois, is also divided by a projecting border, like a distinct orifice, from the outer compartment, in which the clitoris, fig. 302, H, or penis lies: the former is termed the 'urogenital,' the latter the 'vestibular,' part of the cloaca; the urogenital orifice is transverse or semi-lunar. In *Chelydra serpentina* the oviducal orifices are immediately behind the rectal one: the allantoic orifice is in front of it; behind the oviducts are the terminations of the ureters, and behind these, within the vestibule, are the wide orifices of two cloacal sacculi,<sup>5</sup> each of which exceeds the allantois in size. In *Emys europæa*, fig. 302, U, U, they equal the allantoic bladder, U'. The allantois in the *Crocodylia* is reduced to a urinary bladder-like dilatation of the fore part of the cloaca, into which the rectum opens obliquely, and by a valvular protrusion; the genital orifices are behind this,

<sup>1</sup> *Siren*, xx. vol. iv. no. 2695; *Amphiuma*, ib. no. 2397; *Menopoma*, ib. no. 239; *Tortoise*, ib. nos. 2401, 2699; *Salamandra*, ib. no. 2407; *Rana*, ib. nos. 2409, 2702; *Pipa*, ib. no. 2707.

<sup>2</sup> xx. vol. iv. p. 57, no. 2422.

<sup>3</sup> *Ib.* no. 2708.

<sup>4</sup> *Ib.* vol. i. no. 751.

<sup>5</sup> 'Anal sacculi,' xx. vol. iv. (1838) p. 147, no. 2722 B. 'Vessies auxiliares,' CCXLIV. (1839), p. 456. 'Vessies lombaires,' CCXXXIX. tom. vi. p. 363.



and then come those of the ureters.<sup>1</sup> The urogenital compartment opens into the vestibule by a narrow fissure, the lower part of which is continued into the groove of the penis or clitoris lying in the vestibule.

The cloacal outlet, commonly termed the 'anus,' varies in shape in *Reptilia*, but is more constant in position than in *Pisces*; it is never so far forward as in some of that class. In tailed *Batrachia* it is a longitudinal slit in the axis of the trunk; in anourous larvæ it is protected by folds of membrane, which unite to form the lower border of the tail-fin; during the progress of absorption of this natatory organ the anus is somewhat advanced, and assumes a rounded form with a sphincter. In the Sea-snake (*Pelamys*) the anus is longitudinally bilabiate, but the anterior part of the fissure is crossed by a semilunar fold or ridge. In Lizards the corresponding fold, with its scaly covering, is larger, covers more of the orifice, and gives it a transverse semilunar shape. It has a similar form in the Turtle. In *Emys* it is a puckered aperture, with a tunical border beneath the base of the tail; in *Trionyx* it is a longitudinal orifice, and nearer the end of the short tail. In the Iguana the posterior valve of the cloacal opening is approximated, and applied to the anterior one by a muscle which arises from each angle of the fissure or fold between the tail and the thighs. The dilatation of the orifice is produced by two pairs of muscles, attached, the one to the femoro-caudal fold, the other to the lower surface of the tail.

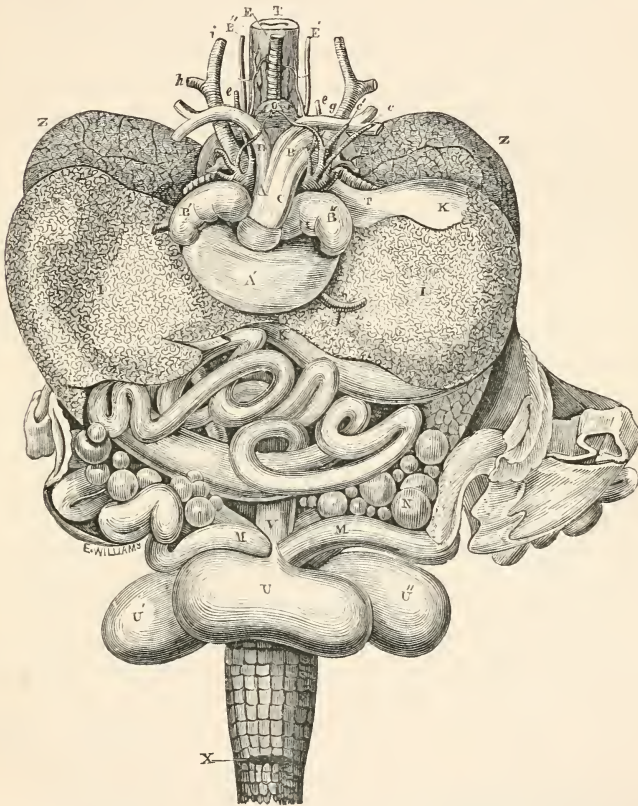
§ 76. *The Liver of Reptiles.*— This organ is proportionally large in all Reptiles: its form is mainly governed by that of the body. In Serpents, fig. 300, *o*, it is unilobate, long, and slender; in Tortoises, fig. 302, *i*, it is short and broad, chiefly composed of two subequal lobes; in Lizards, fig. 292, *k*, it offers an intermediate form.

In the *Lepidosiren* the liver consists of one long lobe, with a transverse notch on the left side, lodging the gall-bladder. In the *Siren* the liver presents a similar form, with the addition of a small left lobe at the anterior end. In the Amphiume the long and slender subtrihedral liver extends through nearly two thirds of the abdominal cavity, and the gall-bladder is an inch distant from the lower end. In the Menopome the liver is shorter and broader, with the gall-bladder lodged in a fissure which makes the posterior end bifurcate. In the Newt the liver has a similar terminal notch into which a peritoneal fold enters. In the Frog

<sup>1</sup> xx. vol. i. no. 747, vol. iv. no. 2438.

the liver is divided into a right and left lobe, with subdivisions of the latter. In the *Pipa* the right and left divisions are quite distinct, and each is subdivided. In *Cæcilia* the elongated liver is divided into several small flattened lobes. The liver, in the Chameleon, consists of one lobe; in the Gecko (*Platydictylus guttatus*) and the *Draco volans*, fig. 292, *h*, it is triangular: the

304

Viscera of the Female Tortoise (*Emys europæa*). XXXVIII.

anterior angle accompanies the vena cava towards the heart: a second angle, *m, m*, enters the curve of the stomach: the third is directed backward, along the right side: the gall-bladder lies in a notch between the last two angles. In some other Lizards this notch is deeper, and the increased size of the left process gives the liver a bilobed character; the vena portæ enters the fissure, the vena cava enters the longer right lobe. In the Iguana the liver extends from right to left, with a convexity forward, and with a

slender prolongation along the right side, into the apex of which the postcaval vein enters. It has a narrow 'falciform' ligament.

In the Crocodile the liver is divided into a right and left lobe, anteriorly, by the heart, which almost wholly enters the fissure. The right lobe is the largest, with the gall-bladder on its concave side. The liver is more equally divided in *Chelonia*, fig. 304, I, I, and chiefly also by the heart, ib. A', B'. The stomach, ib. κ, deeply impresses the left lobe, and is buried in it in some species (*Emys serrata*). In many there is a process, like the 'lobulus Spigelii,' entering the curve of the stomach. In the higher Reptiles the liver is contained in a peritoneal pouch; in *Chelonia* and *Crocodylia* each lobe has its pouch more or less distinct. In the Crocodile the capsule becomes aponeurotic, whence it is continued from the sterno-sacral border of the gland to the abdominal parietes, to be connected, like a diaphragm, with the transversus abdominis muscle.<sup>1</sup>

The lobes of the liver are subdivided into numerous and minute lobules, compactly united by interlobular cellular tissue. The lobules themselves are composed of corpuseles, or 'acini,' occupying the meshes of the vascular network pervading the lobule; these 'acini' are larger in Reptiles than in Fishes. Their secretion finds its way into biliary canals, distinguishable as such, with proper walls, on the exterior of the lobule; these ducts anastomose in the interlobular spaces, and form larger canals, accompanying the hepatic vessels, and, after repeated unions, issuing, as the 'hepatic ducts,' from the portal fissure. The walls of the ducts have no follicular glandules. The hepatic tissue in Reptiles is usually softer than in warm-blooded Verte-

<sup>1</sup> Dr. Jones, CCXLV. p. 113, ascertained the weight of the body and of the liver in the following *Reptilia*, and gives the relative weight of the latter in the subjoined form.

	Weight of the body	Number of times the weight of its liver
	in grains.	
<i>Rana Catesbiana</i> (Bullfrog) . . . . .	9, 800	55
<i>Heterodon niger</i> (Black viper) . . . . .	4, 620	26
<i>Psammophis flagelliformis</i> (Coachwhip snake) . . . . .	5, 141	71
<i>Coluber guttatus</i> (Corn-snake) . . . . .	9, 600	64
<i>Coluber constrictor</i> (Black snake) . . . . .	5, 100	57
<i>Crotalus adamanteus</i> (Rattlesnake) . . . . .	6, 180	55
<i>Alligator mississippiensis</i> (Alligator) . . . . .	76, 507	73
<i>Chelone caretta</i> (Loggerhead Turtle) . . . . .	36, 985	47
<i>Chelydra serpentina</i> (Snapping turtle) . . . . .	16, 985	42
<i>Emys terrapin</i> (Salt-water terrapin) . . . . .	11, 937	53
<i>Emys reticulata</i> (Chicken terrapin) . . . . .	8, 400	18
<i>Emys serrata</i> (Yellow-bellied terrapin) . . . . .	23, 100	48
<i>Testudo Polyphemus</i> (Gopher) . . . . .	45, 500	50

brates, and firmer than in Fishes. It never contains so large a proportion of oil as in plagiostomous and some other Fishes.

A gall-bladder exists in all Reptiles. It lies in a notch on the left side of the elongated liver in the *Lepidosiren*, *Siren*, *Proteus*, and *Amphiuma*, and in a notch at the hind end of the liver in *Menopoma*, *Triton*, and *Salamandra*. In Anurous Batrachia the gall-bladder is imbedded in the right lobe. In the Chameleon the gall-bladder is at the hind border of the liver; in *Draco volans*, fig. 292, *m*, it lies in the notch between the left and hinder angle; in the *Cyclodus* and *Iguana* in the notch between the two hinder divisions of the liver. The gall-bladder is deeply imbedded in the substance of the right lobe of the liver in *Testudo*: it adheres by about one third of its length to the right lobe in *Chelone*: it has a similar attachment in *Crocodylus*, but is less closely connected, and sometimes quite detached, in *Alligator* and *Gavialis*. In true *Ophidia* the gall-bladder, fig. 300, *p*, is removed beyond the liver to the side of the narrow canal connecting the stomach with the intestine. In the snake-like Lizards (*Anguis*, *Amphisbæna*) the gall-bladder is in contact with the liver.

In *Lepidosiren*, *Siren*, and *Amphiuma*, the hepatic ducts communicate with the cystic, or with the gall-bladder (*Siren*), and the bile is conveyed directly by the cystic duct to the beginning of the intestine. In the *Iguana* there is a distinct hepatic duct which enters the duodenum about an inch from the pylorus, a cyst-hepatic duct which enters the side of the gall-bladder, and cystic ducts which leave the globose bladder abruptly. In *Chelonia* the hepatic ducts unite with the cystic: but sometimes one is continued directly to the intestine (*Testudo græca*). In *Chelone Midas* a long hepatic duct from the left lobe unites with a shorter one from the right lobe, and the trunk joins the cystic near its entrance into the duodenum. The cystic is very short and wide, and runs obliquely through the thick walls of the duodenum. In the *Crocodile* the hepatic duct sends a branch to the gall-bladder, and goes to terminate in the duodenum, distinct from the cystic. This arises from the apex of the bladder, and is long and straight. In *Ophidia* the hepatic duct is of great length, and unites with the cystic in the substance of the pancreas, near the termination of the common duct. In some species (*Dispholidus*) it previously sends a branch directly to the gall-bladder. The cystic duct in *Python*, single at its commencement, divides into numerous branches, which penetrate the pancreas, and reunite with each other and the hepatic before terminating in the duodenum. The advantage of this modification of the biliary



receptacle and ducts is obvious. Had the gall-bladder been attached to the liver, as in insectivorous *Anguidæ* and *Lizards*, it would have been compressed by the prey, which in true Serpents is usually of large bulk when introduced into the stomach. The stimulus of such pressure would have led to the expulsion of the contents of the gall-bladder into the intestine before the chyme had been prepared, and passed on into the gut: the relative position of the liver to the stomach subjects the gland to such stimulus to secrete whilst the contents of the distended stomach are undergoing digestion. The bile is conveyed away by the long hepatic duct, but is reflected along the branching cystic ducts to the gall-bladder, which has been transferred to a position beyond the pressure of the stomach. It is so placed, however, as to be affected by the distension of the narrow canal which conveys the chyme to the duodenum, and is thus stimulated to render up the bile to the gut, just at the time when it is wanted for the separation of the chyle from the chyme. This fact in comparative anatomy is significant of the share taken by the biliary secretion in the act of chylification.

The gall-bladder is not, however, a simple reservoir; its vascular and secreting inner surface can operate upon the bile by both subtraction and addition: the more watery part may be diminished by absorption: the cylindrical epithelial cells which form the innermost layer of the mucous membrane may be shed into the liquid, with the contents of mucous follicles which are more or less developed in that membrane. The mucous surface is augmented by minute furrows in the Crocodile: in the *Testudo elephantopus* it is nearly smooth.

The bile in *Chelonia* and most Reptiles is green: Hunter notices its pale yellow colour in the 'Water-snake,' and its want of bitter taste in the Chameleon.<sup>1</sup> Chemical researches on the nature of bile have been almost exclusively confined to that of Mammals, in connection with which class the chief results will be noted. The glycocholic acid is wanting in the bile of the Boa, as in that of the Dog. As might be supposed, from the prevalent colour of the bile in Reptiles, the 'biliverdine' primarily exists in it, not as a transformation of 'cholepyrrhine,' which is the primary colouring principle in most Mammals. The proportion of taurocholate of soda in the bile of a Python is estimated at 8.46 in 100, and in that of a Boa to 6.2 in 100; a trace of the same principle has been detected in the bile of a Tortoise. In

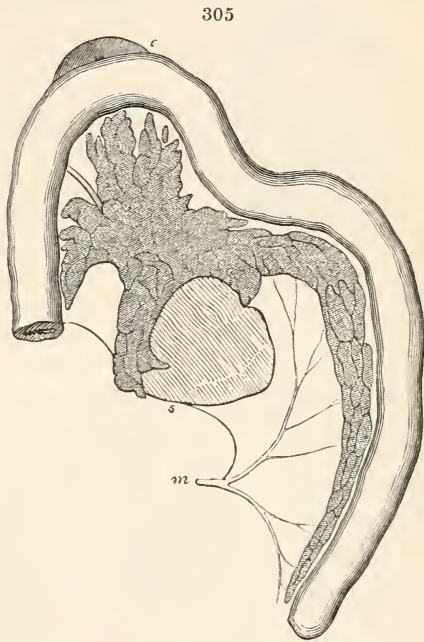
<sup>1</sup> CCXXXVI. vol. ii. pp. 373, 378.

all Reptiles the bile is poured into the gut near to, sometimes close to, the pylorus.<sup>1</sup>

§ 77. *Pancreas of Reptiles.*—The pancreas in Reptiles is a light grey or yellowish, sometimes pinkish, coloured gland, consisting of numerous ‘acini,’ giving origin each to a duct, the acini being united by them, like the short stalks of grapes, in bunches, about a larger duct; such aggregates or ‘lobules,’ further uniting into ‘lobes,’ and their ducts into a common canal, which terminates either with, or close to, the biliary duct in the intestine. The lobes are separate in *Python*, of a subcircular flattened form, suspended cluster-wise by ducts of from six to twelve lines in length, before uniting into the common canal.

The pancreas has a close texture in herbivorous *Chelonia*, forming a thin layer, spread out in the duodenal mesentery, fig. 305, where it branches into numerous lobes. In most Ophidians and in many Lizards it presents a more compact form, fig. 301, *f*.

There are intermediate conditions of structure in the present class. The pancreas is ramified in *Menobranthus*: it is more circumscribed in *Menopoma*, where it forms a long, slender, yellow gland. It is rather broader in *Amphiuma* and *Triton*. In the Frog, fig. 306, *p*, it is flattened, elongate, narrowest at the emergence of the duct (opposite *c*), and sending a process, which surrounds the gall-duct, as far as the gall-bladder. In the Salamander it is long and narrow. It is thick and pyramidal in *Cæcilia albiventer*; straight, elongate, and slightly forked in *Cæcilia interrupta*: it is ovoid in most *Colubridæ*; of a



Pancreas and spleen of the Turtle (*Chelone Midas*). CCXXXI

<sup>1</sup> The relative size of the liver in *Reptilia* does not relate to, or throw light on, its probable accessory function as an elaborator of the albumen and disc-cells of the blood, or as helping to maintain animal temperature by the formation of grape-sugar out of the nitrogenized elements. Dr. Jones, however, detected the presence of grape-sugar in the liver of cold-blooded Animals at all periods of starvation.

compact triangular form in the Rattlesnake,<sup>1</sup> where it is closely attached to the commencement of the intestine, and is perforated by the biliary ducts. The pancreas is small and flattened in Lizards, usually dividing as it recedes from the attachment by the duct to

306



Liver, pancreas, and spleen of the Frog (*Rana*). CCXXXI.

the duodenum into a portion accompanying the biliary duct, and another extending to or towards the spleen. It is very small in the Iguana. In the Crocodile the pancreas is divided into two elongated lobes, and sometimes sends its secretion into the duodenum by two ducts. In *Chelydra serpentina* the pancreas extends from the pylorus some inches along the duodenum, dividing and again uniting, forming a loop, and giving off a process which extends to the spleen. In the Turtle (*Chelone Midas*) the pancreatic duct terminates on a papilla, which projects into the terminal expansion, or 'ampulla,' of the bile-duct.

The pancreas in carnivorous Terrapins (*Emys*) is more bulky and compact in form than in the fucivorous Turtles (*Chelone*).

Thus in the vegetable-feeding Gopher the pancreas is  $\frac{1}{3500}$  of the total weight of the animal: whilst in the carnivorous Snapper it is  $\frac{1}{630}$  of the total weight of the animal. As the proportion of fat consumed by Carnivora must be greater than that by Herbivora, the results of the above comparative observations accord with the view of the use of the pancreas in preparing fatty matters for absorption.<sup>2</sup>

<sup>1</sup> xx. vol. i. p. 235, no. 778.

<sup>2</sup> Dr. Jones, CCXLV. p. 107, ascertained the weight of the body and of the pancreas in several American *Reptilia*, and gives the relative weight of the latter in the sub-joined form.

	Number of times the weight of its pancreas.
<i>Rana Catesbiana</i> (Bull-frog) . . . . .	1088
<i>Heterodon niger</i> (Black viper) . . . . .	537
<i>Psammophis flagelliformis</i> (Coachwhip snake) . . . . .	1353
<i>Coluber guttatus</i> (Corn snake) . . . . .	1371
<i>Coluber constrictor</i> (Black snake) . . . . .	472
<i>Crotalus durissus</i> (Banded rattlesnake) . . . . .	965
<i>Chelone caretta</i> (Loggerhead turtle) . . . . .	518
<i>Chelydra serpentina</i> (Snapping turtle) . . . . .	630
<i>Emys terrapin</i> (Salt-water terrapin) . . . . .	994
<i>Emys reticulata</i> (Chicken terrapin) . . . . .	763
<i>Emys serrata</i> (Yellow-bellied terrapin) . . . . .	1067
<i>Testudo Polyphemus</i> (male Gopher) . . . . .	3500

## CHAPTER VI.

## ABSORBENT SYSTEM OF HÆMATOCRYA.

§ 78. ALL the definite structures of soft parts—acini and simpler gland-follicles, their prolonged outlets or ‘ducts,’—compacted sheets or strata called ‘skin’ and ‘membranes,’ mucous or serous,—bladders, sinuses, and tubes, arterial or venous,—threads or fibres, muscular, ligamentous, or nervous—are covered, coated, or lined, by a loose or soft elastic substance, which, as it connects the better-defined structures together, and fills up their interspaces, is termed ‘connective tissue’ (*tela conjunctiva, tela cellulosa*). It is dispersed in irregular plates, with intervals, cells, or ‘lacunæ,’ and the plates consist of delicate and extremely minute fibrils. The intervals contain a fluid called ‘serous,’ varying in quantity, and also in quality, according to circumstances: and they intercommunicate freely. These cavities are the seat of a transudation from ‘vessels’ and other more definite fluid-holding structures during life: and reciprocally the ‘serosity’ is resumed by the beginnings or pores of sinuses and canals.

The serosity of the cavities of the connective tissue usually consists of—

Water . . . . .	975.20
Albumen . . . . .	5.42
Extractive matters and fat . . . . .	0.76
Mixed salts . . . . .	15.62 <sup>1</sup>

But it is subject to varieties from many causes, mechanical and chemical, operating both within and out of the body.

The vessels or canals which seem to be most closely connected with, or to be most directly traceable from, the connective tissue and its lacunæ are those called lymphatics, lacteals, and absorbent vessels. This system exists as a separate organic vascular apparatus only in the Vertebrate subkingdom: it was first observed in Mammalia,<sup>2</sup> was discovered by John Hunter in

<sup>1</sup> CCLII.

<sup>2</sup> In the dog, by Aselli, in 1622: at least the part of the absorbent system called ‘lacteals,’ in the mesentery of the animal. CCLIII.



Birds<sup>1</sup> and Reptiles,<sup>2</sup> and afterwards described by Mr. Hewson and Dr. Monro in Fishes. The most systematic and detailed descriptions of the absorbent system of the Oviparous Animals, published in the last century, are those of Hewson.<sup>3</sup>

§ 79. *Absorbents of Fishes.*—The lacteal system in Fishes commences by a reticulate or plexiform layer of vessels attached to the connective tissue on the outer or cellular side of the mucous coat of the stomach and intestines: in the Skate<sup>4</sup> the network is so coarse that, when inflated, dried, and cut open, it appears like a subdivided cellular or areolar receptacle. The chyle is conveyed thence in all Fishes by more vasiform lacteals, situated immediately beneath the serous covering of the intestines, to large reticulate receptacles, one in the mesenteric angle along the junction of the small and large intestines, the other extending along the duodenum, its pancreatic appendages, and the pyloric part of the stomach, and often also surrounding the spleen. The presence of the mesentery in the Myxinoids, and its absence in the Lampreys, involve corresponding differences in their lacteal systems: in the Myxinoids the lacteals are supported and conveyed by the mesentery to the dorsal region of the abdomen, and empty themselves into a receptacle above the aorta and the cardinal veins, between these and the vertebral chord: in the Lamprey the lacteals pass forward, and enter the abdominal cavernous sinus beneath the aorta.

The lymphatic system is best demonstrated by injecting the large absorbent trunk which runs upon the inner surface of the

<sup>1</sup> 'It is but doing justice to the ingenious Mr. John Hunter to mention here, that these lymphatics in the necks of fowls were first discovered by him many years ago.' (Hewson, *civ.* 1768, p. 220.)

<sup>2</sup> Hunter's account of this discovery is as follows:—'In the beginning of the winter 1764-5, I got a crocodile, which had been in a show for several years in London before it died. It was, at the time of its death, perhaps the largest ever seen in this country, having grown, to my knowledge, above three feet in length, and was above five feet long when it died. I sent to Mr. Hewson, and, before I opened it, I read over to him my former descriptions of the dissections of this animal relative to the 'absorbing system,' both of some of the larger lymphatics and of the lacteals, with a view to see how far these descriptions would agree with the appearances in the animal now before us; and, on comparing them, they exactly corresponded. This was the crocodile from which Mr. Hewson took his observations of the colour of the chyle.' Hunter here alludes to the note appended to Mr. Hewson's paper on the 'Lymphatic System in Amphibious Animals,' *Philosophical Transactions*, vol. lix. 1769, p. 199 *a*: 'In a crocodile which I lately saw by favour of Mr. John Hunter, the chyle was white.'

<sup>3</sup> *CIV.* 1768, 1769.

<sup>4</sup> In this and other Plagiostomes the gastric lacteals are confined chiefly to the contracted pyloric canal.

ventral parietes of the abdomen, along the median line from the vent forward to the interspace of the pectoral fins, where the size of the vessel best favours the insertion of the injecting-pipe. It receives the lymphatics of the pectorals, and (in thoracic and jugular Fishes) of the ventral fins: then, advancing forward through the coracoid arch, it spreads out into a rich network, which almost surrounds the pericardium. The lymphatic plexus which covers the heart of the Sturgeon and Paddle-fish presents a spongy and almost glandular appearance when uninjected: the tissue between the muscular and mucous coats of the gullet in the Rays,<sup>1</sup> the gland-like mass in the orbit and palate of the Chimæra, and that lodged in a peritoneal fold of certain Sharks, may likewise be appendages to the lymphatic system.<sup>2</sup> Large lymphatic trunks from the upper (dorsal) part of the circumcardial plexus receive the lymphatics of the myocommata by a deep-seated trunk which runs along the ribs, and the lymphatics of the mucous ducts and integuments by a superficial trunk which extends along the lateral line, and gets a penniform character by the regular mode in which its tributary lymphatics join it.

In the Wolf-fish (*Anarrhichas*) the lacteals commence in processes of the edges of the mucous folds by cells or blind ends, from which the vessels proceed to form a close plexus on the outer surface of the intestine, and accompany in a plexiform manner the bloodvessels. In the Turbot there are similar plexiform surroundings of the bloodvessels of the stomach: and in *Silurus glanis* the lacteal network covers all the stomach.<sup>3</sup>

In the Eel the gastro-enteric absorbent plexus communicates with a cavernous sinus upon the lower surface of the stomach, and with a larger one which accompanies the intestinal canal, whence other plexuses pass to the great subvertebral lymphatic trunks. Along the free border of the intestinal spiral valve, in Plagiostomes, there is a varicose lacteal reservoir, from which proceed the vessels forming the reticulate layer beneath the mucous membrane. The lymphatics of the head form minor plexuses at the bases of the orbits, and in the Carp they extend into the basi-cranial canal; those from the cellular arachnoid pass through the occipital foramen to join the lymphatics of the spinal canal, and terminate in the cervical and sub-occipital trunks, which receive the lymphatics from the upper extremities of the gills: these, with the deep-seated lymphatics from the kidneys, join the single or double trunks at the under part of the vertebral

<sup>1</sup> xx. vol. i. p. 126, no. 462.

<sup>2</sup> CCLXI. p. 269.

<sup>3</sup> cv. pp. 27, 30, pl. 6, figs. 1 and 2; pl. 7, figs. 3 and 4.

column, which combine with the lacteal plexiform trunks continued forward along each side of the stomach and œsophagus, to form a large, short, common lacteo-lymphatic trunk on each side, which terminates in the jugular vein near its junction with the short precaval vein. Fohman<sup>1</sup> describes other and minor communications between the absorbent and venous systems of Fishes, as, e. g., in the gastric and intestinal plexuses in the Sheat-fish and Turbot. The lymphatic system of the caudal portion of the body is chiefly received by two caudal sinuses, intercommunicating by a transverse canal, which sometimes perforates the base of the anchylosed compressed terminal tail-vertebra.

The lymphatics of Fishes consist generally of a single tunic: a most delicate epithelial lining may be distinguished in the larger trunks. The only situations where valves have been seen in these vessels are at the terminations of the trunks in the caudal and the jugular veins. There are no lymphatic glands: these are represented by the large and numerous plexuses, and possibly by the gland-like layers or substances above-mentioned. The chyle as well as the lymph of Fishes is colourless and transparent: the plasmic corpuscles or lymph-cells are few in number.<sup>2</sup> The analysis of the lymph in Fishes is still a desideratum.

§ 80. *Absorbents of Reptiles.*—In the intestines of the Frog and Salamander the lacteals form a network of large canals, with minute or close meshes coextensive with the mucous membrane; the vessels continued therefrom accompany the mesenteric arteries, sometimes forming a pair, running along opposite sides, with occasional connecting cross-branches; more commonly having these so numerous as to constitute a continuous reticulate sheath about the artery, the cavity of which sheath seems, in some parts, to be only partially divided by cross threads.<sup>3</sup> These lacteals, or intestinal lymphatics, open into a receptacle at the dorsal line of reflection of the mesentery, of large size in the Frog, but contracted and assuming rather the

<sup>1</sup> cv.

<sup>2</sup> In CXLV. these lymph-corpuscles are described as 'centres of assimilative force, manifesting inherent power of development and change, some being granular, others with a capsule and in the condition of nucleated cells,' p. 249 (1846). Prof. Kölliker testifies to the fissiparous multiplication of the lymph-corpuscles in the lacteals of the dog, cat, and rabbit. The corpuscle, in the condition of the nucleated cell, elongates, the nucleus divides into two; between which the cell contracts and finally divides (CCLXII. p. 639). In Fishes the nucleus undergoes further subdivision before the fission of the cells takes place.

<sup>3</sup> CCLVI. p. 249.

form of a 'thoracic duct' in the Newt; it proceeds along the aorta in both, communicating with lymphatic canals near the liver, and dividing anteriorly, to accompany the right and left aortic arches, and to receive the lymphatic conduits from the head and fore-limbs, before terminating in the subclavian veins. Some of the vessels, both arteries and veins, of the trunk have a similar lymphatic sheath, but the principal conduits of the lymph, in the *Batrachia*, have the form of irregular sinuses or lacunæ, of great capacity between the skin and flesh, and of smaller size in the inter-muscular spaces of the limbs.<sup>1</sup> Air or liquid introduced into these lymph-receptacles finds its way into the veins by the above, and perhaps other, communications. The lymphatics of the hind-part of the body and limbs communicate with a pair of subcutaneous receptacles, with contractile walls, behind each femoral joint; there is a similar pair in front of the scapulæ.<sup>2</sup> These receptacles have a subrhythmical action, not synchronous with one another, or with the pulsations of the heart, or with any of the movements of respiration, which in *Batrachia* are deglutitional chiefly. The muscular fibres of these 'lymph-hearts' are of the striped kind.<sup>3</sup> The cervical pair transmit their lymph into the jugular veins, and distend them at each systole. The pelvic lymph-hearts have been seen to pulsate sixty times in the minute in a frog.<sup>4</sup> In the large *Ceratophrys cornuta* two pairs of ischiadic lymph-hearts have been found.<sup>5</sup>

In the Tortoise the pelvic lymph-hearts are two, of a more circumscribed rounded form, situated on each side of the bodies of the vertebræ, between the femoral joints and the hind-border of the carapace; the valves at the inlets and outlets of the lymph conduits, impressing the course of motion of the fluid, are here readily seen.<sup>6</sup> In Lizards and Crocodiles the pelvic lymph-hearts are situated near or upon the diapophyses of the first caudal vertebra. In *Pseudopus Pallasii* they lie between the muscles upon the sacral diapophyses, receiving the lymph each by a single conduit from the great abdominal sinus, and transmitting it to the umbilical veins; they pulsate about fifty times in the minute.<sup>7</sup> In true Serpents (*Python*, e. g.) the lymph-hearts are elongate, and situated behind the last pair of ribs and upon the rib-like diapophyses of the anterior caudal vertebræ; they receive the lymph by three orifices at one end, and transmit it by two opposite orifices, to conduits com-

<sup>1</sup> CCLVII. p. 28.<sup>2</sup> CCLV. p. 89.<sup>3</sup> CCLVIII. p. 58.<sup>4</sup> LXXIV.<sup>5</sup> *Ib.*<sup>6</sup> CCLV. pl. 1.<sup>7</sup> CCLIX. p. 25, pl. 3.



municating with the caudal vein. The three tunics of these hearts, of which the middle one is muscular, with the inferent and afferent valvular structures, are well displayed in the Python.<sup>1</sup>

The intestinal lymphatics, in Serpents, open into a large receptacle, extending along the root of the mesentery, beginning near the vent where it is narrow, receiving the lymphatics of the tail, and extending forward, greatly expanded, as far as the stomach, where it forms a cul-de-sac. This receptacle is reflected about the aorta, which seems included in it, and receives the lymphatics of the genital organs, kidneys, and intestines. Before reaching the stomach, it sends off a plexiform conduit, which receives the lymphatics of the pancreas, spleen, stomach, and liver, the latter gland being more or less completely sheathed by the lymphatic receptacle; this then contracts into an irregular canal as it approaches the pericardium, where it terminates in a cul-de-sac, but transmits the lymph by several lateral vessels to a large plexus near the great vessels of the heart. The above continuation of the abdominal receptacle has been called the 'right' or 'inferior' thoracic duct. The 'left' or 'superior' or 'dorsal' thoracic duct leaves the great receptacle nearer its anterior extremity, by three or four conduits, and advances along the œsophagus to the pericardium, anastomosing with the right duct, by transverse channels. On reaching the pericardium, the left duct divides into two channels, which reunite in front of the pericardium, and join the lymphatic plexus about the great vessels, from which the lymph is conducted by two or three terminal trunks to the two great precaval veins.<sup>2</sup>

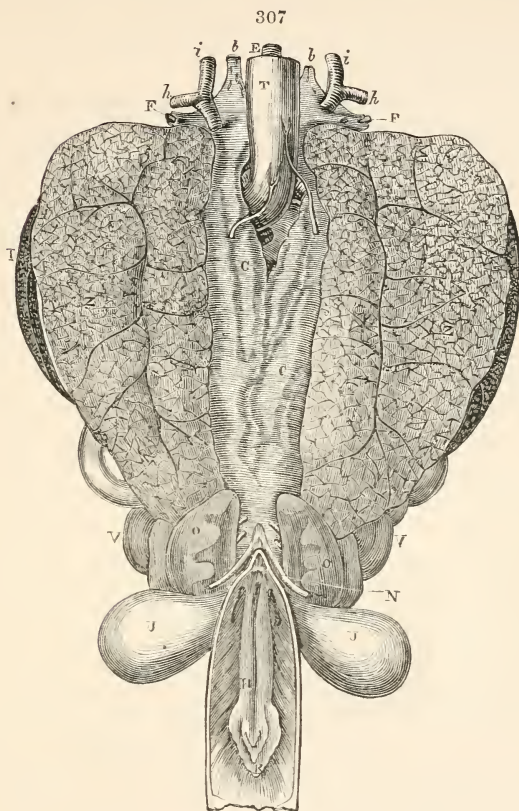
In *Chelonia* the chyle is absorbed into a stratum of intestinal lymphatics, which, in the form of a close network, lies between the muscular and mucous coats;<sup>3</sup> from this the conduits pierce the muscular tunic, and affect a longitudinal course on the exterior of the gut until they quit it, accompanying the mesenteric bloodvessels to the great chyle- and lymph-receptacle, fig. 307, c, c, which extends from the middle of the dorsal part of the abdomen backward to between the vertebræ and rectum. Here it receives the lymphatics of the hinder limbs and tail, and, in succession forwards, those of the cloaca and its appendages, ib. U, U, of the kidneys, ib. O, of the genital organs, ib. H, and intestines, ib. V; it presents the same quasi-capsular relation to the

<sup>1</sup> CCLX. p. 538, pl. 13, figs. 7, 8, 9.

<sup>3</sup> XX. vol. ii. p. 17, nos. 850-858.

<sup>2</sup> CCLVII. p. 15.

aorta as in *Batrachia*, and bifurcates anteriorly, the divisions inclosing the right and left pulmonary arteries and aortæ, and



Viscera in situ, seen from behind, with the lymph-receptacle (*Emys europæa*). XXXVIII.

terminating at the beginning of the two precaval veins, by elliptical orifices guarded by valves. The lymphatic system of the trunk and limbs affects the form of irregular plexuses and dilatations.

The lymphatic system in *Lacertilia* resembles in the main that of *Ophidia* and *Chelonia*. In *Crocodylia* there are several signs of advance. Hunter<sup>1</sup> noted the white colour of the chyle: the 'receptaculum' is more circumscribed; its anterior divisions are more vasiform, more like 'thoracic ducts;' there is a compact gland-like plexus of lacteals at the root of the mesentery. At the base of the tail the lymphatics surround the artery and vein

<sup>1</sup> ccxxvi. vol. ii. p. 335.

by a large plexus, filling up the hæmal canal; they present also a plexiform character at the axillæ and base of the neck, about the jugular veins; but the vasiform character is generally better marked in the lymphatics of the Crocodile than in lower Reptiles, and the valves occur more frequently.

The lymph-corpuses are very few, and rarely visible in the lymphatics of the tail of the Tadpole, but were numerous in the lymphatic canals near the liver in *Salamandra*. By carefully puncturing the large subcutaneous lymph-reservoirs of the Frog, at the upper part of the thigh, the pure fluid may be obtained from the living animal: but analysis of lymph has chiefly been performed on the larger quantities discharged from artificial fistulæ of the thoracic duct in the Horse and Cow, and its results will be given in connection with the Mammalian class.

## CHAPTER VII.

## CIRCULATING AND RESPIRATORY SYSTEMS OF HÆMATOCRYA.

§ 81. *Blood of Fishes.*—The red blood of Vertebrates owes its colour to the albuminoid substance called ‘hæmatosine, existing in the discoid corpuscles called ‘blood-globules,’ ‘blood-cells,’ or ‘blood-discs.’ These float in the light straw-coloured fluid called ‘plasma,’ which consists of water holding in solution proteine principles, hydrocarbonates of the fatty nature, saccharine, and saline matters. The watery solvent predominates in the blood of Fishes and Batrachians. The ‘proteine’ basis exists under the combinations termed ‘albumen’ and ‘fibrin.’

The blood-discs in Fishes are commonly of a full elliptic shape, as in the Cod, fig. 8, *g*, and Skate, fig. 8, *h*, p. 4: but in the Lamprey and Ammocete they are nearly circular. In the Myxine, however, they are elliptic, and some are fusiform. They present the largest size in the Sharks, but are smaller in them in proportion to the body, or mass of blood, than in Batrachia.<sup>1</sup> Besides the red discs there are the larger white corpuscles in the blood of Fishes as in that of higher Vertebrates, but in less proportion than in Saurians, Birds, or Mammals.

The comparison of main physiological importance between the blood in different groups of Vertebrates, is that which relates to the proportion of the organic matters contained in the water.

Prevost and Dumas expressed the general results of this comparison of the blood of the cold-blooded classes in the following

TABLE OF THE PROPORTION OF WATER, CLOT (BLOOD-DISCS AND FIBRIN), ALBUMEN, AND SALTS.

HÆMATOCRYA	Water	Clot	Albumen and Salts
<i>Rana esculenta</i> (Frog) . . . . .	884	69	46
<i>Salmo fario</i> (Trout) . . . . .	864	64	72
<i>Lota lota</i> (Burbot) . . . . .	886	48	66
<i>Anguilla latirostris</i> (Eel) . . . . .	846	94	60 <sup>2</sup>

<sup>1</sup> See CCXXXIX. tom. i. p. 89, for the dimensions, in fractions of a millimeter, of the blood-discs of Fishes.

<sup>2</sup> CCLXV. p. 64.



Dr. Joseph Jones<sup>1</sup> has pushed this kind of analysis further, as shown by the subjoined table.

	MOIST BLOOD-DISCS			PLASMA		
	Total Weight	Water	Solid Matters	Total Weight	Water	Solid Matters
<i>Zygaena malleus</i> (Hammer-shark)	293·44	220·08	73·36	706·56	641·06	65·50
<i>Lepidosteus osseus</i> (Gar-fish)	229·00	171·75	57·25	771·00	714·95	56·05
<i>Salmo fario</i> (Trout)	275·20	206·40	68·80			
<i>Lota lota</i> (Burbot)	192·40	144·30	48·10			
<i>Anguilla latirostris</i> (Eel)	240·00	180·00	60·00			

§ 82. *Veins of Fishes.*—As the blood moves in a circle, it signifies little at what point we commence the description of the parts in which it flows. But as, in tracing the progress of the nutriment through the organs concerned in its chylication and sanguification, we were led by the lymphatics to the veins, we begin with them the account of the circulating system in the present class.

The tunics of the veins of Fishes are unusually thin, and their valves few: though commonly in the form of tubes, yet they more frequently dilate into sinuses than in the higher classes, and traces of the diffused condition of the venous receptacles, so common in the Invertebrates, are not wanting in Fishes; as, for example, in the fissures of the renal organs, where the veins seem to lose their proper tunics, or to blend them with the common cellular tissue of the part; and in the great cavernous sinus beneath the abdominal aorta, receiving the renal and genital veins in the Lamprey. The jugular veins of Osseous Fishes and the hepatic veins of the Rays form remarkable sinuses. The very delicate fibres of the proper venous tunic affect a longitudinal disposition: and in many of the veins of Fishes the walls show pigment, usually in the form of stellate cells.

The veins of Fishes constitute two well-defined systems; viz. the 'vertebral' and the 'visceral,' answering to the division of the nerves and muscles into those of 'animal' and 'organic' life: the portal system is a subdivision of the visceral one, but also frequently includes part of the vertebral system of veins, especially in the Myxines, in which the portal sinus forms a common meeting-point between portions of both systems.<sup>2</sup>

The capillary system of vessels consists in Fishes, as in other Vertebrates, of minute but similar-sized tubules, capable of carrying

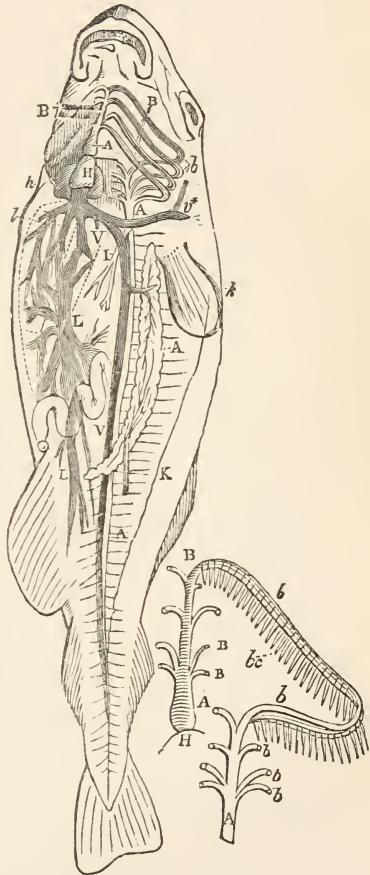
<sup>1</sup> CCXLV. p. 27.

<sup>2</sup> Retzius, in XXI. 'Gefäßsystem,' 1841, p. 16.

a single file of blood-discs, and connecting the termination of the arteries with the commencement of the veins, figs. 328, 329.

The vertebral system of veins commences by a series of capillary roots in the integuments and muscles, which unite to form branches corresponding with the muscular and osseous segments of the body: these 'segmental' veins consist, in the tail, of upper or neural, and lower or hæmal branches; in the abdomen, of upper and lateral branches; in the head, where the vertebral segments are more modified, the veins manifest a less regular and appreciable correspondence with these segments. The cephalic veins, returning the blood from the cranial vertebræ, their appendages and surrounding soft parts, from the brain, the organs of special sense and their orbits or proper cavities, from the mouth and pharynx, and, receiving also the whole or part of the 'venæ nutritiæ' from the branchial arches, unite together on each side to form a pair of 'jugular' veins, fig. 308, *v*<sup>\*</sup>, each of which usually dilates into a larger sinus, and again contracts and resumes the vasiform character, as it descends to beneath the parapophyses of the atlas and axis, in order to join the corresponding trunk of the vertebral veins of the body.<sup>1</sup> This great trunk, called 'vena cardinalis,'<sup>2</sup> fig. 308, *v*, commences at the base of the tail-fin, where it receives blood, and some affirm also lymph, from the pulsating sac there present in the Eel-tribe. The vein-trunk is

308



Circulation of the blood in the Fish. CCLXVI.

<sup>1</sup> In the Lamprey the corresponding jugular trunks lie above the aponeurotic representatives of the vertebral parapophyses.

<sup>2</sup> 'La veine cave' of Cuvier; but it is not homologous with either the 'inferior' or 'superior venæ cavæ' of Man.

double, there being one for each side of the body, and both right and left 'venæ cardinales' extend forward, in close contact, along the hæmal canal in the tail, then through the abdomen, and in both regions immediately beneath the aorta and vertebral bodies, to near the first vertebra, where each trunk diverges and descends to join its corresponding 'vena jugularis,' fig. 308, *v*, forming the short 'precaval' vein,<sup>1</sup> *ib. v*, which empties itself in the great auricular sinus between the aponeurotic layers of the pericardial and abdominal septum. In the Lamprey the vena cardinalis is single along the tail, but it bifurcates on entering the abdomen into two veins, each of which is six times as large as the aorta. The left cardinal vein is larger than the right in the Myxinoids: but the symmetrical disposition of the vertebral venous system is more disturbed in many Osseous Fishes, at the expense of the right side; the right cardinal vein, after some transverse connecting channels with the left, finally terminating or losing itself therein anteriorly: part of the right jugular vein, also, in this case enters the left or common cardinal vein.<sup>2</sup> In the Tunny the two 'venæ jugulares' unite and form a common trunk, which enters the auricular sinus independently.<sup>3</sup> The Shad, the Pike, and the *Lucioperca* are examples where the jugular veins are symmetrical, and terminate distinctly in the precaval veins. With regard to the vertebro-venal system of the trunk, not all the segmental branches terminate in the 'vena cardinalis;,' the neural twigs form with the myelonal veins a trunk which runs parallel with the cardinal veins, but above the vertebral bodies in the neural canal. This trunk, the 'vena neuralis,' communicates by short lateral and vertical canals with the venæ cardinales, and in the region of the abdomen these short anastomosing veins perforate the substance of the kidneys, and receive the 'renal veins' before terminating in the abdominal cardinal veins. The neural vein gradually exhausts itself by these descending branches, and does not extend to or terminate anteriorly in the precaval trunk. Jacobson, observing that the abdominal anastomotic branches of the neural vein, in transferring its contents to the cardinal veins, perforated the kidneys, thought

<sup>1</sup> *Ductus Cuvieri*, Rathké; *quervernenstämme*, Müller. The precaval veins are the homologues of the two 'superior cavæ' in Reptiles and Birds, which receive the so-called 'azygos' veins or reduced homologues of the 'venæ cardinales' of Fishes: in the higher Mammals and in Man they are concentrated into a single 'superior vena cava,' receiving the 'venæ cardinales' by a common trunk, thence called 'azygos' in Anthropotomy. The anatomical student is usually introduced to the cardinal veins, as represented by their single homologue in the human subject, where their normal symmetrical character becomes masked by an extreme modification, and where the name 'azygos' is applicable only to so exceptional a condition.

<sup>2</sup> *xxi. p. 38.*

<sup>3</sup> *Ib. p. 37.*

that those branches ramified in the renal tissue, like the portal veins in the liver; but my observations concur with those of Meckel and Cuvier,<sup>1</sup> in showing that they rather receive or communicate with the renal veins *in transitu* in Osseous Fishes. In the Lamprey the renal vein assumes the form of a cellular or cavernous sinus, of a very dark colour, extending along the mesial margin of the kidney, uniting with its fellow posteriorly, and communicating by small orifices with the contiguous cardinal vein.

The visceral system of veins commences in Osseous Fishes by the capillaries of the stomach and intestines, of the pancreatic cæca and spleen, of the generative organs and air-bladder: these by progressive union and reunion, constitute either a single trunk which forms the portal arterial vein, fig. 308, L, of the liver; or, as in the Perch, a second trunk, the true homologue of the 'inferior vena cava' which returns the blood from the genital organs and air-bladder to the auricular sinus, without previous ramification in the liver; the portal trunk being formed only by the veins of the alimentary canal and its appendages. The portal trunk is single in the Ling, the Burbot, the Pope, the Eel, the Lamprey, and the Plagiostomes; but, in the Carp, where the lobes of the liver interlace with the convolutions of the intestine, the veins of this canal pass directly into the liver by several small branches, which ramify therein without forming a portal trunk.

In the Plagiostomes with the longitudinal spiral valve the main root of the portal vein is concealed in the free, thickened, muscular margin of that valve:<sup>2</sup> the trunk of the intestinal vein is lodged also in an internal fold of the mucous coat in the Lamprey: in the Plagiostomes and Ganoids with transverse coils of the spiral valve, the venous blood is collected into an external intestinal vein. In the Paddle-fish this vein joins the vein of the spleen (fig. 276, *n*), and then, with the duodenal, pancreatic, and gastric veins, forms the portal trunk.

Professors Eschricht and Müller<sup>3</sup> found, in the Tunny, that the veins of the stomach, intestine, pyloric appendages, and spleen, respectively subdivided into numerous minute venules, which interlaced with corresponding 'retia mirabilia' of the arterial branches sent from the cœliac axis to the same viscera, and formed pyriform masses of vessels before entering the liver.

In a few Osseous Fishes, as the Shad, some of the caudal branches of the vertebral system of veins anastomose with the

<sup>1</sup> XXIII. p. 381.

<sup>2</sup> XCVIII. p. 274.

<sup>3</sup> CIII.



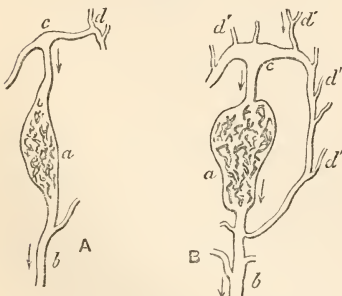
veins of the rectum, and thus form part of the roots of the portal system. But the most interesting modification of the portal system of Fishes is that discovered by Retzius in the Glutinous Hag. In this and also in other Myxinoids, the genital and intestinal veins form a common trunk along the line of attachment of the mesentery: all the gastric veins that do not empty themselves into the cardinal vein also join the great mesenteric vein. This vein advances to the space between the pericardium and the right suprarenal body, receives the anterior vein of that body (its posterior one joining the cardinal vein), and dilates into an elongated sinus, which is said to contract, as if it were a portal heart. The anterior part of this sinus receives a vein from the right anterior parietes of the body, which is formed by the union of all those of the muscular parts there which do not join the right jugular vein: the portal arterial vein is sent off from the posterior end of the pulsating sac, near the entry of the mesenteric vein, and goes backward to beneath the two livers, and there divides, enters, and ramifies in each. The hepatic vein of the hinder and larger liver enters the common trunk or sinus formed by the union of the two cardinal veins with the left jugular: the hepatic vein of the smaller liver joins the termination of the left jugular vein, and they together end in the opposite side of the same common sinus.

In the Plagiostomes the right jugular and cardinal veins unite, and, receiving the vein of the pectoral fin (brachial vein), and a superficial vein from the head (external jugular), form a short transverse 'precaval' trunk. A corresponding precaval trunk is formed in the same way on the left side, and the great auricular sinus is constituted by these and by the wide hepatic veins, which contract before they terminate. In many Osseous Fishes, as *Salmo*, *Silurus*, *Belone*, *Anguilla*, *Ammodytes*, and *Accipenser*,

the hepatic veins terminate in the common sinus by a single trunk; in others, as *Thynnus*, *Gadus*, *Esox*, and *Pleuronectes*, by two trunks; and in a few Fishes, as *Clupea*, *Cottus*, and certain Cyprinoids, by three or more trunks.

The pulsatile sac in the Eel, fig. 309, is situated near the beginning of the cardinal vein on the hæmal side of the caudal vertebræ at the end of the tail. It is of a yellowish colour,

309



Caudal venous heart of Eel: magn. 20 diam.  
CCLXIV.

checquered more or less with stellate pigment; in shape fusiform, fig. 309, A, or pyriform, ib. B; at the distal end it is connected with a small vein, *c*, which collects the blood from the capillaries of the tail, *d*, *d'*: at its proximal end it is connected with the commencement of the cardinal vein, *b*. The blood, which is deep red, appears to flow into the sac in a continuous stream from *c*; it is forced out at each contraction in an interrupted current, quickly, in successive portions, into *b*, where the movement soon subsides into a continuous stream. During the systole the veins *c* and *b* are lengthened, being drawn out; in the diastole they resume their size, and assist in elongating the sac; which, both by its contents and connections, is to be regarded as a 'venous heart.'<sup>1</sup>

Thus in Fishes the chyle, having already begun to manifest its independent life by the development of distinct microscopic granular corpuscles, as primitive centres of assimilative force, before it enters the lacteals, undergoes in those vessels and their receptacles a further stage of conversion into blood by the reaction and, as it were, impregnation of the lymph, and by the interchange of properties therewith: the vitalising stimulus of which interchange and reaction is manifested by the repeated spontaneous fission of the corpuscles, many of which now acquire a capsule, and thus become nuclei of cells. Then the mixed chyle and chyme enter the veins, where a further interchange of properties with the venous blood and a new course of action and reaction takes place. The primitive pale chyle-corpuscles are here few in number; they have a capsule, and the granular character of their contents shows them to be in the course of change. The venous blood undergoes some change, probably, in its passage through the kidneys, by virtue of the anastomoses of the renal vascular system: it undergoes further change in its circulation through the liver, in so far as the bile, a fluid highly charged with carbon and hydrogen, is eliminated from it: that in some fishes (*Myxine*, *Bdellostoma*) a contractile receptacle accelerates its course through the portal circulation. The venous blood now shows a marked accession of coloured corpuscles; and it has finally to be submitted to the influence of the atmosphere, and especially to the reaction of the oxygenous element; and for this, the most important and efficient cause of its conversion into arterial blood, a contractile cavity, with strong muscular walls, is provided, in order to impel the blood to the organs especially destined to effect its decarbonisation and oxygenation.

<sup>1</sup> cXLV. p. 253 (1846).

§ 83. *Heart of Fishes.*—The propelling organ is called the ‘heart,’ fig. 308, H; the respiratory organs the ‘gills’ or branchiæ, ib. B, *b*; fig. 312, 1, 6; fig. 323, 2, 3, 4, 5; they submit the blood to the influence of the air through the medium of the water in which it is suspended or dissolved.

There is only one known fish, viz. the Lancelet, in which a venous or branchial heart is not developed as a compact and predominant muscular organ of circulation: a great vein answering to the ‘vena cardinalis’ extends forward along the caudal region, beneath the chorda dorsalis, above the kidney, fig. 169, *h*; and as it extends along the branchial œsophageal sac gives vessels to or receives them from the ciliated vertical bands or divisions of that sac, which vessels communicate with a vascular trunk along the inferior part of that sac. This trunk at its posterior end dilates into a small sinus, *ov*, which pulsates rhythmically, and represents rudimentally the branchial heart of the Myxinoids: the cardinal vein, *ba*, divides anteriorly, and supplies the short vascular processes, *gg*, which project above the pharyngeal orifice, *ph*, into the wide buccal cavity: the blood oxygenized in these processes is transmitted to the cerebral portion of the neural axis, to the organs of sense, especially the sensitive integument of the head, and to the jointed labial tentacula, *f, f*, whence it returns to the pharynx by the labial vessels which there unite together, and with the inferior trunk of the vascular system, or arches, of the branchial pharynx.

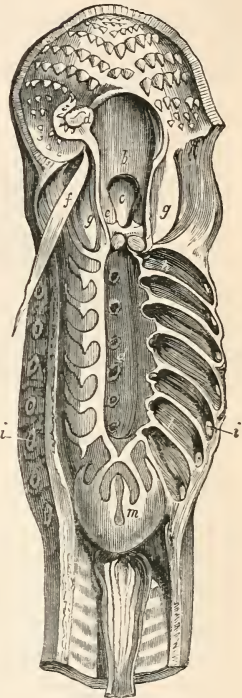
In the Myxinoids a heart consisting of an auricle and a ventricle is situated, like the pulsating tube or sinus of the Lancelet, far back from the head, in the beginning of the abdomen, where it is inclosed by a fold or duplicature of the peritoneum, extending between the cardiac end of the œsophagus above, and the anterior liver below, and forming the homologue of the pericardium, which sac communicates freely by a wide opening with the common peritoneal cavity. The auricle is much longer than the ventricle: it receives the blood from the common sinus by an orifice defended by a double valve. The auricle communicates with the left side of the rounded ventricle, the ‘ostium venosum’ having also a double valve. There are no ‘columnæ carneæ’ or ‘chordæ tendineæ.’ The artery, single here as in all Fishes, rises from the fore-part of the ventricle with a pair of semilunar valves at the ‘ostium arteriosum’ behind its origin, beyond which it slightly dilates, but has no muscular parietes constituting a ‘bulbus arteriosus.’ In a large Myxinoid (*Bdellostoma cirratum*, Dum.) the vessel from the heart divides at once into two branchial trunks, reminding one of the

separate branchial arteries of the Cephalopods.<sup>1</sup> In other species of *Bdellostoma* the artery extends beyond two or three pairs of gills before it bifurcates; and Müller<sup>2</sup> saw one instance in the *Myxine glutinosa*, where the branchial artery continued single as far as the anterior gills.

The pericardium of the Ammocete communicates by one wide orifice with the peritoneum: that of the Lamprey is a shut sac, and is supported by a perforated case of cartilage, formed by the last modified pair of branchial arches, fig. 310, *m*. Not any of the Dermopteri possess the 'bulbus arteriosus': this is present, and forms, as it were, a third compartment of the heart, 311, *B*, beyond the ventricle, *ib.* *A*, and auricle, *ib.* *C*, in all other Fishes: nay, if we include the great 'sinus communis,' *ib.* *D*, as part of the heart, then we may reckon four chambers in that of Fishes; but these succeed each other in a linear series, like the centres of the brain, and their valves are so disposed as to impress one course upon the same current of blood from behind forward, driving it exclusively into the branchial artery and its ramifications. This is very different from the arrangement and relations of the four compartments of the human heart. Physiologically the heart of Fishes answers to the venous or pulmonary division, *viz.* the right auricle and ventricle of the mammalian heart, and its quadripartite structure in Fishes illustrates the law of vegetative repetition, rather than that of true physiological complication. The auricle and the ventricle are, however, alone proper to the heart itself: the sinus is a development of the termination of the venous system, as the muscular bulb is a superaddition to the commencement of the arterial trunk. The heart of Fishes with the muscular branchial artery is the 'homologue' of the left auricle, ventricle, and aorta in higher Vertebrates; but it performs a function 'analogous' to that of the pulmonic auricle and ventricle in them.

Some of the higher organised Fishes, which present the normal structure of the heart, have, like the Myxinoids, a perforated

310



Heart and gills, Lamprey  
(*Petromyzon*). cxx.

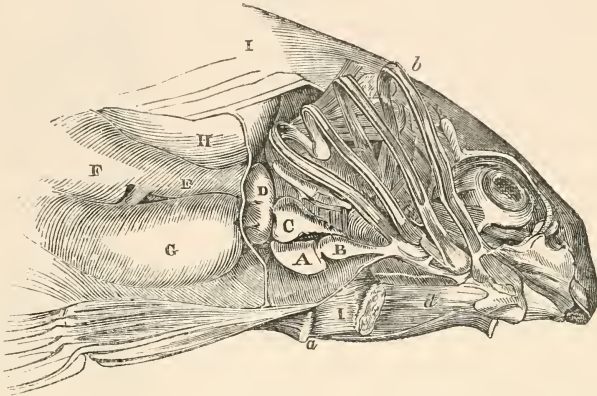
<sup>1</sup> xx. vol. ii. p. 78, prep. no. 1018.

<sup>2</sup> xxi. p. 9.



pericardium. In the Sturgeon the communication with the peritoneum is by a single elongated canal extending along the ventral surface of the œsophagus. In the Planirostra and Chimæroids the pericardio-peritoneal canal is also single. In the Plagiostomes

311



Heart and gill-arches, Perch. XXIII.

it bifurcates, after leaving the pericardium, into two canals, which diverge and open into the peritoneum, opposite the end of the œsophagus: no ciliary movements have been noticed on the surface of these remarkable conduits. The serous layer of the pericardium is defended by an outer aponeurotic coat in Osseous Fishes and Plagiostomes, which adheres to the surrounding parts. In the Sturgeon, Wolf-fish, Loach and *Muræna*, short fibrous bands supporting vessels pass from different parts of the pericardium to the surface of the heart: in most other fishes the heart hangs freely except at the two opposite poles, viz. where the sinus communicates with the auricle, and where the *bulbus arteriosus* is continued into the branchial artery.

In the Plagiostomes the sinus itself is situated within the pericardium; but in Osseous Fishes between the layers of the posterior aponeurotic partition between it and the abdomen. The heart is situated below the hind-part of the gills, and, as these are more concentrated in the head in all Fishes above the *Dermopteri*, so the position of the heart is more advanced, fig. 308, H. In the Plagiostomes, the Sturgeons, and many Osseous Fishes, e.g. the Perch, the Angler (*Lophius*), and the Sun-fish (*Orthogoriscus*), the orifice by which the great sinus communicates with the auricle is guarded by two semilunar valves; but these are far from being constant in the *Teleostomi*. The auricle, when distended, is larger in proportion to the ventricle

in Fishes than in higher Vertebrates. Its relative position to the ventricle varies in different species, and permanently represents as many similar variations displayed temporarily during the course of the heart's development in birds and mammals; thus in the heart of *Scorpena scrofa*, as in the Myxinoids, the auricle is posterior to and in the same longitudinal line with the ventricle: in the Perch, fig. 311, c, Carp, Sole, and Eel, it has advanced to the same transverse line, on the dorsal and left side of the ventricle: in the Sturionidæ and other Ganoids it extends more forward, dorsad of both ventricle and bulbus arteriosus, and the heart, including the venous sinus, is now bent into a sigmoid form. The walls of the auricle are membranous, with thin muscular fasciculi decussating and forming an open network; but these are closer and stronger in the Sun-fish, Sturgeons, and Plagiostomes. The cavity is simple, but its inner surface is much fasciculated in the Sun-fish and Sturgeon, where the ends of the valves of the sinus are attached to the strongest muscular bands. Only in the Lepidosiren is there any vestige of a septum, and this is reticulate. The auricle communicates by a single orifice, commonly with the dorsal or the anterior part of the ventricle: this is guarded usually by two free semilunar valves; but in the Sturgeon, their margins and their surface next the ventricle are attached to numerous 'chordæ tendineæ.' In the Orthogoriscus the auricular aperture is guarded by four semilunar valves, the two smaller ones being placed at right angles with and on the auricular side of the two larger and normal valves: their margins are free.

The ventricle, fig. 311, A, usually presents the form of a four-sided pyramid, one side dorsad toward the auricle; one angle ventrad, and the base forward. In the Lepidosteus and Polypterus, however, it is pyriform: in the Pike it is lozenge-shaped: in the Lophius, as in the Myxinoids and Lampreys, it is oval: in most Plagiostomes its transverse diameter is the longest, as if preparatory to a division. Its cavity is, however, simple in all fishes. The parietes of the ventricle are very muscular, and the fibres are redder than those of any other part of the muscular system; but the colour is less deep in the ground-fishes than in those that swim nearer the surface, and enjoy more active locomotion and respiration. The exterior muscular fibres decussate and interlace together irregularly and inextricably; but the deeper-seated ones form more regular layers, the innermost being transverse and circular, and separating readily by slight decomposition from the outer and more longitudinal layers. Some of

the internal fasciculi send off the 'chordæ tendineæ' above mentioned in the Sturgeon; but in almost all other fishes those 'chords' are absent, and the auricular valve is free. In most Osseous Fishes the orifice at the base of the bulbus arteriosus is provided with a pair of semilunar valves: the Sun-fish (*Orthogoriscus*) has four such valves there.<sup>1</sup> But the Ganoids, Holocephali, and Plagiostomes have two or more transverse rows of semilunar valves attached to the inner surface of their long and muscular bulbus arteriosus. There are two rows of three valves in the Grey Shark (*Galeus*), in the Blue Shark (*Carcharias*), in the Dog-fish (*Scyllium*), and in the Chimæroids: the *Amia* has two rows of six valves: in the genera *Sphyrna*, *Mustelus*, *Acanthias*, *Alopias*, *Lamna*, *Rhinobatus*, *Torpedo*, and *Accipenser*, there are three rows of valves: the Sturgeon's heart<sup>2</sup> shows five valves in the anterior row, and four valves in each of the other rows; and the free margins of the valves are connected by short 'chordæ tendineæ' to the parietes of the bulb. The genera *Hexanthus*, *Heptanchus*, *Centrophorus*, and *Trygon* have four rows of valves. The heart of the *Raia Batis*<sup>3</sup> shows five rows, the valves increasing in size to the last row, which is at the termination of the bulb. *Scymnus*, *Squatina*, and *Myliobat's* have also five rows of valves. In *Cephaloptera* the large bulbus arteriosus<sup>4</sup> presents internally three longitudinal angular ridges, at the sides of which are small valves disposed in pairs, and in four or five rows: besides these there are three larger valves at the beginning, and three at the end of the bulb. The valves are still more numerous in lepidogonoid fishes, and are arranged in longitudinal rather than in transverse rows: the *Polypterus* shows three such rows of nine or ten larger semilunar valves alternating with as many rows of smaller valves. The *Lepidosteus* has five longitudinal rows of sub-equal valves: those at the end of the bulb being always the largest and most efficient. In the *Lepidosiren* the place of valves is supplied in its long and twisted bulbus arteriosus by two longitudinal ridges, fig. 312, *c*;<sup>5</sup> the interesting stages, which we have been tracing through the highly organised Ganoids and Plagiostomes, in the partition of the bulb into distinct arterial trunks for the systemic and pulmonic circulation, being most advanced in this amphibious fish.

The auricle in the *Lepidosiren annectens*, *ib. a*, is essentially single, but has two ear-like appendages.<sup>6</sup> The venous sinus

<sup>1</sup> xx. ii. p. 37, prep. no. 905.    <sup>2</sup> *Ib.* p. 38, prep. no. 908.    <sup>3</sup> *Ib.* p. 38, prep. no. 909.

<sup>4</sup> I found its cavity more capacious than that of the contracted ventricle.

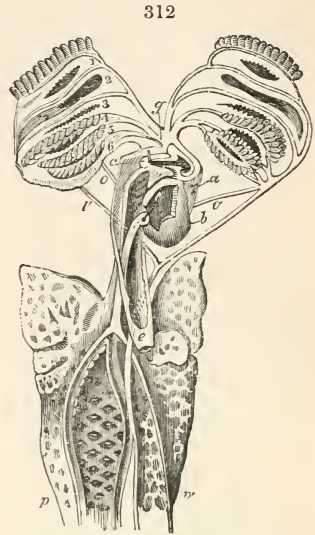
<sup>5</sup> xxxiii. p. 343. p. pl. xxvi. fig. 2. *c*.

<sup>6</sup> *Ib.* p. 345.

communicates with it without any intervening valve; the auricle receives the vein from the air-bladder by a distinct aperture, close to the opening into the ventricle; regurgitation into the vein being prevented by a hard valvular tubercle, which also projects into the ventricle. The ventricle (fig. *b*) is single, like the auricle; its inner parietes are very irregular: a 'trabecula' projects from the lower part of the cavity, like a rudimental septum: a smaller transverse 'trabecula' arches over and acts as a valve to the single auriculo-ventricular opening, but there are no proper membranous semilunar valves.

The muscular parietes of the 'bulbus arteriosus' are distinct in all fishes from those of the ventricle; they may be overlapped by these, but an aponeurotic septum intervenes between the origin of the bulb and the overlapping ventricular fibres.<sup>1</sup>

§ 84. *Gills of Fishes.*—The primary division of the branchial artery in the Myxinoids has been already described. Each gill-sac receives, either from the trunk or its bifurcations, its proper artery. The leading condition of the gills in other fishes may be understood by supposing each compressed sac of a Myxine, fig.



Circulating and respiratory organs,  
Lepidosiren

313



Two gill-sacs, *Bellostoma*

314



Two gill-sacs, Lamprey

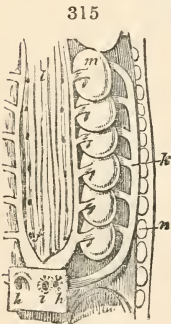
313, *m*, to be split through its plane, and each half to be glued by its outer smooth side to an intermediate septum, which would then support the opposite halves of two distinct sacs, and expose their vascular mucous surface to view. If the septum be attached by

<sup>1</sup> xx. vol. ii. p. 39, prep. no. 910.



its entire margin, the condition of the plagiostomous gill is effected. If the septum be liberated at the outer part of its circumference and the vascular surfaces are produced into pectinated lamelligerous processes, tufts, or filaments, proceeding from the free arch, the gill of an ordinary osseous or teleostomous fish is formed. Such a gill is the homologue, not of a single gill-sac, but of the contiguous halves of two distinct gill-sacs, in the Myxines. Already, in the Lampreys, the first stage of this bi-partition may be seen, fig. 314, *m*, and the next stage in the Sharks and Rays: consequently in these fishes, a different artery goes to the anterior branchial surface of each sac or fissure from that which supplies the posterior branchial surface of the same fissure; whilst one branchial artery is appropriated to each supporting septum or arch between the fissures, as it is to the liberated septum or branchial arch in the *Teleostomi*.<sup>1</sup> Before describing the branchial vessels it will be necessary to describe the organs upon which they ramify.

In the Lampreys and Plagiostomes each supporting septum of the two (anterior and posterior) branchial mucous surfaces is attached to the pharyngeal and dermal integuments by its entire peripheral margin, and the streams of water flow out by as many fissures in the skin, *ib. k*, as those by which they enter from the pharynx, *ib. f*: these are called 'fixed gills,' and the species possessing them are characterised as 'pisces branchiis fixis.' In the *Teleostomi*=Osseous, Plectognathic, Lophobranchiate, Ganoid, and Holocephalous fishes, the outer border of the supporting branchial arch is unattached to the skin, and plays freely backward and forward, with its gill-surfaces, in a common gill-cavity which has a single outlet, usually in the form of a vertical fissure: the species with this structure are called 'pisces branchiis liberis.'



Branchial organs, Myxine

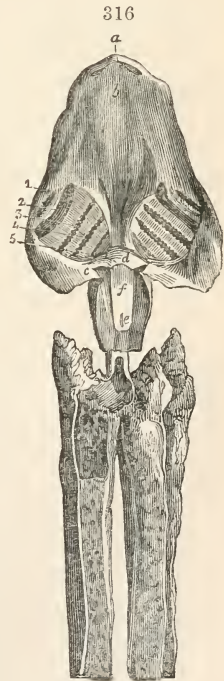
In the Myxine the outlets of the six lateral branchial sacs, fig. 315, *m*, on each side are produced into short tubes, which open into a longitudinal canal, *h*, directed backward, and discharging

<sup>1</sup> *CXLV.* p. 258. Prof. Milne Edwards has exemplified this homology by the subjoined formula:—

Osseous Fishes	B. ac.	B 1	B 2	B 3	B 4
		b . b	b	b	b .
Plagiostomous Fishes					
		b . b	b	b	b .
		B 1	B 2	B 2	B 4
				B 4	B 5

the branchial stream by an orifice, *h*, near the middle line of the ventral surface: between the two outlets of these lateral longitudinal canals, but nearer the left one, is a third larger opening, *i*, which communicates by a short duct with the end of the long œsophagus, *l*, and admits the water, which passes from that tube by the lateral orifices, *f*, leading into the branchial sacs. This is the first step in development beyond that simpler condition which prevails in the Lancelet, where the whole parietes of a much dilated œsophagus, fig. 169, *rr*, are organised for respiration; and besides the pharyngeal opening, *ph*, the sac communicates by a short and wide ‘ductus œsophago-cutaneus,’ *ib. od*, with the external surface, and also with the peritoneal cavity. The common respiratory surface of the œsophagus is ciliated in the Lancelet. The sacs developed from the œsophagus, and specially set apart for respiration in the Myxinoids, have a highly vascular, but not a ciliated mucous surface: this is disposed in radiated folds, and is further increased by secondary plicæ. The seven branchial sacs on each side of the œsophagus have short external ducts, fig. 313, *k*, which open by as many distinct orifices in the skin in a species of *Bdellostoma* hence called *heptatrema*: the internal branchial ducts communicate by as many openings, *ib. f*, with the œsophagus. In the Lampreys there are, also, seven stigmata on each side; but another stage in the separation of the respiratory from the digestive tract is here seen, for each internal duct communicates with a median canal, fig. 310, *d*, beneath and distinct from the œsophagus, terminating in a blind end behind, and communicating anteriorly with the fauces by an opening guarded by a double membranous valve.

In all higher fishes the inlets to the branchial interspaces are situated on each side the fauces, and are equal in number with those interspaces, fig. 316, 1—5. The outlets are, with the exception of the Plagiostomes, single on each side: they vary much in size; are relatively largest in the Herring and Mackerel families, smallest in the Eels and Lophioid fishes; in some of the small Frog-fishes, *Antennarius*, the circular branchial pore is produced into a



Branchial slits and lungs,  
Lepidosiren. XXXIII.

short tube above each pectoral fin. The power of existing long out of water depends chiefly on these mechanical modifications for detaining a quantity of that element in the branchial sacs; for fishes perish when taken out of water, chiefly by the cohesion and desiccation of their fine vascular branchial processes, through which the blood is thereby prevented from passing.<sup>1</sup> If sufficient water can be retained to keep the gill-plates floating, the oxygen which is consumed by the capillary branchial circulation is supplied to the water retained in the branchial sac directly from the air. In some of the Eel tribe the small branchial outlets are closely approximated below, as in *Sphagebranchus*; and they are blended into a single orifice in *Symbranchus*, analogous to that in the Myxine. In some Ganoids, many Plagiostomes, fig. 137, *br*, and all Sturgeons, a canal leads from the fore part of each side of the branchial chamber to the top of the head; the outlets are called 'spiracles,' the canals 'spiracular.' The nasal sac communicates in the Lamprey with the single homologous canal, the inner or faucial aperture of which is shown at *c*, fig. 277.

The branchial chamber is largest in the fishes which have the smallest outlets, as, e.g., in the Eel tribe, the Uranoscopi, the Blennies, and especially the Lophioids: extending backward in the Angler (*Lophius piscatorius*) towards the hind part of the abdomen, with a proportional elongation of the branchiostegal rays; and still further back in *Halieutea*. The opercular flaps forming the outer wall of the gill-chambers are described at pp. 123, 124, fig. 84; the branchial arches at p. 106, fig. 85. The basibranchials are usually present only in the two or three anterior arches, the others joining below directly, or by the medium of a gristly plate (*Trigla*) to the last basibranchial; or terminating loosely, as in *Murenophis*. The hypobranchials are usually present only in the first or second arches: the most constant elements, both as to existence and shape, are the ceratobranchials, fig. 85, 47, and epibranchials, *ib.* 48. The pharyngo-branchials, *ib.* 49, vary in shape and tissue; they attach the arches to the base of the skull, and develope, with the anterior epibranchials, fig. 325, the complex labyrinthic appendages of the branchial apparatus in the Climbing Perch (*Anabas*) and its allies. In *Lophius* and *Diodon* there are only three pairs of branchial arches. The fissures between the arches become shorter as they recede in position, the last being commonly a mere foramen: their vertical extent shows an agreement with that of the outer gill-slit: they

<sup>1</sup> *CVI.* p. 124.

are long, e.g. in the Mackerel; short in the Eel: in the Lophobranchs they are one-third the length of the arches: in the Plectogonaths they are half that length; in the Carp-tribe they are nearly as long, in the Salmon-tribe quite as long, as the branchial arches themselves.

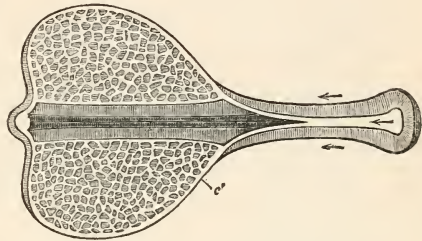
The main purpose of the gills of fishes being to expose the venous blood in a state of minute subdivision to streams of water, the branchial arteries rapidly divide and subdivide until they resolve themselves into microscopic capillaries. These constitute a network in one plane or layer, fig. 317, supported by an elastic plate, and covered by a tessellated and non-ciliated epithelium. This covering and the tunics of the capillaries are so thin as to allow the chemical interchange and decomposition

to take place between the carbonated blood and the oxygenated water. The requisite extent of the respiratory field of capillaries is gained by various modes of multiplying the surface within a limited space. In the *Marsipobranchii* and *Plagiostomi*, for example, by folds of membrane on plane surfaces: in the *Lophobranchii* by clavate processes grouped into tufts: in the *Protopteri*, by double or single fringes of filaments: in the rest of the class by the production of the capillary-supporting plates from each side of long, compressed, slender, pointed processes, extending, like the teeth of a comb, but in a double row, fig. 318, *d, d*, from the convex side of each branchial arch, fig. 311, *b*.

Each pair of processes has its flat sides turned toward contiguous pairs, and the two processes of each pair stand edgewise toward each other, and are commonly united for a greater or less extent from their base: hence Cuvier describes each pair as a single bifurcated plate, 'feuillet.'

In the Swordfish (*Xiphias*), the processes of the same pair stand quite free from each other; whence Aristotle described this fish as having double the

317



A branchial leaf, with the respiratory capillaries on side, Cod. CCLXVIII.

318

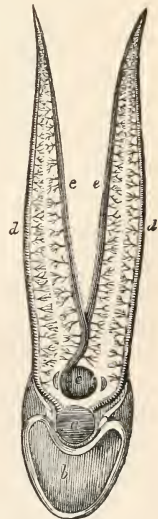


Diagram of the circulation of the blood through the branchial leaflets. Fish. XXIII.



usual number of gills.<sup>1</sup> But to compensate for this independence, and to prevent the inconvenience of mutual pressure, the processes of the same series are united together by little vascular lamellæ, so that the surface of the gill is reticulate rather than pectinate. In the *Orthogoriscus* the processes of each series are not opposite, but alternate. In a few species the processes of each pair are joined together to near their apices, as in the Sturgeon, in which the musculo-membranous medium of union extends from pair to pair throughout the entire gill, forming a true 'septum branchiale,' and presenting a transition to the more complete septum which divides the respiratory vascular surfaces in the Plagiostomes.

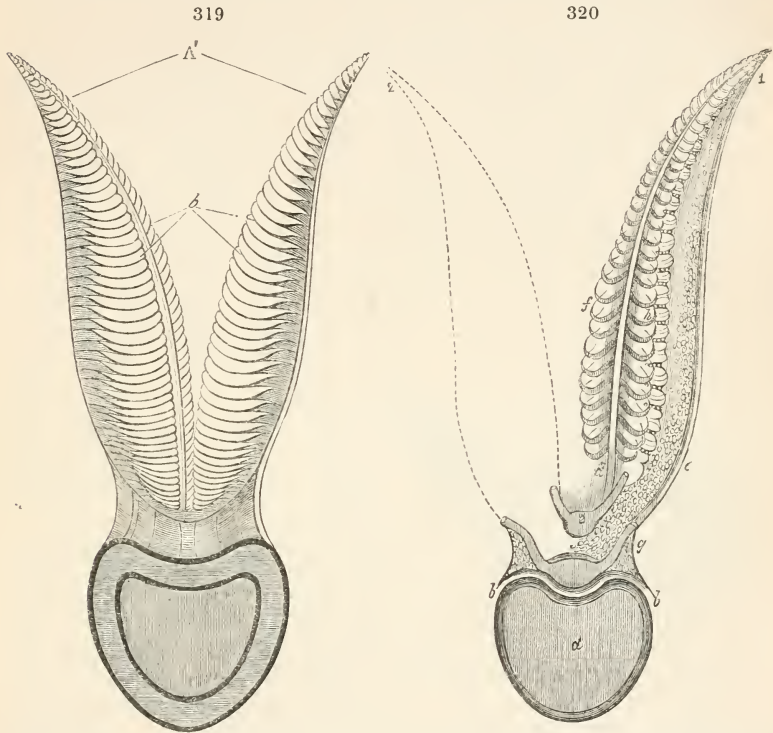
In fig. 318, the course of the blood through a pair of branchial processes is diagrammatically shown: *a* is a section of the branchial artery; *d* is the branch sent along the outer margin of the process; *e* is the vessel receiving the blood from the capillaries after the respiratory change has been effected, and returning it, along the inner border of the process, to the branchial vein, the sectional area of which is shown at *c*. In fig. 319 are shown the vascular plates or lamellæ, *b*, of the branchial processes,  $\Delta'$ , in the Cod (*Morrhua vulgaris*), in which they are confined to the inner half or two-thirds of the process. Fig. 317, representing a transverse section of the process, shows the degree and form in which the plates extend from it on each side: the arrows indicate the course of the blood from the outer to the inner border of the plate-bearing process. Fig. 320 represents the frame-work supporting the vascular structure of the gill: *a* is a section of the branchial arch; *b* is the base of the branchial process attached to but distinct from the arch: *c* its outer obtuse border; *d* its inner border, from which are continued the elastic cords, *f*, extending along the outer margin of the lamellæ, fig. 317, *i*, and maintaining them outstretched.<sup>2</sup> The number of plates on one process has been estimated at 55 in the Gudgeon, 96 in the Tench, 106 in the Barbel, 135 in the Carp, 700 in the Eel, 1000 in the Cod, 1400 in the Salmon, 1600 in the Sturgeon.

In some Osseous Fishes certain of the branchial arches support only one series of processes; such are called 'uniserial,' or 'half' gills; but, as a general rule, they support 'biserial,' or 'whole' gills. Most of the Labroids, the genera *Cottus*, *Scorpena*, *Sebastes*, *Apistes*, *Zeus*, *Antennarius*, *Polypterus*, *Gobiesox*,

<sup>1</sup> XXIII. t. viii. p. 192.

<sup>2</sup> For the histology of these structures, see Dr. Williams's minute description in CCLXVIII. pp. 288-290.

*Lepadogaster*, and the *Cyclopterus liparis* have three biserial gills and one uniserial gill; the genera *Lophius*, *Batrachus*, *Diodon*, *Tetrodon*, *Monopterus*, *Cotylin*, have three biserial gills; *Malthæa* and *Lepidosiren* have two biserial gills and one uniserial gill; the



Section of branchial arch with a pair of processes, A', supporting the branchial plates, b, Cod.  
CCLXVIII.

Section of branchial arch, a, with supporting framework of the plate-bearing processes, Cod.  
CCLXVIII.

Cuchia (*Amphipnous*) has only two gills. The above enumeration refers to the branchial organs of one side; they are symmetrical in all fishes, and the uniserial opercular gill is not counted, as not being attached to a proper branchial arch.

The branchial processes are bony, at least along the outer and thicker border, in most Osseous Fishes (e.g. *Salmo*, *Alosa*, *Gadus*). They are gristly, like the arches which support them, in the Sturgeon, where they break up into delicate branched fringes, along their outer margin. Small 'interbranchial' muscles extend, through the uniting septum, between the bases of the processes, for effecting slight reciprocal movements.<sup>1</sup>

<sup>1</sup> CXII. CXIII.

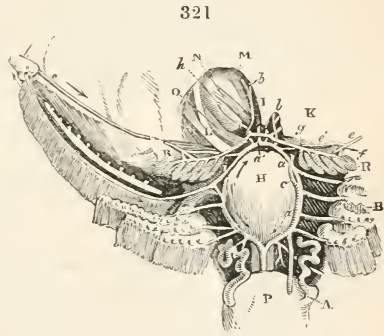
The concave borders of the branchial arches are usually beset with defensive processes, fringes, or tubercles, and these sometimes support small teeth which aid in deglutition; but the chief office of these appendages, which project inward toward the mouth, is to prevent the passage of any particles to the interspaces of the gills, which might injure or irritate their delicate texture. In the edentulous Sturgeon and Paddlefish each arch supports a close-set series of such retroverted slender tapering filaments, fig. 276, which are longer than the opposite branchial processes, *ib. u*: they are developed even from the fifth or pharyngeal arch, which has no gill. Similar fringes of extreme delicacy defend the branchial slit in the Gray Mullet. Frequently such a fringe is developed only from the first branchial arch, Mackarel, Perch, fig. 85, 63, the rest supporting dentated tubercles, fig. 321, and the last or pharyngeal arch being beset with teeth only. In the Remora and many other Fishes, the defensive tubercles on opposite sides of the same branchial fissure interlock, like the teeth of a cog-wheel. In the *Lepidosiren annectens*, fig. 316, short valvular processes are developed from the sides of those branchial fissures only which lead to the gills, the first and second arches having no gills. In the Conger, all the branchial arches are devoid of defensive fringes or tubercles.<sup>1</sup>

The immediate force of the heart's contraction is applied by a short and rapidly divided arterial trunk, fig. 308, B, upon the branchial circulation. Only in a few fishes is the heart removed backward from the close proximity of the gills, and then the branchial artery is proportionally elongated; as in the Eel tribe, especially the *Synbranchidæ*: the artery is long in the *Planirostra*, fig. 276, *s*. The primary branches are always opposite and symmetrical, but vary in number in different species. Very commonly, as in the Perch, they are three in number on each side; the first branch dividing, as in fig. 308, B B, to supply the fourth and third gills, the second going to the second, and the third to the first gill, *ib. b, bc*. In the Polypterus and Skate there are only two primary branches on each side: the first supplies the three posterior gills; the second, formed by a terminal bifurcation of the branchial trunk, supplies the anterior gill in the Polypterus, and in the Skate bifurcates to supply also the uniserial, opercular, or hyoid gill. The Fox-Shark (*Alopias*) and the *Lepidosteus* give examples of four pairs of primary branches from the branchial

<sup>1</sup> See prep. 1038. (Conger), and its description, xx. 1834, p. 83.

trunk. In the Shark the first pair come off close together from the dorsal part of the trunk: the arteries of the last pair quickly bifurcate, and thus each of the five branchial fissures receives its artery. The Myxinoids offer the exceptional instances of the bifurcation of the branchial trunk by a vertical division into two lateral forks, extended in one species to near its base: the *Lepidosteus* presents the still rarer example of the trunk being cleft horizontally into an upper and lower primary division; the upper or dorsal division sends off two branches on each side, the posterior dividing to supply the fourth, fig. 323, 5, and third, ib. 4, gills, the anterior going to the second gill, ib. 3: the lower division sends off the pair of arteries to the first pair of gills, ib. 2, then extends forward and bifurcates to supply the uniserial opercular gills, ib. 1, which are present in this ganoid genus, as in the Sturgeon.<sup>1</sup> In the Cod and other Osseous Fishes the vessels on each side, which are analogous to the pulmonary veins in man, unite to form the 'aortic circle,' fig. 321, *a*, which encompasses the basisphenoid, *H*. The current of arterialised blood flows forward at the fore-part of this circle into the hyo-opercular, *e'*, and orbito-nasal, *b*, arteries; but the main streams are directed backward, and converge in the direction of the arrows to the aortic trunk. The carotids, *c*, the homologues of the subclavians, *d*, sent to the pectoral fins, and sometimes the coronary vessels of the heart, are sent off from the aortic circle. But no systemic heart or rudiment of a propelling receptacle is developed in any fish at the point of confluence of the branchial veins.

Small vessels are sent off from the marginal branchial venules by short trunks, which ramify beneath the branchial membrane, and become the 'arteriæ nutritiæ' of the gills: their capillaries are collected into venous trunks, which quit the gills commonly at both their extremities, those from the dorsal ends joining the jugular veins, those from the ventral ends emptying



Commencement of Systemic Circulation, Dorsæ  
(*Gadus Callarias*). XXV.

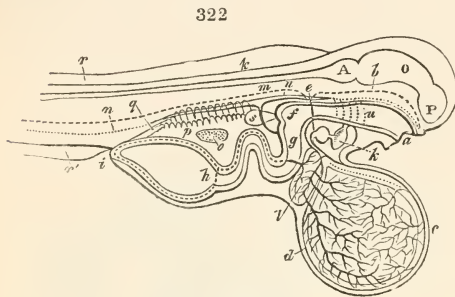
<sup>1</sup> XXV.



themselves into the præcavals, or directly into the great auricular sinus.<sup>1</sup>

Such is the outline of the general structure of the beautiful and complex mechanism of the normal or pectinated gills of fishes. Of this there are many minor modifications; some of which receive explanation from known phenomena in the development of the gills;<sup>2</sup> others, teleologically, from the habits of the species.

Five branchial arches and arteries, or vascular hoops, are developed on each side in the embryo of all fishes above the Der-mopteri, as a general rule.<sup>3</sup> At first the trunk of the branchial arteries simply bifurcates, the divisions passing round the pharynx



Embryo Osseous Fish

and reuniting on its dorsal surface, to form the aorta. Behind this primary circle, which corresponds with the fold developing the hyoid and mandibular arches, four additional arterial hoops are sent off, fig. 322, *u*, which traverse, without further ramifications, the convex side of the four

anterior simple branchial arches, and reunite above in the aortic trunk, *ib. m*. If a sixth arterial arch be developed, corresponding with the fifth branchial arch, as its presence in the *Lepidosiren* would indicate, it has not been observed, and must soon disappear in most Osseous Fishes. In these the gills make their appearance as leaflets budding out from the convexity of the four anterior branchial arches, each leaflet supporting a corresponding loop of the branchial artery; and, as the bifurcation and extension of the primary leaflets and the pullulation of secondary laminae and loops proceed, the vascular arch begins to separate itself lengthwise into two channels, traversed by opposite currents, and thereby establishing an arterial, fig. 318, *d*, and a venous, *ib. e*, trunk in relation to the loops and their vascular developments on the branchial processes. In Osseous Fishes

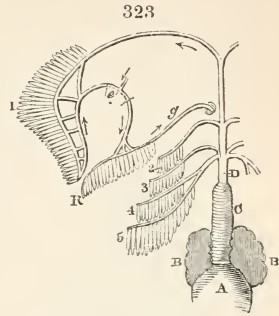
<sup>1</sup> These 'venæ nutritiæ' are unusually large in the *Carp*; but are not, as *Du Verney* supposed (CVIII.), directly continued from the true 'venæ branchiales;' and they do not, therefore, divert any of the stream of arterialised blood from the aorta to pour it directly into the venous sinus. See *Müller*, XXI. 1841, p. 28.

<sup>2</sup> CXI. CXII. CXIII.

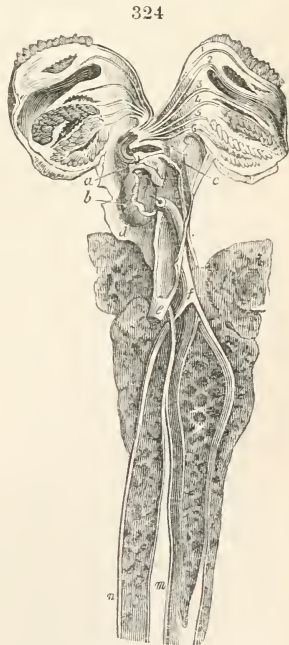
<sup>3</sup> The six-gilled Shark (*Hexanchus*) and the seven-gilled Shark (*Heptanchus*) are among the few exceptions.

the primary arterial arch, corresponding with the anterior or hyoid one, develops either a simple (uniserial) gill, or a plexiform, plumose, rudiment of a gill, or both, or neither. In the *Lepidosteus* this arch retains its primitive connection with the extremity of the branchi-arterial trunk, and develops on each side a small uniserial pectinated gill, fig. 323, 1, from the membrane clothing the inner surface of the cerato-hyoid and preopercular bones: the vein or efferent vessel, *e*, of this gill goes to a smaller pectinated organ, *ib. R*, consisting likewise of one series of vascular filaments, which agrees with the 'pseudobranchia' of other fishes in being supplied with arterial blood. In the Sturgeon, the *Lepidosiren*, and the Plagiostomes the representative of the primary vascular arch has become, by partial bifurcation of the branchi-arterial trunk, a secondary branch, sent off by the artery of the first branchial arch: but it nevertheless develops a simple gill, of one series of filaments in the *Lepidosiren*, fig. 324, 1, and of the anterior series of lamellæ in the first gill-bag of the Plagiostomes: and this series is attached, like the opercular gill of the *Lepidosteus* and Sturgeon, to the membrane supported by the hyoid arch.

In most Osseous Fishes we recognise the reduced homologue of the anterior primary vascular arch in that vessel, fig. 321, *e*, which is continued from the venous or refluxing division of the second primary vascular arch; not, as in the foregoing fishes, from the arterial division of that arch, or from the branchial trunk. The vessel in question carries, therefore, arterial blood: it manifests its primitive character by returning into the circulus aorticus, as at *e'*, fig. 321, but now receives blood from it, and is called 'arteria



Branchiæ and pseudo-branchia,  
*Lepidosteus*. XXII.



Respiratory and circulatory organs,  
*Lepidosiren annectens*. XXXIII.

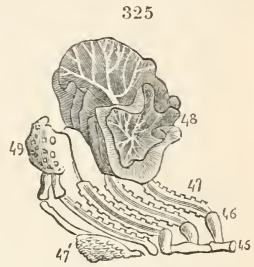
hyo-opercularis:’ the pseudo-branchia, when present, as at fig. 321, r, is developed from it.

In Osseous Fishes the four normal biserial pectinated gills are developed only from the four anterior branchial arches; the fifth and last arch has no gill developed from it, but is converted, as we have seen, into a pair of accessory jaws. In the *Lepidosiren*, as in *Hexanchus*, the fifth arch supports a uniserial gill, fig. 324, 6. In the *Planirostra*, although the branchial pecten is not developed from it, yet the same kind of long slender filamentary processes project inwards from its concavity, as from that of each of the anterior four pairs of branchial arches. The five interspaces between the hyoid arch and the five branchial arches are originally exposed on the sides of the head of the embryo osseous fish; the opercular and branchiostegal appendages are later developements, and the single branchial outlet is the result of the formation of the gill-cover. Thus the numerous branchial apertures in the cartilaginous fishes, like the substance of their skeleton, are retentions of embryonic structures. Very interesting arrests of development are also found in bony fishes. We have seen that the primary vascular hoops sweep over their respective arches without sending off any branches, the (subsequently) branchial veins being, in the embryo, direct continuations of the branchial arteries. This primitive condition is persistent in the fourth branchial arch of certain Muræoid fishes of the Ganges, *Monopterus*, *Symbranchus*;<sup>1</sup> it is persistent in the first and second branchial arches of the eel-like *Lepidosiren*, fig. 324. 2, 3. Such arches are, therefore, gill-less, and a certain proportion only of the blood transmitted from the heart is aerated in the gills: about one fourth, e. g. in *Monopterus*, goes directly to the aorta in its venous state; a larger quantity would pass into the roots of the aorta, fig. 312, o, o, and mix with the general circulation in the *Lepidosiren*, were no part of the current diverted by the vessels l, l', into the lung-like modification of its air-bladder.

A tuft of filaments, supporting each a single vascular loop, and covered with non-ciliate epithelium, extends from each branchial plate, protruding from the outer slit, in the embryo of the Plagiostomes; <sup>2</sup> and a similar tuft also extends from the spiracle in those species which possess it, e. g. *Mustelus* and *Acanthias*; but these preliminary branchial organs soon disappear.<sup>4</sup> Three seemingly analogous filaments are retained on each side, for a longer period, in the *Lepidosiren annectens*; but lose that vascular and

<sup>1</sup> CXIX.<sup>2</sup> XX. vol. v. p. 72.<sup>3</sup> LXIX. p. 88, pl. 14.<sup>4</sup> LXXXII. CXXV. CXIII. p. 97.

respiratory character before they are absorbed. Accessory respiratory organs, acting chiefly as a reservoir or filter of water,<sup>1</sup> are developed from the upper part of the pharynx in the Climbing Perch (*Anabas scandens*) and allied fishes of amphibious habits; they are complex folds of slightly vascular membrane supported on sinuous plates developed from the pharyngo- and epi-branchials of the anterior branchial arches, fig. 325, 48; whence this family of fishes is called *Labyrinthibranchii*. An accessory branchial ramified vascular organ is similarly situated in the genus thence called *Heterobranchus*. It resembles a miniature tree of red coral, is hollow and muscular, and serves not only for respiration, but, as Cuvier suggests, to aid in propelling the arterialised blood into the aorta. In the Cuchia (*Amphipnous*), a finless snake-like fish, which lurks in holes in the marshes of Bengal, the second branchial arch supports a few long fibrils, and the third a simple lamina fringed at its edge; the first and fourth arches have not even the rudiment of a gill. The branchial function is transferred to a receptacle on each side of the head, above the branchial arches, covered by the upper part of the opercular membrane; these receptacles have a cellular and highly vascular internal surface; the cavity communicates with the mouth by an opening between the hyoid and first branchial arch, and receives its blood from the terminal bifurcation of the branchial artery, and also from the efferent vessels of the rudimental gills. Those from the supplemental lung-like vascular sacs are collected into two trunks, which unite with the posterior unbranched branchial arteries to form the aorta. Thus about one half of the volume of blood transmitted from the heart is conveyed to the aorta without being exposed to the action of the air. This amphibious fish is, as might be expected, of a sluggish and torpid nature, and remarkable for its tenacity of life. The homologues of the superior branchial sacs extend in a Gangetic Siluroid fish, the Singio, beyond the cranium, backward beneath the dorsal myocommata upon the neural arches of the vertebræ to near the end of the tail, where they terminate in blind ends. The inner tunic of the sacs is a delicate vascular membrane, supplied by a continuation of the posterior branchial artery. The position of the palatal opening of the sac, in relation to the laminae of the



Branchial arches and labyrinthine reservoir, *Anabas*. XXXIII.

<sup>1</sup> CLXXIV, vol. iii. p. 372.



second and third arches, is such that water can with difficulty penetrate them, and they are usually found to contain air. They are not, however, the homologues of the air-bladder or of lungs, though they are analogous to the latter in function. By this extreme modification of the opercular gill the Singio (*Saccolabrus*, Cuv.) is enabled to travel on land to a great distance from its native rivers or marshes, and, like the Cuchia, is remarkable for surviving the infliction of severe wounds.<sup>1</sup> In most fishes a rich developement of follicles on the walls of the gill-chamber supplies the branchial machinery with a lubricating mucus.

The mechanism of branchial respiration differs from that of swallowing, only in the streams of water being prevented from entering the gullet, and being diverted to the branchial slits on each side the pharynx.

The mouth opens by the retraction of the premaxillary and the depression of the mandible. Almost simultaneously the mandibular rami are divaricated behind by the action of the 'levatori tympani,' fig. 134, 24, upon their pedicles; the opercular flaps are drawn outward by the 'levatori operculi,' ib. 25; the branchiostegal membrane is dilated by divarication of the rays, the 'levatori branchiostegarum,' fig. 135, 28, opposing the 'depressorii,' ib. *d*, in this action; the branchial arches are successively drawn forward and outward by the 'branchi-levatori,' fig. 137, 3, and 'mastobranchiales,' ib. 26; and the branchial chamber being thus expanded, the water rushes in through the sieve-like inner slits, and fills the chambers, floating apart the gills and filtering between every branchial process and fold. The inner slits are, then, closed by the protraction of the hyoid and depression of the branchial arches, the 'geniohyoidei,' fig. 135, cooperating with the 'branchi-depressorii,' fig. 137, 25, in this action; the branchial processes are approximated and divaricated by special muscles, and elastic parts. The respiratory currents are driven out by the contraction of the branchiostegal membranes and the depression and adduction of the opercular flaps, which, on the expulsion of the currents, close like a door upon the 'sill' formed by the scapular arch. In the Plagiostomes the branchial currents are moved and directed by muscles, combined with elastic structures, more immediately acting on the inner and outer slits and the intermediate chambers.

§ 85. *Arteries of Fishes.*—The first structure to be noticed in connection with the arterial system, is the vascular body already alluded to under the name of 'pseudobranchia.' *Mormyrus*, *Tinca*,

*Cobitis*, *Nandus*, *Silurus*, *Batrachus*, *Gymnotus*, *Muraenopsis*, and *Muraena* are examples of genera in which it has not been detected. In almost all other Osseous Fishes it is present, situated on each side of the head, in advance of the dorsal end of the first biserial gill, under the form either of a small exposed row of vascular filaments, like a uniserial gill (as in all Sciaenoids and many other *Acanthopteri*, the *Pleuronectidæ*, and the *Lepidosteus*, fig. 323, R); or, like a vaso-ganglionic body, composed of parallel vascular lobes, and covered by the membrane of the branchial chamber (as in *Esox*, *Cyprinus*, *Gadus*, fig. 321, R). In both cases the vein or efferent vessel of the pseudobranchia becomes the ophthalmic artery, ib. *h*, and the choroid 'vaso-ganglion,' when present, is developed from it. The Sturgeon, like the *Lepidosteus* and *Lepidosiren*, has a uniserial opercular gill, the homologue of the first so-called 'half-gill' of the Plagiostomes; and, on the anterior wall of the 'spiracular canal,' a small vascular lamellate body receives arterialised blood by a vessel sent off from the vein of the first biserial gill; which blood, after being subdivided amongst innumerable pinna-tifid capillaries is collected again into the efferent vessel of that body, and divides into the artery for the brain (encephalic), and that for the eye (ophthalmic). The pseudobranchia is thus a kind of 'rete mirabile' for both the cerebral and ophthalmic circulation in the Sturgeon<sup>1</sup>: in Osseous Fishes it stands in that relation to the eye only, and is most generally associated with the more immediate ophthalmic 'rete mirabile,' called 'choroid gland,' fig. 216, *o*. The pseudobranchia, in the Plagiostomes that have the spiracula, is developed, as in the Sturgeon, on the anterior wall of each of those temporal outlets from the branchial cavity: its 'vena arteriosa' supplies the eyes and part of the brain: it coexists in the Plagiostomes, Chimæroids, Sturgeons, and some Osseous Fishes, with the vaso-ganglion supplied by vessels from the anterior branchial veins, which lies between the anterior basi-branchials and the sternohyoid muscles. Besides the small nasal and orbital arteries, and the hyo-opercular, from which the proper ophthalmic artery is derived, the carotids are usually sent off from the 'circulus aorticus.' In the Chimæra the carotids are transmitted directly from the anterior branchial veins; and, in the Pike, the artery of the pectoral fins (brachial) is transmitted from the common trunk of the two anterior branchial veins. In the Myxines an anterior, as well as a posterior, aorta is continued from the common confluence of the branchial veins. In all higher fishes the posterior aorta is the only systemic trunk so formed.

<sup>1</sup> XXI. pp. 41-67, 75.

This aorta extends beneath the bodies of the vertebræ along the abdomen and through the hæmal canal to the end of the tail. In many Cyprinoid fishes it dilates beneath each abdominal vertebra into a sinus. It gives off intercostal arteries, which in many adult fishes become fewer in number than the intercostal spaces; it supplies numerous small branches to the kidneys. In the Syngnathi the aorta grooves the kidney in its course, and in the Anchovy sinks into the renal substance. The first principal visceral branch is the 'cæliac;' which sometimes, as in the Burbot, is sent off from the posterior part of the 'circulus aorticus,' and in some Sharks by two trunks from the same part. The next branch is a posterior mesenteric, which varies in size according to the extent of the intestinal canal supplied by the cæliac. Between these, in some fishes, the brachial arteries are sent off from the abdominal aorta: these vessels in the large-finned Torpedos and Chimærae have a partial investment of muscular fibres, like secondary bulbs, but without any valvular structure to give effect in onward flow to their action.<sup>1</sup>

In the Porbeagle Shark (*Lamna cornubica*) the two cæliac arteries each split into a bundle of small arterioles, which interlace with a similar resolution of the hepatic veins to form a mixed fasciculate 'plexus mirabilis' between the pericardial septum and the liver. The arterial blood is collected again into a trunk on the outer side of each plexus; and is distributed by the ramifications of those trunks in the ordinary way to the stomach and intestines.<sup>2</sup> The arterial branches to the spiral valve in the Fox Shark are remarkable for the rich bundles of twigs by which they distribute the blood to that production. In the Mediterranean Tunnies (*Thynnus* and *Auxis*) the branches of the cæliaco-mesenteric artery sent to the stomach, the pancreas and the intestines, severally split up into similar fasciculate plexuses, which are interlaced with corresponding plexuses of the veins from those viscera prior to the formation of the portal trunk.

But the most common modification of the visceral vascular system is the sudden division and termination of a branch, usually of the gastric artery, in a small body chiefly composed of the cellular beginnings of the returning veins, forming the vasoganglion so constant in all higher Vertebrates, and called the 'spleen,' fig. 276, *n*; fig. 281, *g*. It is not present in the Lancelet; and the gland-like bodies near the cardia in the Cyclostomes, and near the pylorus in the Lepidosiren, which some have called 'spleen,' are more like the recognised remnants of the vitellicle in Osseous Fishes, where a true spleen is actually present. The

<sup>1</sup> xcviij.

<sup>2</sup> xxi. p. 99, pl. 5.

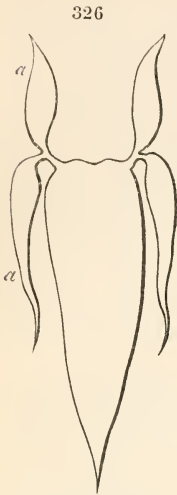
vein of the spleen always contributes to form the 'vena portæ;' but it is important to note that it is not essential to the formation of that vessel. The absence of the spleen in fishes is concomitant with the absence of the pancreas; and the increased size and complexity of the spleen is associated in some fishes with a corresponding development of the pancreas. Thus there is an accessory spleen in the Sturgeon; and the spleen is divided into numerous distinct lobules in Lamna, Selache, fig. 278, *d*, and some other highly organised Plagiostomes. In most Osseous Fishes the spleen is appended by its vessels, and a meso-splenic fold of peritoneum to the hinder end or bend of the stomach, or to the beginning of the intestine: it is of variable but commonly triangular shape; of a deep red or brown-red colour, and soft and spongy: the venous cells of which it is chiefly composed are filled with granular corpuseles.

§ 86. *Air-bladder of Fishes.*—The organ so denominated is found, in most Osseous Fishes, in the form of an elongated bladder, tensely filled by air, extending along the back of the abdomen, between the kidneys and the chylopoietic viscera, fig. 281, *k*, and sometimes (*Gymnotus*, fig. 233, *d*, *Ophiocephalus*, *Coius*) beneath the caudal vertebræ to near the end of the tail. It is sometimes bifurcate (as we see it in most Scomberoids and Carangoids,<sup>1</sup> in some species of *Diodon*, *Tetrodon*, of *Dactylopterus*, *Pimelodus*, *Prionotus*); seldom divided lengthwise into two bladders (*Arius*, *Gagora*, *Polypterus*, *Lepidosiren*, fig. 324, *p*, *p*): more often divided crosswise into two compartments, which intercommunicate by a contracted orifice (*Cyprinidæ*, fig. 229, *p q*, *Characinidæ*), or are quite separate (*Bagrus filamentosus*, *Gymnotus equilabiatus*). In the Siluroid genus *Pangasius* the air-bladder is divided into four longitudinally succeeding portions. In the *Trigla hirundo* the swim-bladder is notched anteriorly by one indent, and posteriorly by two indents, from which notches septa project inwards: sometimes the air-bladder is divided partially, both lengthwise and crosswise (*Cobitis fossilis*, *Auchenipterus furcatus*, some species of *Pimelodus*). Sometimes the bladder sends forward two blind processes from its forepart (*Sphyræna barracuda*, *Trigla cuculus*, *Conodon antillanus*, some species of *Micropogon* and *Otolithus*); sometimes from its hind part (*Cantharis vulgaris*, *Lethrinus atlanticus*, *Heliases insolatus*, some species of *Sillago*, *Mæna*, and *Smaris*); sometimes from both ends (*Dules maculatus*, *Pimelipterus*

<sup>1</sup> Dr. Günther tells me that all the species of these families with a short and elevated body, with a short abdominal cavity, and with strong first hæmal and inter-hæmal spines, have the air-bladder bifurcate behind, extending backward between the muscles of the tail, to or beyond the middle of its length.



*altipennis*, *Lactarius delicatulus*). *Corvina trispinosa*, fig. 326, has two slender caecal processes from each side of its air-bladder; the Bearded Umbrina has three such processes; the allied 'Maigre' and other species of *Sciæna*, with most of the *Corvinae*, have very numerous lateral pneumatic caeca, which, as in *Johnius lobatus*, fig. 327, are more or less ramified.<sup>1</sup> In some species of *Cheiloneurus* and *Gadus* blind processes are continued from both the sides and ends of the air-bladder (see the anterior ones in *Gadus callarias*, fig. 321, A, p). In *Gadus Navavaga* the lateral productions expand, and line corresponding expansions or excavations of the abdominal parapophyses, thus foreshadowing the pneumatic bones of birds. In *Kurtus* the air-bladder is encircled by expanded ribs, curving and meeting below it.<sup>2</sup>



Air-bladder, *Corvina trispinosa*

layers fig. 229, *q r*; they are contractile and elastic; but the walls of the



Air-bladder, *Johnius lobatus*

anterior compartment of the air-bladder of Cyprinoids, *ib. p.*, are much more elastic than those of the posterior one. The air-bladder is lined by a delicate mucous membrane, with a 'plaster epithelium'; it is more or less covered by the peritoneum. Its cavity is commonly simple; in the Sheat-fish it is divided by a vertical longitudinal septum along three-fourths of its posterior part.<sup>3</sup> The lateral compartments are subdivided by transverse septa in many other Siluroids (e. g. genus *Bagrus*): the large air-bladder of some species of *Erythrinus* (e. g. *E. salvus*, *E. taniatus*) is partially subdivided into smaller cells. The cellular subdivision is such in the air-bladder of the *Amia*, that Cuvier compared it to the lung of a reptile<sup>4</sup>; and the transition from the air or swim-bladder

<sup>1</sup> XXXIX. i. p. 94, after Cuvier and Valenciennes, xxiii. pl. 138, 139. The most complex form is that described by Günther (CLXXIV, vol. ii. p. 313) in *Collichthys lucida*, where the air-bladder forms a second investment of the abdominal viscera, within the peritoneum.

<sup>2</sup> CLXXIV. vol. ii. p. 10. <sup>3</sup> CXVI. vol. ii. p. 33, pl. 6, fig. 4. <sup>4</sup> XXIV. vol. ii. p. 377.

to the lung is completed in the *Lepidosiren*, in which the cellular subdivision and multiplication of the vascular surface are combined with a complete bilateral partition of the bladder into two elongated sacs, with a supply of venous blood from a true pulmonary artery, and with the communication of the ductus pneumaticus, as in the *Polypterus*, with the ventral surface of the œsophagus.

At the first introduction into the Animal Kingdom of a true lung, or air-breathing organ communicating with the pharynx or œsophagus, much variety of form and structure, much inconstancy even as to existence, might be expected, especially in that class in which the normal function of the new organ could be so seldom in any degree exercised, and in which, therefore, different accessory or subordinate offices predominate in such rudimental representative of the pulmonary organ. There is no swim-bladder, for example, in the orders *Dermopteri*, *Holocephali*, and *Plagiostomi*; it is present in one of the families (*Gadidæ*) of the thoracic sub-order of *Anacanthini*, and not in the other family (*Pleuronectidæ*); here we can associate its absence with the peculiar flattened form and grovelling habits of the species. In like manner we may account for the absence of the air-bladder in the Angler (*Lophius*), which habitually keeps the sea-bottom: but the mechanical explanation of the absence or rudimental condition of the swim-bladder is not so obvious in regard to the Acanthopterous genera *Percis*, *Percophis*, *Eleginus*, *Auxis*, *Trachypterus*, and *Gymnetrus*. A large and often complex air-bladder exists in most of the Siluroid fishes; but the genera *Loricaria*, *Rhinelepis*, and *Hypostoma* are exceptions in that family, having no air-bladder. What is more inexplicable is, that while some species of the same genus, *Polynemus* and *Scomber* for example, have a large swim-bladder, others want it, or have it of extremely small size.

The variation in respect to the presence or absence of an air-duct (*ductus pneumaticus*) is expressed in the characters of the orders in the Classification of Fishes, pp. 10—12. The duct, which is shown by its place of communication with the beginning of the œsophagus, and by the rudimental larynx, in *Polypterus* and *Lepidosiren*, fig. 316, *e*, to be the homologue of the trachea of air-breathing Vertebrates, is a simple and delicate membranous tube; but it presents considerable variation in its length, diameter, and place of communication with the alimentary tract. In the Herring the ductus pneumaticus is produced from the posterior attenuated end of the cardiac division of the stomach, fig. 281, *i*, and opens into the fusiform air-bladder at the junction of the

middle and posterior thirds of that organ.<sup>1</sup> The long, narrow, and flexuous ductus pneumaticus is continued from the forepart of the posterior division of the air-bladder in the Cyprinoids, and opens into the dorsal part of the œsophagus, fig. 229, *su*: the short, straight, and wide ductus pneumaticus, in the *Lepidosteus*, opens also into the dorsal part of the œsophagus, the orifice being served by a sphincter: in the *Erythrinus* the air-duct communicates with the side of the œsophagus; in *Polypterus*, as in *Lepidosiren*, with the under or ventral part of the beginning of the œsophagus.<sup>2</sup>

The principal seat of the vascular ramifications in the air-bladder, like that in a true lung, is the mucous lining membrane; but the modes of ramification in the primitive piscine form of the air-breathing organ are as variable as any of its other properties. The arteries of the air-bladder are derived sometimes directly from the abdominal aorta, sometimes from the cœliac 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, fig. 312, *l'*, and therefore convey venous blood to the cellular, lung-like, double air-bladder. 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*, *ib. p'*, they penetrate, by a common trunk, the great post-caval vein, *ib. e*, formed by the confluence of the visceral and vertebral veins of the trunk; but instead of terminating there, the pulmonary venous trunk passes forward, through the sinus and auricle, to the entry into the ventricle, and there terminates above the valvular cartilaginous tubercle. Thus the aerated blood from the lungs enters the ventricle directly, instead of being previously mixed with the venous blood in the auricle.

The vascular system of the lung-like air-bladders of the Protopteros and Ganoid Fishes forms no 'retia mirabilia' or vaso-ganglions, but resolves itself into a generally diffused reticular capillary system, which is much richer and closer in the more subdivided and thicker cellular structure of the anterior than of the posterior parts of the bladders in the *Lepidosiren*.

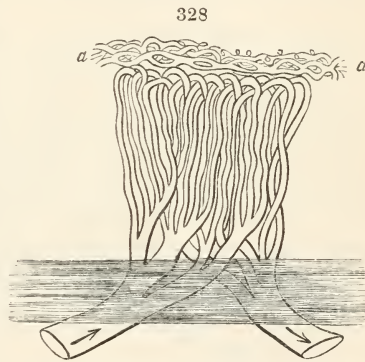
In the Osseous Fishes the principal forms of the terminal divisions of the arteries of the air-bladder are as follows:—1. A resolution of the smaller ramifications into fan-like tufts of capillaries over almost every part of the inner surface (*Carp*). 2. The formation of similar, but larger and more localised,

<sup>1</sup> cxiv. vol. ii. pl. viii. fig. 1.

<sup>2</sup> xxi. 1841, p. 194.

radiating tufts (Pike); in both without any special aggregation of the capillaries to form a 'vaso-ganglion.' 3. The conversion of the tufts by rapid subdivision into capillaries aggregated so as to form red gland-like bodies; the capillaries reuniting into larger vessels, which again ramify richly round the border of the gland-like body; the rest of the inner surface of the air-bladder having the ordinary simple capillary system (Perch and Cod). 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 swim-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 together, and the venules as frequently anastomose with each other: both are inextricably interwoven, and form the basis of the so-called 'air-gland,' which is essentially a large 'bipolar rete mirabile,' or vaso-ganglion. The ultimate

vessels of this body form loops, where the arteries return into veins, fig. 328, and these loops are covered by a layer of vessels and epithelium, *a, a*. This organ, however, is further composed of a number of peculiarly arranged, elongated corpuseles, which depend in two rows from each vascular branch, and are bound together by a loose cellular tissue: the corpuseles are beset with fine villiform processes. The blood returns from the vaso-



Superficial and looped vessels of the vaso-ganglion  
air-bladder, Cod. CCLXVIII.

ganglions by small veins which rarely accompany, more commonly cross, the arteries. 4. The two chief 'retia mirabilia,' or vaso-ganglions, in the air-bladder of the Eel and Conger, which are situated at the sides of the opening of the air-duct, are also 'bipolar,' and consist of both arterioles and venules: they consist of straight parallel capillaries, as in fig. 329: their efferent trunks do not ramify in the immediate margin of the vaso-ganglion from which they issue, as in the vaso-ganglions of the Cod, Burbot, Acerine, and Perch, but run for some distance before they again branch to form the common capillary system of the lining membrane of the air-bladder.

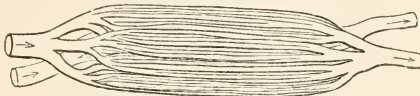
Rathk<sup>1</sup> failed to detect the opening of the air-duct with the

<sup>1</sup> cxi. 'Ueber die Schwimm-blase einiger Fische,' p. 98.



oesophagus in the Eel; but De la Roche had well described the oblique aperture,<sup>1</sup> and accurately cites the whole family of the Eels as fishes having both the so-called 'air-gland' and the pneumatic duct. It had been supposed that the vascular 'air-gland' was present only in those fishes which could not derive the gaseous contents of their swim-bladder from without; and unquestionably in those fishes which have the shortest and widest ducts (Sturgeon, *Amia*, *Erythrinus*, *Lepidosteus*, *Lepidosiren*, *Polypterus*) the supposed air-secreting vaso-ganglions are not developed. Since Professor Magnus has determined the

329



Parallel vessels of the vaso-ganglion of the air-bladder,  
Eel. CCLXVIII.

existence of free carbonic acid gas, of oxygen, and of azote in the blood, and dissolved in different proportions in the venous and the arterial blood, it may be readily conceived that the

venules of the vaso-ganglions may withdraw carbonic acid gas from the arterioles, and that these may reach the inner surface of the air-bladder richer in oxygen and poorer in carbonic acid than when they penetrated the vaso-ganglions.<sup>2</sup>

The air-duct may allow the gas to escape under certain circumstances; and the small size and obliquity of its orifice in many Osseous Fishes (Carp, Eel) seem only to adapt it to act as a safety-valve against sudden expansion of the gas when the fish rises to the surface:<sup>3</sup> but in the higher organised species above-cited, with short and wide air-ducts, these may, likewise, convey air to the bladder.

The contents of the air-bladder consist, in most freshwater-fishes, of nitrogen, and a very small quantity of oxygen, with a trace of carbonic acid gas: but in the air-bladder of sea-fishes, and especially of those which frequent great depths, oxygen predominates.<sup>4</sup>

In the genera *Auchenipterus*, *Synodon*, *Malapterurus*, and some other Siluroids, the axis vertebra sends out on each side a slender

<sup>1</sup> cxvii. p. 201. <sup>2</sup> xxi. 1841, p. 98. See also Dr. J. Davy, in Phil. Trans. 1838.

<sup>3</sup> Neither the air-duct nor the elasticity of the air-bladder are equal to prevent the consequences of a too rapid removal from the enormous pressure which fishes sustain at great depths in the sea; those that are drawn up quickly by the hook are often found to have the air-bladder ruptured, and sometimes the stomach is protruded from the mouth by the pressure of the suddenly extricated and expanded gas.

<sup>4</sup> Humboldt found the gas in the air-bladder of the electric *Gymnotus* to consist of 96° of nitrogen and 4° of oxygen. Biot found 87° of oxygen in some of the deep-sea Mediterranean fishes, the rest nitrogen, with a trace of carbonic acid. No hydrogen has ever been detected in the air-bladders of fishes.

process, which expands at its end into a large round plate: this is applied to the side of the air-bladder, and can be made to press upon it, and expel the air through the duct by the action of a small muscle arising from the skull. In some species of *Gadus* muscular fibres extend from the vertebral column upon the air-bladder. The nerves of the air-bladder are derived from the vagus after it has received organic fibres from the sympathetic, fig. 229, *t*.

Viewing the general modifications and relations of the air-bladder throughout the class of Fishes, we cannot but discern and admit, notwithstanding some seeming capricious varieties, that its chief and most general function is a mechanical one, serving to regulate the specific gravity of the fish, to aid it in maintaining a particular level in its element, and in rising or sinking as occasion may serve. The general law of its absence in the parasitic and suctorial *Dermopteri*, and in all ground-fishes, as the *Pleuronectidæ* and Ray-tribe, supports the above conclusion. Borelli<sup>1</sup> found that those fishes whose air-bladders were burst sank to the bottom and were unable to rise. Nor does the absence of the air-bladder in the surface-swimming Sharks militate against this view of its physical function: for though the air-bladder serves, it also enslaves. It opposes, for example, those Fishes that possess it in their endeavours to turn on one side, and it demands a constant action of the balancing fins to prevent that complete upsetting of the body which it occasions from the weight of the superimposed vertebral column and muscles when life and action are extinct. The Sharks require, by the position of their mouth and in their common pursuit of living prey, freedom in turning and great variety as well as power of locomotion: if they are not aided by a swim-bladder, neither are their muscular exertions impeded by one; whilst their swimming organs acquire that degree of developement and force which suffices for all the evolutions they are called upon to perform. With regard to the accessory offices of the air-bladder in relation to the sense of hearing, the chief of these remarkable modifications by which it is brought into communication with the acoustic labyrinth have been already described, p. 344. In a few genera (*Trigla*), the air-bladder and its duct are subservient to the production of sounds.

Under all its 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 upon the air-bladder,

<sup>1</sup> CXXXI. cap. 23.

by which it becomes also analogous in function to the lungs of the air-breathing Amphibia.

The *Lepidosiren annectens*<sup>1</sup> inhabits a part of the river Gambia, which in the rainy season overflows extensive tracts, that are again left dry in the dry season. Those which do not follow the retreating waters escape from the scorching rays of the African sun by burrowing in the mud, which is soon baked hard above them; but they maintain a communication with the air by a small aperture, and, coiling themselves up in their cool chamber, clothe themselves by a layer of thick mucous secretion, and await, in a torpid state, the return of the rains and the overflowing of the mud-banks. The advent of their proper element wakes them into activity: they then emerge from the softened mud, swim briskly about, feed voraciously, and propagate.

The peculiar modifications of the gills and air-bladder of the *Lepidosiren* are precisely those which adapt them to the peculiar conditions of their existence. In the inactive state into which they are thrown by their false position as terrestrial animals, the circulation, which would have been liable to be stopped had all the branchial arteries developed gills, as in normal fishes, is carried on through the two persistent primitive vascular channels, fig. 312, 2 and 3. Whatever amount of respiration was requisite to maintain life during the dry months is effected in the pulmonary air-bladders; its short and wide duct or trachea, the œsophageal orifice of which is kept open by a laryngeal cartilage, fig. 316, *f*, introduces the air directly into the bladders: the blood transmitted through the branchial arches to the pulmonary arteries, fig. 312, *l*, is distributed by their ramifications over the cellular surface of the air-bladders; and is returned arterialised by the pulmonary veins, *ib. p, p'*. A mixed venous and arterial blood is thence distributed to the system, and again to the air-bladders. True arterial blood exists only in the pulmonary veins, and unmixed venous blood only in the system of the venæ cavæ; whence the necessity, apparently, for that peculiar arrangement by which the arterial blood is conveyed directly to the ventricle by the pulmonary vein. When the *Lepidosiren* resumes its true position as a fish, the branchial circulation is vigorously resumed, a larger proportion of arterialised blood enters the aorta, and both the nervous and muscular systems receive the additional stimulus and support requisite for the maintenance of their energetic actions.

Anatomists and physiologists have expressed different views as to the homologies and analogies of the respiratory organs of

fishes. Indeed the essential distinction of those relations has seldom been clearly kept in view. When we read in the latest edition of the Comparative Anatomy of Cuvier: 'the gills are the lungs of animals absolutely aquatic;'<sup>1</sup> and, with regard to the cartilaginous or osseous supports of the gills, 'they are in our opinion, to the gills of fishes, what the cartilaginous or osseous tracheal rings are to the lungs of the three superior classes:'<sup>2</sup> we are left in doubt whether it is meant that the gills and their mechanical supports merely perform the same function in Fishes which the lungs and windpipe do in Mammals, or whether they are not also actually the same parts differently modified in relation to the different respiratory media of the two classes. Geoffroy St. Hilaire leaves no doubt as to his meaning where he argues that the branchial arches of fishes are the modified tracheal rings of the air-breathing classes; we perceive that he is enunciating his belief in a relation of homology. The truth of his proposition will be best tested by first considering the homologies of the air-bladder of fishes. In the *Lepidosiren* the notochord, the parapophyses, the attachment of the scapulæ to the occiput, the branchiostegal covering of the permanent gills, the opercular bones, the presence of a spiral intestinal valve, the relative position of the anus, the extra-oral nasal sacs, the scaly integuments, the mucous tubes on the head, the 'lateral line,' in short, the totality of the organisation of the *Lepidosiren*, exemplify its fundamental ichthyic nature. It is extremely interesting to find the Ganoid *Polypterus*, which of all osseous fishes most closely resembles the *Lepidosiren* in its spiral intestinal valve, in the bipartition of the long air-bladder, the origin of the arteries of that part, and the place and laryngeal mode of communication of the short and wide air-duct or windpipe, also presenting the closest agreement with the *Lepidosiren* in the important character of the form of the brain. The common objection to the view of the air-bladder of fishes being the rudimental homologue of the lungs of air-breathing Vertebrates has been, that the artery of the air-bladder carries arterial blood, that of the lungs venous blood. But in the *Polypterus* and *Lepidosiren*, in reference to this character, the arteries of air-bladders are derived from the returning dorsal portions of the branchial vascular arches before their union to form the aorta. In the

<sup>1</sup> 'Les branchies sont les poumons des animaux absolument aquatiques.' (XIII. t. vii. p. 164.)

<sup>2</sup> 'Elles sont, à notre avis, aux branchies des poissons, ce que les cerceaux cartilagineux ou osseux des voies aériennes sont aux poumons des trois classes supérieures.' (Ib. p. 177.)



Polypterus the artery of each air-sac is formed by the union of the efferent vessels of the last gill: the blood is, therefore, arterialised before entering the artery of the air-sac. In the Lepidosiren, by reason of the non-developement of gills on two of the branchial arches, the blood transmitted to the air-sac is venous. But this difference relates only to the presence or absence of a particular developement of the branchial vascular arches, from which the air-bladders of the two species are supplied with blood: it is a difference which modifies the function without at all changing the essential nature of the air-bladders themselves: the relative position of these vascular sacs, their form and size, their mode of communication with the œsophagus,—in short, every character by which relations of homology are determined,—are the same in both Polypterus and Lepidosiren.<sup>1</sup> The lungs of the Lepidosiren being, then, unequivocally the homologues of the air-bladder of the Polypterus, it follows that they must be homologous with the air-bladders of other fishes, whatever be the modifications of form or function of such air-bladders. Between the completely divided air-bladder of the Polypterus and the undivided air-bladder of the Lepidosteus there are numerous degrees of bifurcation in the series of fishes: it is to the undivided state of the air-bladder in the Lepidosteus that its more strictly dorsal position, and its communication with that aspect of the œsophagus, are due: these modifications, however, do not affect its relation of homology with the divided air-bladder of the allied genus Polypterus, any more than with the divided air-bladders of the *Cobitis barbatula* or *Arius gogora*, in which the divisions are confined to the fore part of the abdomen, and are inclosed in osseous cups developed from anterior trunk-vertebræ. Thus, the series of transitions traceable in the air-bladders of fishes proves those of the Lepidosiren to be the homologous organs; whilst the developement, relative position, and connection of the lungs of the Batrachia equally prove those lungs to be the homologues of the air-bladders of the Lepidosiren. Consequently, the air-bladder of the Fish is homologous with the lungs of the Batrachian and of all air-breathing Vertebrates; although the air-bladder of the fish does not perform the function of a lung, but is analogous to the air-chambers in the Nautilus shell.

§ 87. *Blood of Reptiles.*—The blood of Reptiles has red corpuscles of a flattened sub-biconvex elliptical shape; proportionally smallest in *Ophidia*, roundest in *Chelonia*, and largest in *Batrachia*:

<sup>1</sup> Compare xxxiii. pl. xxvii. figs. 3 and 4, with xxv. pl. ii. figs. 5 and 6, and fig. 54, xxxiii. p. 182, with xxv. pl. ii. fig. 7.

in these the size is greater in the ratio of the persistence of the branchial apparatus; and the perennibranchiates present the biggest blood-discs absolutely, as well as in proportion to the size of the body, of all vertebrate animals. The two extremes in the relative size of the blood-discs in pulmonated *Hematoerya* are shown in those of a Crocodile, which was twenty feet in length, p. 4, fig. 8, *e*, and in those of a *Siren lacertina*, which was two feet in length, *ib. f*. The latter, which are just visible to the naked eye, serve to demonstrate the highly refractive divisions of the nucleus, and the nuclear capsule.<sup>1</sup>

There is less blood in cold-blooded than in warm-blooded animals, and more blood in some fishes, the Tunny, e. g., than in any reptile. Dr. Joseph Jones<sup>2</sup> estimates the average quantity of blood to be:—

In Serpents . . . .	$\frac{1}{10}$ to $\frac{1}{13}$	of the weight of the body.
<i>Emys terrapin</i> . . . .	$\frac{1}{11}$ to $\frac{1}{14}$	” ”
<i>Emys serrata</i> . . . .	$\frac{1}{13}$ to $\frac{1}{16}$	” ”
<i>Testudo polyphemus</i> . . . .	$\frac{1}{14}$ to $\frac{1}{17}$	” ”

Blood drawn from a living Batrachian is of a purplish red colour, and coagulates into a clot including the discs, floating in clear serum. The clot is firmer than that of fishes, but less firm than in allantoic reptiles; in a few hours the clot dissolves and liberates the discs. In the recently drawn blood of *Chelonia* most of the discs settle at the bottom of the vessel, and are not included in the clear clot which forms above them. The fibrin in this clot speedily passes into albumen. The colour of the serum in most reptiles, e. g. *Batrachia*, *Ophidia*, *Crocodilia*, and some *Chelonia* (*Testudo polyphemus*), is a light yellow: in many carnivorous *Chelonia* (*Emys serrata*, *E. reticulata*, *E. terrapin*), it is of a golden colour. When treated with a drop of sulphuric acid, and gently heated, the peculiar smell of the species, due, e. g. in the Alligator, to the musk-glands, and in the Rattlesnake to the anal glands, is plainly developed.

The blood of *Ophidia* contains the greatest proportion of solid constituents, in the cold-blooded Vertebrates.<sup>3</sup>

§ 88. *Veins of Reptiles*.—The capillary blood-vessels having a calibre proportionate to the diameter of the blood-discs which flow along them in single file, are largest in the *Batrachia*, in which class the best examples are afforded for demonstrating to

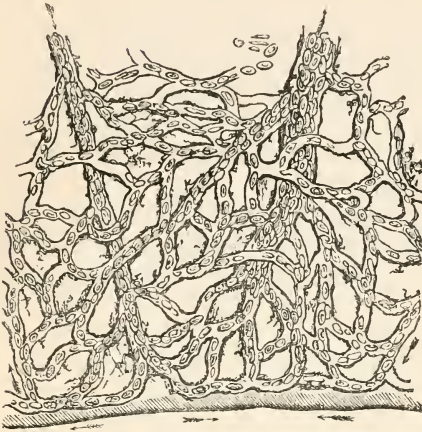
<sup>1</sup> CCLXXIII. and CCLXXIV.

<sup>2</sup> CCXLV.

<sup>3</sup> Dr. Joseph Jones, from whose excellent and original work (CCXLV.) most of the above particulars are taken, suggests that the richness of the ophidian blood may be due to the fact of serpents seldom, if ever, drinking. The comparatively unimportant details of the diameters of reptilian blood-discs may be seen in CCXXXIX, tome i. p. 89.

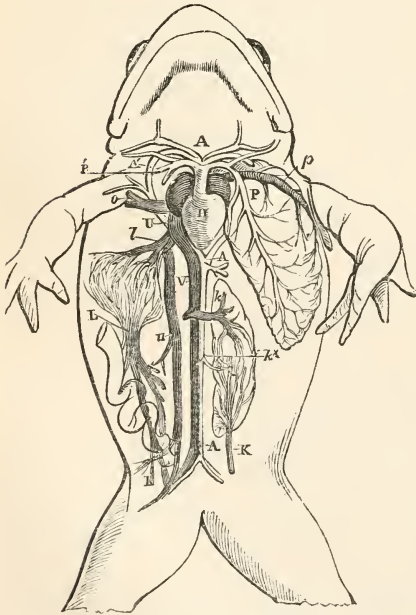
the eye the circulatory motion of the blood, flowing constantly from the arteries to the veins, as seen, e.g. by transmitted light in a membranous part of the frog's or newt's structure, under the microscope, fig. 330.

330



Capillaries with blood-discs of the web of the foot, Frog, magn. CCLXVII.

331



Circulation in the Frog. CCLXVII.

The venous system of Batrachians resembles that of Fishes in the degree in which the species retain the piscine character. The cardinal veins, essentially those which return the blood from the osseous and muscular segments of the trunk, are largest in the Perennibranchs, and decrease, as the hind-limbs acquire more size and power, in the Newts and Land-Salamanders, until, in the tail-less and long-legged Frogs and Toads, the primitive venous trunk of the body is reduced to the condition of the 'azygos' vein in Mammals, and the great bulk of the blood is submitted to the influence of the kidneys and liver before it is returned to the heart.

In the Frog, fig. 331, the blood being collected from each hind-limb into an ischiadic and iliac vein, these unite into a common iliac vein, which divides. One branch joins that of the opposite iliac, and receives the vein of the great allantoic bladder, to form the

'umbilical vein,' fig. 331, *u*: the other branch, *k*, goes to the

kidney of its own side. It inclines to the outer border of the gland, and divides into two branches, which ramify in the renal tissue. The vein of the genital glands and conduits, and a vein from the lumbo-dorsal segments, also enter and ramify in the kidneys. The blood of this 'reni-portal' system is collected into a sinus at the inner border of each gland, and is conveyed by the vein, *k*, into the postcaval trunk, *v*. The umbilical vein ascends along the ventral aspect of the abdomen, attached to the mid-line of the muscular walls of the cavity: as it approaches the liver it sends branches which penetrate directly the hepatic tissue, and a branch which receives the veins of the intestines, spleen, and stomach; but, before completing the portal system, *L*, it sends a small vein directly to the postcaval, near the auricle. The hepatic vein, *l*, joins the postcaval trunk, *v*. The blood from the head and fore-limbs is collected into a right and left jugular and axillary trunk, which unite to form a precaval vein, *o*, on each side. The postcaval vein, in the Perennibranchs, after receiving the renal veins, is suspended by a duplicature of peritoneum to the back of the abdomen, the fold being continued from the vein to the mesentery: it enters a groove or canal in the liver, and receives the hepatic veins and the left precaval, before terminating in the auricular sinus. There are a few valves in the venous trunks of *Batrachia*; but their chief characteristic is the presence of 'striped fibre' in the muscular coat.<sup>1</sup> This is associated with the faculty of rhythmical pulsation in the postcaval, axillary, and iliac trunks, independently of the pulsations of the heart.<sup>2</sup> The abdominal venous trunks traverse wide lymph-reservoirs; and their exterior is here and there roughened by little vascular loops, floating in the lymph, but communicating exclusively with the mother-vein.<sup>3</sup>

In *Ophidia* the cutaneous veins of the trunk and intercostal veins communicate with a large abdominal vein which runs along the under part of the abdominal walls, and answers to the umbilical vein in *Batrachia*. The caudal vein bifurcates on entering the abdomen, each division after receiving blood from the genital ducts and contiguous intestine, attaches itself to the kidney, and ramifies upon its several overlapping lobes: the efferent renal veins unite to form a trunk, which, on emerging from the inner and fore-part of the kidney, joins its fellow to form the postcaval vein. The veins of the intestinal canal, genital glands, and fatty appendages, which have not contributed to the reni-portal system, unite with those of the pancreas and spleen to form the hepato-

<sup>1</sup> CCLXXVII.<sup>2</sup> CCLXX.<sup>3</sup> CCLXXVII.

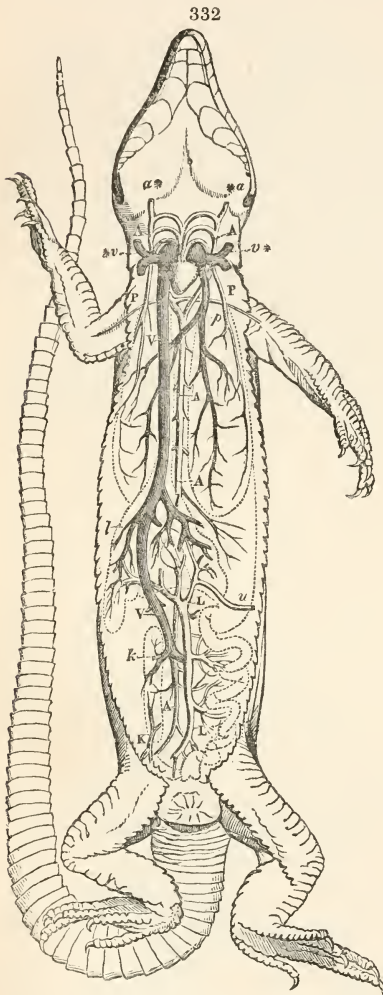


portal vein: this dilates and describes a spiral curve on entering the liver, and has a valvular structure ensuring the onward flow of blood to the elongated gland, during the compression exercised in the contortions of the Snake. The hepatic veins enter the

postcaval, and this large trunk terminates in the hind end of the long auricular sinus.

The blood from the head and fore-part of the body is returned to the fore-part of the sinus by a jugular vein and an inferior azygos vein, each of which has a pair of valves at its termination: and by a superior azygos vein, which has three valves at its termination: there is a fourth vein, answering to the left precaval, which passes behind the left auricle to terminate in the right sinus auriculæ near the postcaval orifice: it receives the coronary vein before its termination.

In Lacertians the blood from the hind limbs is partly conveyed by a reni-portal vein, fig. 332,  $\kappa$ , to the kidneys, and partly by a trunk, which communicates with the caudal vein to an umbilical or sub-abdominal vein,  $L$ : this, as it advances, collects blood from the ventral walls of the trunk, and receives a recurrent thoracic vein: it then communicates with the trunk of the gastro-intestinal, pancreatic, and splenic veins,



Circulation in a Lizard (*Lacerta ocellata*). CCLXVII.

to form the great portal vein which penetrates the liver. The renal veins,  $k$ , unite to form the postcaval,  $v$ , which afterwards receives the hepatic veins, and proceeds to the auricular sinus. A small cardinal or azygos vein, returning part of the blood from the tail, advances along the back part of the abdominal

cavity, receiving the segmental or vertebral veins, and terminates in the left precaval vein. The jugular and the axillary trunks unite to form a precaval vein, fig. 332, *v*<sup>\*</sup>, on each side, the left of which as usual passes behind the auricles to the postcaval orifice of the sinus.

In the *Chelonia* the blood from the tail and hind limbs is conveyed along the plastron by a pair of 'umbilical' or sub-abdominal trunks, which receive the veins of the large allantoic bladders, and the meseraic veins, to form the great portal trunk. A small derivative branch from the posterior part of each umbilical communicates with lumbo-dorsal vertebral veins, and with some veins from the genital organs to form the reni-portal veins. The renal veins unite with the ovarian or testicular veins to form the postcaval, which traverses the liver and receives there the hepatic veins: the wide and short trunk, fig. 336, *v*, then terminates in the auricular sinus. The blood is returned from the head and fore-limbs by the jugulars, figs. 302 and 304, *i, i*, and from the axillary veins, *ib. h, h*. Each axillary unites with the jugular of its own side to form a precaval vein: the right and left precavals enter separately the auricular sinus, the left precaval opening near the postcaval vein.

In the *Crocodile*, the caudal vein, on entering the abdomen, divides into two trunks: each unites with the ischial and iliac veins of its own side and advances towards the kidney. Here the trunk sends off a reni-portal vein, and is then continued towards the hepato-portal system. The renal veins from the inner side of the kidneys unite to form the postcaval, fig. 339, *v*, which receives the left precaval, fig. 340, *v*<sup>\*\*</sup>, at its entry into the auricular sinus, *ib. s*: the hepatic veins open separately into the contiguous end of the sinus, fig. 339, *s*. The blood from the head and forelimbs is conveyed to the heart, as in other Reptiles, by a pair of precavals, of which the right, *ib. v*, terminates in the fore-part of the sinus, and the left traverses the back part of the heart, receiving the coronary veins, to join the postcaval or to terminate near its auricular orifice.

§ 89. *Heart of Reptiles*.—In *Lepidosiren* the vein from the lung-like air-bladders traverses the auricle and opens directly into the ventricle. In *Siren* the pulmonary vein dilates, before communicating with the ventricle, into a small auricle, which is not outwardly distinct from the much larger auricle receiving the veins of the body.<sup>1</sup> This is remarkable for its large size, thin walls, and hollow, fimbriated processes, which overlap and almost

<sup>1</sup> XXXIII.

conceal the ventricle. The two precavals and the postcaval terminate in a sinus, which the pulmonary venal trunk seems to enter, but to the inner surface of which it adheres in its course to its proper auricular chamber. The ventricle is obtuse and sometimes sub-bifid at the apex: it is connected to the pericardium by the usual reflection of the serous layer upon the *bulbus-arteriosus*, and also by a fold reflected from the apex upon the coronary vein, which is thence continued to the venous sinus. The muscular parietes of the ventricle are about a line in thickness, and loosely fasciculate. The cavity is partially divided by an incomplete septum, terminating by a concave border opposite the orifice of the artery, on each side of which are the valves closing the two auriculo-ventricular orifices. The aorta, narrow, and with thin walls at its commencement, after a short subspirial course, thickens into an elongate '*bulbus arteriosus*,' which includes a longitudinal valvular prominence, grooved at its fore-part in correspondence with the origins of the branchial arteries. There is a pair of valves at the origin of the aorta, and a second pair near the beginning of the bulb. The distinction of the pulmonary from the systemic auricle, first observed in *Siren*, has been since determined in *Menobranthus*<sup>1</sup>, *Axolotes*<sup>2</sup>, *Amphiuma*, and *Menopoma*.<sup>3</sup> In *Proteus*, in which some of the blood of the puny lungs is conveyed to systemic veins, the auricular septum is not complete, according to Hyrtl.<sup>4</sup> In *Amphiuma* the auricle is smaller and less fimbriated than in *Siren*. The ventricle is similarly connected to the pericardium by the apex, as well as by the artery. This forms a half spiral turn at its origin, and dilates into a broader and shorter bulb than in *Siren*.

In *Menopoma* the auricles are still more reduced in size, and lie, as in *Salamandra*, fig. 333, *a*, when undistended, to the left of the ventricle: their outer surface, as in *Menobranthus*, is entire. The ventricle is of a flattened triangular form: its cavity is occupied by the loose fasciculate muscular structure through which the blood filters, as through a sponge, from the small contiguous auricular apertures, each of which has a simple valve, to the '*ostium arteriosum*.' The artery inclines, with a slight twist, to the left, and swells into a subspherical bulb. The valves are confined to the narrower part, and are in two transverse rows, four in each row, each valve of a conical shape, pointing forward.<sup>5</sup> The first row is just above the ostium: the second is halfway between this and the bulb.

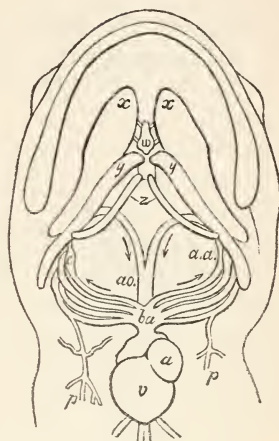
<sup>1</sup> CCLXXVIII. p. 73.<sup>2</sup> CCLXXIX. p. 45.<sup>3</sup> CCLXIX. p. 215.<sup>4</sup> CCLXXX. p. 258.<sup>5</sup> XX. ii. p. 45, pl. xxiii. fig. 2.

The pulmonic auricle augments in size with the more exclusive share taken by the lungs in respiration: but the auricular part of the heart shows hardly any outward sign of its division in Batrachians. It is small, smooth, and situated to the left and in advance of the ventricle, in Newts and Salamanders, fig. 333, *a*. In Frogs and Toads the auricle is applied to the base of the ventricle, and to the back and side of the aorta and its bulb. The ventricle, usually of a more rounded form than in fig. 331, II, is occupied by the muscular fasciculi, except at a small part between the auriculo-ventricular and aortal orifices. The bulbus arteriosus is incompletely divided by opposite longitudinal folds, the margins of which meet, but remain free.

In Serpents the heart agrees with other organs in its elongate form. The auricles are in advance of the ventricle, their lower obtuse ends slightly overlapping its base: they are separated anteriorly by the co-elongate intrapericardial origins of the arteries called 'conus arteriosus,' answering to the bulbous part in *Batrachia*; a slight 'auricular' production of the right auricle is tied down to the arteries by the serous layer of the pericardium.

The right auricle consists of a sinus and auricle proper. The sinus receives three veins at its fore part; the orifice of the right jugular and of the inferior azygos is guarded by a pair of valves: in the orifice of the superior azygos I found three semilunar valves; two veins open at the back or hind part of the sinus, the largest being the postcaval, the smaller one the left precaval. The aperture of communication with the auricle is longitudinal, near the middle of the sinus, of a full elliptical shape, guarded by a pair of membranous valves, situated within the proper auricle. The sinus has the structure of the large veins, with the serous layer of the pericardium reflected over it. The auricle has a finely fasciculate muscular wall, thickest at its lower and fore part. The auriculo-ventricular aperture is a semilunar slit, opening into the base of the ventricle, near the origin of the pulmonary artery, and defended by a short membranous valve, having one or two chordæ tendineæ attached to its free margin. The left auricle is shorter than the right, but of equal breadth

333

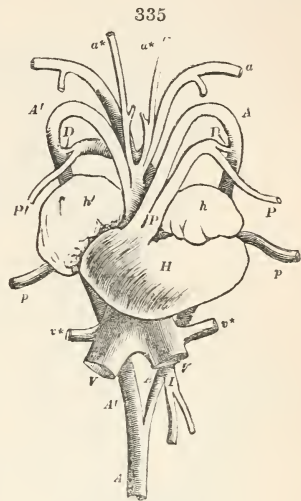


Heart, vascular arches, and hyo-branchial apparatus, Salamander

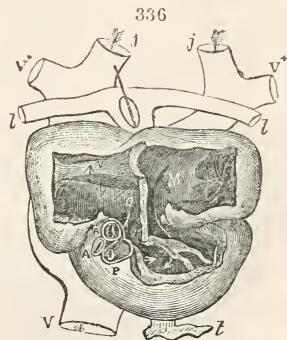




shape of the body, shows its greatest breadth, figs. 304, A, 335. The two auricles, when distended, are of nearly equal size, and of a subquadrate form, fig. 336, M, O. The bivalved orifice between the sinus and the auricle, ib. *v, o*, is a transverse slit. The white arrow, *o*, shows the course of the blood from the right auricle, past the valve supported by the base of the auricular septum, into the aortic cavity of the ventricle. In fig. 337 a bristle passes through the orifice left by the incomplete septum between the aortic and pulmonic cavities into the latter, which is the largest in *Emys*, as in *Ophidia* and *Lacertilia*: the bivalved orifice of the pulmonary artery, P, is shown. In fig. 338 that of the left aorta, A, is similarly exposed, and the incomplete septum is cut through: the root of the right aorta, A', is behind that of the left. The relative position of the origins of the three arteries from the chelonian ventricle is shown in fig. 336, where P is the pulmonary, A the left aorta, A' the right aorta, the most posterior, or dorsal, of the three arteries. The ventricle is almost wholly occupied by a spongy muscular structure, and the cavities are smaller in *Testudo* than in *Emys*. The left auricle, fig. 336, M, receives the arterial blood from the lungs by a single vein, the common trunk of the pulmonary veins, ib. *l, l*: it opens into the back part of the auricle near the septum, and is guarded by a single oblique membranous fold, ib. *m*. Each auriculo-ventricular orifice is guarded by a fold which extends across it from either side of the base of the inter-auricular septum; to that of the left auricle a small part of the muscular structure is attached by chordæ tendineæ. Opposite to the right valve a semilunar ridge projects, in *Testudo indica*, which is the rudiment of the second auriculo-ventricular valve in the Crocodile, and of the fleshy valve of that orifice in the right ventricle

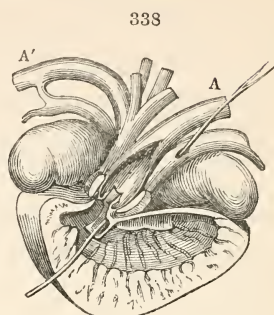
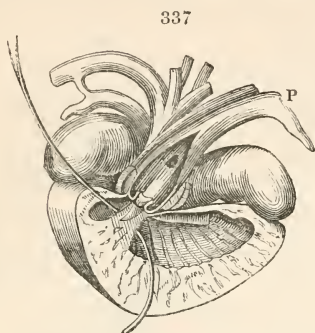
Heart of *Testudo graeca*

The left auricle, fig. 336, M, receives the arterial blood from the lungs by a single vein, the common trunk of the pulmonary veins, ib. *l, l*: it opens into the back part of the auricle near the septum, and is guarded by a single oblique membranous fold, ib. *m*. Each auriculo-ventricular orifice is guarded by a fold which extends across it from either side of the base of the inter-auricular septum; to that of the left auricle a small part of the muscular structure is attached by chordæ tendineæ. Opposite to the right valve a semilunar ridge projects, in *Testudo indica*, which is the rudiment of the second auriculo-ventricular valve in the Crocodile, and of the fleshy valve of that orifice in the right ventricle

Structure of auricles: heart of *Chelys Ambrata*

Opposite to the right valve a semilunar ridge projects, in *Testudo indica*, which is the rudiment of the second auriculo-ventricular valve in the Crocodile, and of the fleshy valve of that orifice in the right ventricle

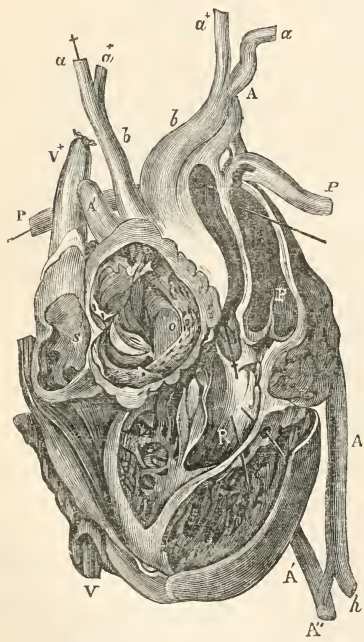
of Birds.<sup>1</sup> The apex of the ventricle is attached by a short fold of the serous membrane to the pericardium, fig. 336, *t*.



Structure of ventricle, *Emys europaea*. XXXVIII.

In all the foregoing modifications of the reptilian heart the venous blood from the general system and the arterialised blood from the lungs are transmitted by distinct auricular reservoirs into the ventricle, where,

339



Right auricle and ventricle, *Crocodilus acutus*

through the spongy character of the receptacle, and the free intercommunication between the basal spaces into which the auricles open and from which the arteries proceed, the blood is transmitted, in a more or less mixed state, to the lungs and to the general system.

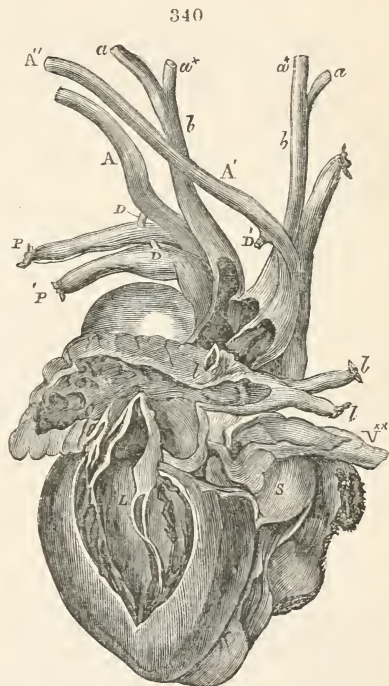
In the Crocodilian order a marked advance is made in the structure of the heart. The blood from the general system is poured by the veins into a sinus, fig. 339, *s*, whence it passes into a right auricle, *ib. o*, by the usual bivalved aperture. The auricle has a more distinct 'appendix,' and its muscular walls are thicker than in lower reptiles. The auriculo-ventricular orifice is defended

<sup>1</sup> XX. vol. ii. p. 48, prep. no. 920.



not only by the ordinary valve on its left side, which is attached to the base of the auricular septum, but by a similar though smaller fold on the opposite or right side: this fold becomes the fleshy auriculo-ventricular valve in birds. To the junction of the two valves at their lower angle a fleshy column is attached. The ventricular cavity, *ib. R*, which receives the venous blood, propels it to the left aorta, *A*, and to the pulmonary artery, *P*: the origin of each is guarded by a pair of semilunar valves. Immediately above the larger of those of the left aorta is an orifice leading into the right aorta: in fig. 339, a bristle is passed from the left aorta through this orifice into the right axillary branch, *a*, of the right or brachio-cephalic aorta.

In the figure, the valve is drawn down to show the orifice; in its natural state, it conceals and would cover the orifice as the blood flowed from the ventricle into the left aorta. Some openings lead from the pulmonic cavity of the ventricle into a spongy structure, which has been defined as a particular cavity (*spatium interventriculare*) of the ventricle; but it is essentially a part of the pulmonic chamber: bristles are passed through the orifices or intercolumnar spaces, leading from *R* to this structure, in fig. 339. The left auricle, fig. 340, *M*, when distended, is smaller than the right, and of a more transverse form: its muscular part is produced into an appendage, which almost meets that of the right auricle in front of the 'conus arteriosus,' embracing the 'sulcus coronalis' of the heart. There is a small pulmonary sinus receiving the short trunks of the pulmonary veins, fig. 340, *l, l*. The left auriculo-ventricular aperture is defended by a broad membranous fold continued into the ventricle from the middle of the base of the interauricular septum: to its margin are attached a few chordæ tendineæ: the



Left auricle and ventricle, *Crocodilus acutus*

fig. 340, *M*, when distended, is smaller than the right, and of a more transverse form: its muscular part is produced into an appendage, which almost meets that of the right auricle in front of the 'conus arteriosus,' embracing the 'sulcus coronalis' of the heart. There is a small pulmonary sinus receiving the short trunks of the pulmonary veins, fig. 340, *l, l*. The left auriculo-ventricular aperture is defended by a broad membranous fold continued into the ventricle from the middle of the base of the interauricular septum: to its margin are attached a few chordæ tendineæ: the



cavity into which it opens, fig. 340, L, is distinct from the pulmonic cavity, the septum being complete: its walls are smooth, or less broken by 'columnæ carneæ' than in other Reptiles; and the free walls of this ventricle are more compactly muscular. The ventricle is produced in a subconical form, from its base to the origin of the right or brachiocephalic aorta: the auriculo-ventricular valve is slit, in fig. 340, to show the course of the ventricle to the origin of that aorta: this has a pair of semilunar valves, above which is the intercommunicating orifice with the left aorta.

Thus the heart, in *Crocodylia*, consists of two auricles and two ventricles, corresponding to the 'right' and 'left' auricles and ventricles of Mammals. But, through the origin of an aorta from the right as well as from the left ventricle, and their intercommunication, it follows that whenever, from an impeded state of the pulmonary circulation, the right ventricle and its arteries become over-distended, the venous blood flows through the inter-aortic orifice into the arterial trunk, which, after supplying the head and fore-limbs, bends, at A', over the right bronchus and effects an union at A'', fig. 339, with the left aorta, A, h. Such a state of the circulation coincides with and facilitates the long submersion of the Crocodile. When the animal is on land and breathing the air directly, the arterialized blood flows freely into the ventricle, fig. 340, L, and the synchronous currents from this and the opposite ventricle throw forward the valves at the respective origins of the two aortæ and close the interaortic orifice. The arterial and venous streams flow on unmixed; the former to the brain and other parts of the head and fore-limbs; the latter, by the branch, h, fig. 339, chiefly to the liver and contiguous viscera; a small part mixing with the arterial blood in A', to be transmitted by A'' to the other abdominal viscera, hind limbs, and tail. To convert the heart of the Crocodile into that of the bird, it needs only to obliterate the left aorta; fig. 339, R, to appropriate the right or pulmonic ventricle, exclusively to the service of the pulmonary artery; and the 'left' or systemic ventricle to the service of the aorta, which in *Hæmatotherma* is the exclusive distributor of arterial blood, in an unmixed state, to the general system.

§ 90. *Gills of Batrachia*.—The blood is conveyed in all Reptiles from the ventricular part of the heart, really or apparently by a single trunk, which, in the one case, is called the 'bulbus arteriosus,' in the other the 'conus arteriosus.' The interior developments by which the 'bulbus' is converted into the 'conus,' are interestingly gradational, and the insulation of the pulmonary

artery to its ventricular origin is not effected until the batrachian type is passed.

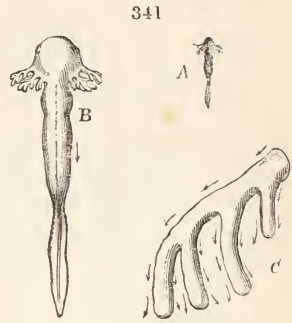
In the lower or perennibranchiate members of the order, the single artery from the ventricle sends, as in Fishes, the whole of the blood primarily to branchial organs, throughout life, and, in all *Batrachia*, at the earlier aquatic period of existence; a description of the gills, permanent or deciduous, will, therefore, be premised. At page 87 are described and figured, fig. 69, the hyo-branchial arch and appendages of the larva of the Frog. The basihyal, *b*, suspended by ceratohyals, *a*, to the tympanic pedicle, *e*, supports a pair of cerato-branchials, *c*, which each send off four branchial arches. All these parts are cartilage. The heart distributes the blood by a short trunk through four pairs of vascular arches, which, bending round the gullet, reunite behind to form the aorta. Before the larva quits the egg, a tegumentary tubercle buds out in front of the branchial cleft, and soon shoots into a trifold appendage, fig. 341,

A and B, each process lengthening and bifurcating after the larva is extricated. These filaments, of cylindrical shape, *ib. c*, each

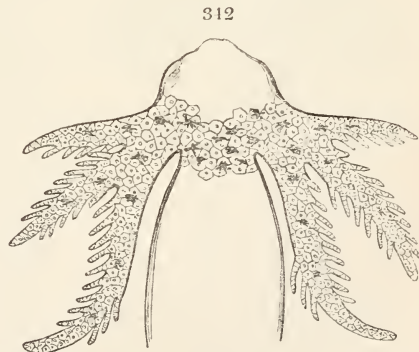
support a single capillary loop, pushed out from the primitive vascular arch, and are covered by ciliated epithelium, producing the currents indicated by the arrows in *c*. The branchial cavity communicates at first, as in *Branchiostoma*, with the abdominal one, as well as with the outer surface by the branchial clefts. About the fourth day these simple outer gills begin to shrink; they are absorbed by the

seventh day. The cartilaginous arches, also beginning to shrink, become more internal by the progressive growth of the head.

In the Newt (*Triton*, fig. 342), three pairs of external gills are developed, at first as simple filaments, each with its capillary

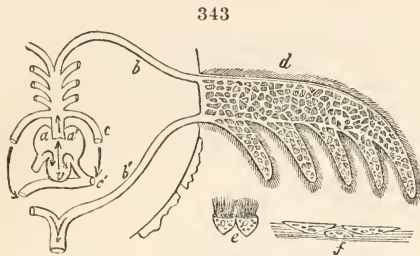


External gills, larva of Frog. CCXXXVIII



Head and branchial appendages of the larva of a Newt (*Triton*) magn. CCLXVIII.

loop, but speedily expanding, lengthening and branching into lateral processes with corresponding looplets; these blood-channels intercommunicating by a capillary network, as at *d*, fig. 343. The

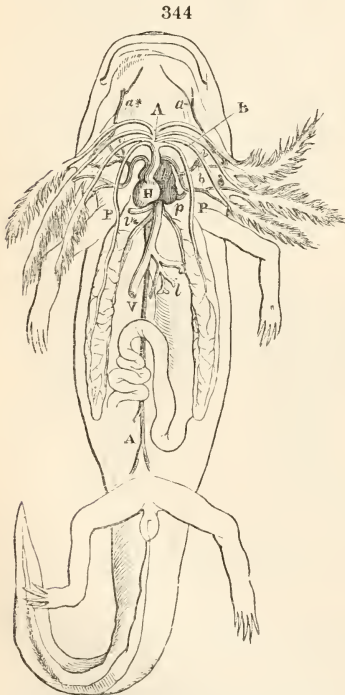


One of the gills of the Newt, magn. CCLXVIII.

gill is covered by ciliated scales, *ib. e*, which change into nonciliated epithelium, *f*, shortly before the gills are absorbed.

The size of the gills is as the proximity of their developing vascular arch to the propelling organ of the blood. In the *Proteus anguinus* three pairs only of branchial and vascular arches are developed, corresponding with the number of external gills. In *Siren lacertina*, as in caducibranchiate Batrachians, there are four pairs of branchial arches; the first and fourth being fixed, the second and third free:

their contiguous borders on the concave side are provided with small interlocking processes. The gills are in three pairs, increasing in size, according to the above-stated dynamic condition, from the first to the third, which is attached to both the third and fourth arches: the upper or outer surface is entire and covered by ordinary integument; the under or inner surface is produced into pinnatifid fringes, supporting the capillary branchial vessels and covered by thin epithelium. Each gill is attached by its base anterior to and above the gill-slit, which it overhangs. In the *Axolotl*, fig. 344, the fringes of the gills are longer and more slender. In the *Menobranthus* they resemble those of the Triton. In the *Siren*, *Proteus*, and *Menobranthus* the outer gills are persistent, and, perhaps, also in *Axolotes*. In each of these



Circulating and respiratory organs, Axolotl, *Axolotes mexicanus*. CCLXVII.

'perennibranchiate' Batrachians, arteries are developed from the last pair of branchial vascular arches, as at P, fig. 344, to convey blood to the lungs.

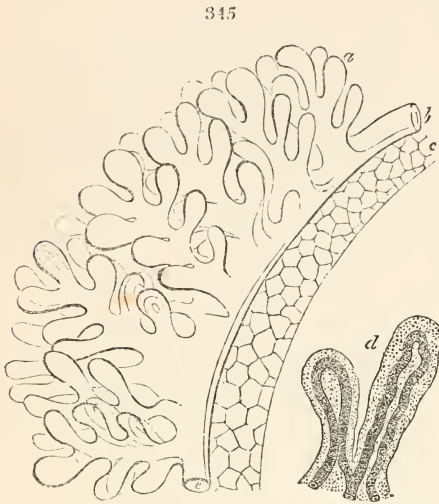
In *Menopoma* and *Amphiuma* the gill-opening persists on each side; but of the original four pairs of vascular arches only the second and third accompany remains of branchial arches, circumscribe the gullet, and reunite behind to form the beginning of the aortic trunk. The extent of the ossification of the hyobranchial framework in some measure corresponds with the degree in which the branchial organs of respiration are retained. In *Proteus* the ceratohyals, urohyal, two pairs of basibranchials, and three pairs of ceratobranchials become bony. In the *Siren* the ceratohyals, urohyal, one pair of basibranchials, and two pairs of ceratobranchials are bony. The Menopome and Cryptobranchus agree with the Newts and Salamanders (fig. 333), in having the basihyal, *w*, the ceratohyals, *x, x*, and two pairs of ceratobranchials, *y* and *z*; but the latter pair is proportionally longer and shows two elements of the arch, on each side, ossified. In the Anouros Batrachians the branchial arches are reduced to the basal portions of a single pair of ceratobranchials (p. 91, fig. 74), which persist, in most higher Vertebrates, as the 'posterior cornua' of the 'hyoid bone.'

The parts of the branchial framework in immediate relation with the support of the deciduous gills never pass beyond the cartilaginous stage; and a histological test is thus afforded of the temporary or permanent character of the branchiæ in a Batrachian presenting them. The deciduous gills offer many modifications in the larvæ of the caducibranchiate species. In a tropical South American Frog (*Opisthodelphys ovifera*), e. g., the external gills are formed before the larva is excluded, and expand into a broad membranous disc at their extremity.

But whatever the form or structure of the external gills, they are fitted only to their office as such: that being discharged, they turn to no other use, but lose their ciliated and vascular structure, and disappear. The Tadpole, meanwhile, being subject to a series of changes in every system of organs concerned in the daily needs of the coming ærial and terrestrial existence, still passes more or less time in water, and supplements the early attempts at pulmonary respiration by pullulating loops and looplets of capillaries, fig. 345, *a*, from the branchial vessel, *b, e*, supported by the cartilaginous arch, *c*, and coated by delicate non-ciliated epithelium: the terminal processes of these 'internal gills' support a single capillary loop, *d*. They resemble the commencing gills of



Teleostomous Fishes, especially of the Lophobranchs; and the analogy to the piscine respiratory structures is enhanced by the growth of an opercular fold of membrane, protecting the branchial chamber; but this, by progressive adhesion of its posterior border to the cervical integument, reduces the lateral fissures to one inferior foramen. In the Newts, the side-slits are longer retained. The young of *Cæcilia* show a branchial pore on each side, with traces of branchial fringes. The embryo Salamander shows external gills while in the womb; and, when these disappear, the branchial arches adhere to the opercular fold of skin, the external outlet being an inferior transverse slit.



The internal branchia of the Tadpole of the Frog, magn.  
CCLXVIII.

In Newts, Salamanders, *Cæcilia*, and Anourans, the branchial orifices become obliterated after the absorption of the internal gills. The gigantic Newt of Japan (*Cryptobranchus*) equally differs from *Menopoma* and *Amphiuma* in the closure of those orifices. Their retention in these large American Newts, with the superadded persistency of the branchia themselves in *Menobranchus*, *Siren*, and *Proteus*, are amongst the most significant evidences of the manifestation of generic characters through arrested stages of one general course of transmutational development.

§ 91. *Arteries of Reptiles*.—In the Axolotl, fig. 344, the three anterior pairs of vascular arches rise distinctly from the ‘bulbus,’ A; the fourth pair blend their origins with those of the third: the three anterior pairs are, functionally, branchial arteries, ib. B, course along the corresponding branchial arches to the sides of the neck, and then quit them to enter the base of the pendent gill, running along the antero-inferior border: they there send off a double series of branches, which penetrate and ramify in the branchial fringes, and constitute at their end and margin a capillary net-work, like that in fig. 343. From this the returning

channels converge to form the 'branchial veins,' *ib. b*, which re-enter the neck, course along the dorsal walls of the pharynx, and unite to form the right and left aortæ, or roots of the common median arterial trunk, *ib. A*. From the first or foremost branchial vein is given off the carotid or cephalic artery, *a\**. The fourth pair of vascular arches pass outward and backward, and each divides, the larger portion, *P*, going to the lungs, the smaller division pursuing its course to the back of the œsophagus, where it unites with the third 'branchial vein,' and adds a small proportion of unrespired blood to the contents of the aorta.

In the *Proteus* the bulbus arteriosus divides into a pair of vessels, each of which, as it diverges, again divides; the anterior division supplies the anterior gill: the posterior division bifurcates, to supply the second and third gills. But, before distributing the branchial capillaries, each artery communicates by a direct anastomosing channel with the branchial vein; in other words, only a portion of each primary vascular arch is appropriated to the gills, and a certain proportion of the blood goes from the heart to the aortic trunk without being submitted to the respiratory process. The small artery to the slender simple pulmonary sac is sent off from the hindmost branchial vein. The cephalic arteries arise from the foremost branchial veins, and consequently supply the brain with purer arterial blood than that which goes to the body.

The changes in the vascular arches, consequent on absorption of the gills, are chiefly due to the enlargement of anastomosing channels, between the inferent and efferent branchial trunks, like those in *Proteus*. The course of these changes reduces the arterial system in *Menopoma* to the condition of which Hunter left the illustrations published in *xx. vol. ii*. The bulbus is shortened, and the origins of the primary vascular arches approximated: those of the third and fourth are blended together. The foremost arch is smaller than the second or third: it sends off an artery to the intermandibular space, a second to the side of the head, a third to the pharynx, beyond which it bends abruptly back, to enter the aortal root. The second and third vascular arches are of equal size, wind round the wide pharynx, anterior to the branchial opening, and unite on reaching its back part to form the aortal root: this sends forward a small artery to the side of the mouth, and, a little further on, the main carotid artery, beyond which the roots converge backward, and unite to form the aortic trunk. The hindmost vascular arch is the smallest, and courses round the œsophagus, below or behind the branchial

opening, behind which it sends off the pulmonary artery, and returns, at an acute angle, to join the third vascular arch near its termination in the aortic root; or, the pulmonary artery may be said to be formed by a small branch from the third arch, in conjunction with the fourth arch. The branchial arteries are sent off from the aortic trunk, about an inch beyond its origin.

In the Newt the small anastomosing vessel at the base of each gill, between the ingoing and outcoming trunks, enlarges as the flow of blood is checked by the stunting of the gill in the course of its absorption; so that, when this is complete, the blood flows from the 'bulbus' round to the aorta in a continuous unchecked stream, fig. 333, as at its first appearance.

In the Frog this course of change issues in the following persistent disposition of the primitive vascular arches:—The anterior, originally the fourth, pair, which have their origins brought back so as to seem to rise from the pair preceding, are sometimes called its 'carotid branches:' they diverge outward, as in their primitive course, have a partial enlargement, and send off the 'lingual,' pharyngeal, and entocarotid arteries. The next pair of vascular arches, answering to the third of the primitive pairs, sends off the laryngeal and brachial arteries, also a tributary to the subcutaneous cervical, and are continued backward and inward, supplying the œsophagus in this course, to form by their union the aorta, A. The first pair, answering to the second and first of the primitive pairs, send off the second root of the artery which ramifies on the subcutaneous cervical gland, and the pulmonary artery; the dorsal part of the second primitive arch now appears as the accessory root of the subcutaneous cervical artery given off from the aortic root, as above mentioned.

The brachial artery sends off an external thoracic, distributed to the muscles of the fore-part of the abdomen, a subscapular branch, a circumflex artery, supplying the muscles of the shoulder, and is then continued to the fore-arm, where it becomes 'radial,' sends off a recurrent branch, and divides near the wrist into a dorso-carpal and palmar branch, which terminates in the digital arteries and the intervening web of capillaries.

The aortic trunk gives off the gastro-mesenteric artery, dividing into 'cœliac' and mesenteric branches; then the suprarenal and renal arteries, the lumbar, and the genital arteries (spermatic or ovarian), and bifurcates to form the common iliacs. From each of these are sent off a vesico-epigastric artery continued from the allantoic bladder forward upon the abdominal walls, the external and internal circumflex arteries, and the femoral, which, on reaching

the leg, divides into posterior and anterior tibial, terminating in the digital arteries and capillaries of the webs.

In Ophidian, Lacertian, and Chelonian Reptiles the 'bulbus' of the embryo heart becomes divided into three distinct tubes, which remain closely united together by their outer fibrous tissue, and covered anteriorly by the reflected serous layer of the pericardium. The extent of this union, or length of the 'conus vasculosus,' is greatest in the Serpents. In the Python it may exceed two inches in length; and, when the serous and fibrous tunics are dissected away, the origin of the pulmonary artery is seen to the left, next to it is the origin of the left aorta, and to the right of this, about an inch above the ventricle, the trunk of the right aorta appears, which, as it diverges from the left, sends off the single carotid artery. This artery is the remnant of the anterior of three primitive vascular arches. The right aortic arch and the left aortic arch, which unite behind and beyond the pericardium to form the abdominal aorta, are the proceeds of the middle primitive arches: the pulmonary artery is the issue of the changes of the posterior or first pair of vascular arches.

In the *Lacertilia* the extent of modification is somewhat less. Looking on the sternal surface of the heart, the pulmonary trunk is the foremost, the left aorta is the next, the right aorta is the hindmost. The left and right aortic arches converge, and unite or intercommunicate, behind and usually below or beyond the heart, to form the abdominal aorta. In *Lacerta ocellata*, fig. 334, P marks the origin of the pulmonary artery, which ascends and divides: the left branch, P, passing in front of the left descending aorta, with which it is connected by a ductus arteriosus, D, before proceeding to the left lung, p, fig. 332; the right pulmonary artery, fig. 334, P', passes behind the 'arterial cone,' and in front of the right descending aorta, A', with which it communicates, or is connected, by a ductus arteriosus before proceeding to the right lung. These 'ductus arteriosi' exist in the *Python*, are shown in the Tortoise, fig. 335, D, D, and in the Crocodile, fig. 340, D, D'. The third primitive arterial trunk, called 'right aorta,' divides into the right arch (below A' in fig. 334), and into the common trunk of the two cephalic or carotid arteries, ib. a, a\*, describing the upper arches: the common trunk of the brachial arteries is usually given off from the right aortic arch. In *Psammosaurus griseus* the common trunk of the carotid does not bifurcate until it has ascended the neck as far as the origin of the bronchial tubes: and not until after the right aorta has arched over the right bronchus does it send off, at an acute



angle, the common trunk of the right and left brachials. The left aortic arch, in *Psammosaurus*, sends off a gastric and mesenteric artery before it joins the right aortic arch; and this is the case also in the Tortoise, fig. 335, *l*, and Crocodile, fig. 339, *h*, the left aorta being then so reduced in size as to resemble a 'ductus arteriosus.'

In the Tortoise the right aorta, soon after its origin, sends off a common trunk, which quickly subdivides into the carotids, fig. 335, *a*\*, *a*\*, and brachials, *ib. a, a*; and the same is the case with *Emys*, in which the four arteries are seen cut short near their origins, between  $\Lambda'$  and  $\Lambda$ , figs. 337 and 338.

In the Crocodile the two 'arteriæ innominatæ,' figs. 339, 340, *b, b*, are longer before they divide into the brachial, *a*, and carotid, *a'*: both innominatæ arise by a short common trunk from the right aorta, which divides, soon after its origin, into that trunk and the right aortic arch, *ib. \Lambda'*. This arch winds over the right pulmonary artery, fig. 339, *p'*, with which it is connected by a 'ductus arteriosus' (the arch is reflected upward and the 'ductus' *D'*, severed from the pulmonary artery, *p'*, in fig. 340). The origin of the right or brachi-cephalic aorta is hidden by that of the left aorta, fig. 339,  $\Lambda$ , which is anterior, or on the sternal side of it. The left aorta, as it winds over the left pulmonary artery, is attached to it by a 'ductus arteriosus,' the remnant of the channel by which the first vascular arch originally communicated with the second, to aid in forming the aorta, before its current of blood was diverted to the uses of the well-developed lung, after exclusion. The continuation of the main part of the left aorta into the great visceral artery, fig. 339, *h*, reduces its original union with the right aortic arch,  $\Lambda'$ ,  $\Lambda''$ , to a small anastomotic channel.

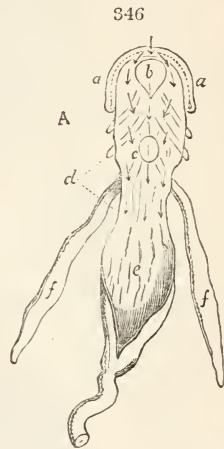
The following particulars are notable with regard to the distribution of arterial blood by the right aorta in Reptiles. The anterior vascular arch, in *Ophidia*, is converted into a pair of cephalic or carotid arteries in the young Snake, and this structure is retained in the common Snake (*Coluber natrix*); in *Python tigris* I found the right carotid much reduced in size; in the Viper (*V. verus*), and some other Serpents, the cervical part of the right carotid is obliterated: but the cephalic portion remains, and receives blood by the anastomosis of one of its branches with the left carotid.<sup>1</sup> In the Viper, and some other venomous Serpents, the internal maxillary branch of the carotid forms a rete mirabile behind the poison-gland.<sup>2</sup> The right aortic arch,

<sup>1</sup> CCLXXXI.<sup>2</sup> CCLXXXII. p. 260.

soon after it has curved over the right pulmonary artery, sends off the trunk of the vertebral and anterior intercostal arteries: in its origin and position, this trunk resembles the common brachial trunk in Lizards.

The relation of the origin of the right aorta to the ventricular compartment, first receiving the arterialised blood from the pulmonary auricle, and the distribution of the branches of the right aorta, are such, that the head, neck, and fore-limbs receive chiefly arterialised blood, and the abdominal viscera, the trunk, hind-limbs, and tail, are supplied with mixed venous and arterial blood. But this localised distribution of the two kinds of blood is more completely effected in the Crocodiles, through the modification of the heart and arteries before described.

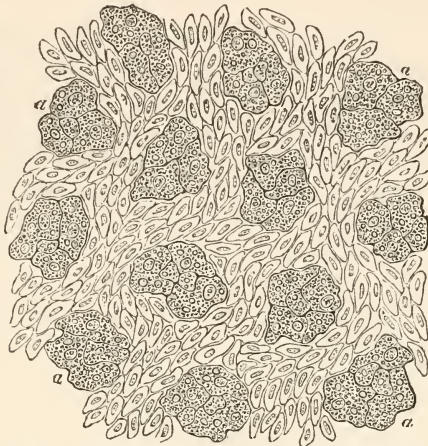
§ 92. *Lungs of Reptiles.*—An opening on the midline of the ventral side of the pharynx, fig. 346, *c*, receives air introduced into the mouth, and conveys it to the receptacles which, in Reptiles and all higher Vertebrates, are called ‘lungs,’ *ib. f, f*. The opening, usually a short longitudinal slit, leads, in the Newt and Proteus, to a small crescentic membranous sac, from the angles of which are produced the long slender pulmonic bags. In the Axolotl a short tube, strengthened by a few feeble subannular cartilages, conducts the air to the lungs, which commence just beyond the heart: in the Siren and Land-Salamander a similar trachea divides into two branches, one to each lung.<sup>1</sup> In all these tailed *Batrachia* the pulmonary bags have simple or even walls. The artery, formed as above described, from the hindmost vascular arch, joined by a branch from the next arch, runs along one side or border, and the vein returns along the opposite border of the lung. The branches proceed from the artery, fig. 348, *a*, transversely, with regular intervals, midway in which the venules are formed which course half-round the cylinder to open into the longitudinal vein: fibres of elastic tissue accompany the arterioles and venules. The intervening capillaries constitute a regular network, uniformly over the pulmonary surface; they seem to be mere channels for the passage of the blood discs, fig. 347, with intervals or islets of compacted cells, containing nuclei



Respiratory organs, Newt.  
CCXXXVIII.

and granules, *ib. a*. This vascular surface is covered by a delicate carpet of epithelial cells, fig. 348, certain linear tracts of which,

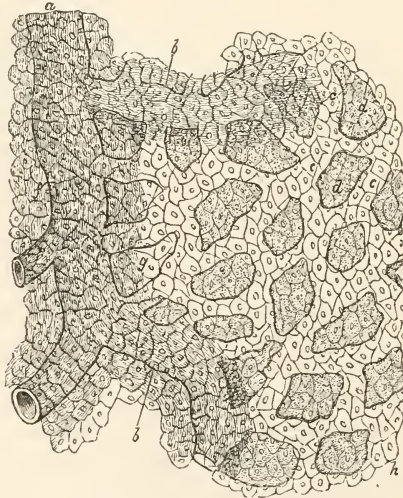
347



Respiratory surface, lung of Newt, magnified, with the epithelium out of focus. CCLXVIII.

*ib. b, b*, are ciliated. The exterior of the lung is covered by delicate peritoneal nonciliated scales.

348



Respiratory surface, lung of Newt, magnified, with the epithelial covering in focus. CCLXVIII.

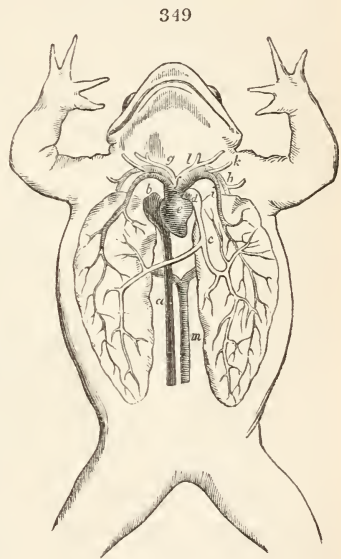
In the *Siren* the lungs are narrow bags, coextensive with the

long trunk; and the ciliated tracts upon the inner surface begin to be raised therefrom, and to mark out shallow depressions on the vascular surface, at least along the anterior half of the sac. In the Axolotl, in which the lungs terminate at the hinder third of the abdomen, the alveolar depressions or cells are more marked. In the Amphiume the lungs are narrow, and terminate in a point, within a short distance of the anus: on the inner surface elastic bands are developed in the inter-alveolar partitions, and the alveoli begin to be subdivided into smaller cells. In the Menopome the lungs have a similar structure, but are proportionally smaller, and with larger alveolar depressions.

The lungs of the Frog, fig. 349, are wider in proportion to their length, and extend along the dorsal part of the abdominal cavity, with the vertebral bodies and vascular trunks intervening. They are continued by short bronchiæ or bronchial apertures, fig. 350, *f*, directly from the larynx. The proper tissue of the bag is composed of very elastic fibre, covered by peritoneal epithelium, and lined by the capillary network and its epithelial covering; the pulmonary artery takes its course beneath the peritoneal layer, the pulmonary vein runs beneath the internal epithelium; the one on the fore and outer part, the other nearer the inner or mesial side of the lung.

The whole inner surface is honeycombed, and the alveoli are subdivided into smaller cells. The arterioles run along the attached borders of the septa, the venules along the free borders. The ciliary epithelium is limited to the margins of the alveoli supporting the larger venules: the capillary network, covered by non-ciliated delicate epithelial scales, is disposed upon the sides and bottom of the ultimate cells, the septa having a layer of the capillary network on each side. Thus the lungs of the tailless Batrachia, and more especially of the *Pipa*, in which they are very broad and the bronchial tubes long, have a more extensive respiratory surface in proportion to their size than in the tailed species.

But the pulmonary artery is not exclusively distributed to the



Heart and lungs, Frog. CCLXVIII.



lung: it sends a branch to the 'rete mirabile' of the parotoid, or group of subcutaneous cervical glands, and, in the Frog, the branch from the pulmonary artery joins one from the aorta to form a large subcutaneous artery, more extensively distributed upon the skin, which exercises a respiratory office in these naked Batrachia. In the Siren, Menopome, and Amphiume, the pulmonary artery distributes some small twigs to the œsophagus.

In the poisonous, colubrine, and marine Snakes the lung is, functionally, single, one only being developed, but of great length, for the respiratory purpose, the other becoming aborted into a small or scarcely discernible rudiment. The trachea, fig. 300, *a*, has numerous and entire cartilaginous rings along a certain proportion of its course, and the lung, *ib.* *B*, seems to be formed by a dilatation of the membranous part of the tracheal tube, after the rings become incomplete: but these may be traced supporting a narrow and shallow kind of air-canal to the hind end of the lung in *Pelamis bicolor*.<sup>1</sup> A similar structure has been observed in Vipers (*Echidna arietans*), and, for a shorter extent, in Rattlesnakes, in which the trachea is shorter than in non-venomous Snakes. The expanded membranous part of the lung is honey-combed, with subdivisions of the alveoli at the fore-part of the lung, for a varying thickness and extent in different species. The rudiment of the atrophied lung is often indicated by an orifice in the trachea, at or near its entry into the functional lung, leading to a small pouch. This adheres to the terminal whole-rings of the trachea in *Coluber natrix* and *Naja tripudians*. In the great constricting Serpents both lungs are functionally but unequally developed. In *Python tigris* the left lung is nearly half as long as the right: but, by its structure, it takes almost an equal share in the respiratory function, the vascular and honeycombed parietes being of nearly the same extent as in the right lung. So much of this as is prolonged beyond the left lung has thin, simple, and comparatively unvascular walls, performing the office of a reservoir of air, which may be useful during the period, when the delicate windpipe is squeezed flat by a large prey in progress of slow deglutition.<sup>2</sup> The proper parietes of the lungs almost everywhere adheres, by lax cellular tissue, to the contiguous organs. In the Slow-worm (*Anquis fragilis*) the lungs are relatively shorter than in true *Ophidia*, but the left is only half the length of the right lung. A similar difference is presented by the lungs

<sup>1</sup> xx. vol. ii. p. 93, prep. no. 1089.

<sup>2</sup> *Ib.* p. 94, prep. no. 1093 A.

of *Bipes lepidopus*. In *Pseudopus Pallasii* the lungs are of nearly equal length.

In most Lacertian Reptiles the lungs are equal, are broader in proportion to their length, and the short bronchus terminates abruptly in the single pulmonary cavity. The parietes are honey-combed and vascular, but in a less degree as they extend from the heart: in Geckos and Agamas the alveoli are deepest on the mesial side of the lungs. In the Iguana the pulmonary cavity is divided by a few deep partitions into primary lodges, the parietes of which are honeycombed by secondary and tertiary cells.<sup>1</sup> In a Monitor (*Regenia ocellata*) the bronchus is continued some way along the interior of the lung.<sup>2</sup> The lungs of the Chameleon are remarkable for their great extent, for the delicacy of their parietes, and the number of cæcal processes continued from their anterior and inferior margins. Each lung is partially divided longitudinally at its fore part into two cavities, which have their vascular surface increased by subdivision into cellular alveoli; the posterior appendiculated part of the lung is of a simpler and less vascular structure, and may serve as a reservoir of air. Marginal cæcal productions of the pulmonary bag exist also in the Geckos (e. g. *Ptyodactylus fimbriatus*) and in *Polychrus marmoratus*. In Geckos and Scinks the trachea terminates in the lungs without dividing into bronchi.

In the Chelonia the lungs present a further stage of complication, and are adherent to the surrounding parts. In those of *Chelydra serpentina*, e.g. the general cavity of each lung is divided into eight compartments, the walls of which are honeycombed and vascular, especially at their fore part. The bronchial tube extends to the hindmost compartment of the lung,<sup>3</sup> communicating by special orifices with the anterior ones, and sending continuations of its fibrous structure along the free border of the septa.

In the Sea-Turtles (*Chelone*) the lungs extend over the back part of the abdomen to the pelvis, and must act as an air-bladder during their swimming: 4 the bronchial tubes are continued, gradually decreasing, to near the end of the lungs, and retaining cartilaginous rings or half-rings along three-fourths of their course. They communicate with numerous primary divisions of the pulmonary cavity, each of which is divided into cells, which are subdivided to the third or fourth degree, with proportionate extension of the vascular respiratory surface. The ultimate cells

<sup>1</sup> xx. ib. p. 96.

<sup>2</sup> cccxxi. p. 525.

<sup>3</sup> Ib. p. 96, prep. no. 1109 A.

<sup>4</sup> Ibid. p. 96, prep. no. 1110.

along the outer margin of the lung are the largest and their parietes the least vascular.

Subjoined is a tabular view<sup>1</sup> of the capacity of the lungs in examples of different families of the Chelonian order, 'obtained by pumping out the air of the lungs, then pumping in water, then pumping out the water again and measuring its amount in cubic inches.'<sup>2</sup> This table shows that aquatic *Chelonia* require less air in their lungs, in proportion to the weight of the body, than land *Chelonia*; and that in mud-dwellers and the soft-turtles (*Trionycidae*) other parts are auxiliary to the lungs in the act of breathing. Thus the more permeable texture and minor thickness of the epiderm in the *Trionycidae* suggest the aptness of the skin for respiratory influence on the blood, analogous to that of a gill. The integument of the under side of the body in these estuary turtles, which seldom leave the water except to lay their eggs, is highly vascular.

Dr. Sager found 'arranged along the surface of the tongue of *Trionyx*, and somewhat in rows, as well as on the fauces and about the rima glottidis, and also over the edges of the cornua hyoidea, a number of delicate fringes, resembling, especially on the hyoid arches, the fimbriated gills of the *Menobranchus*.'<sup>3</sup> Professor Agassiz remarks that, 'after seeing this Turtle remaining under water for half-an-hour without showing the least sign of oppression, it seems plausible to assume that these fringes may be similar to the internal gills of Tadpoles, not only in their shape but also in their function.'<sup>4</sup>

In the Crocodile (*Crocodylus acutus*) the bronchial tube enters the middle of the lung and is continued for a short distance into its substance before losing the cartilaginous annular structure,

<sup>1</sup> TABLE SHOWING THE CAPACITY OF THE LUNGS COMPARED WITH THE WEIGHT OF THE BODY. CCC. p. 283.

Species	Mode of Life	Weight of body	Capacity of the lungs	Length of Carapace
<i>Testudo polyphemus</i> , fœm.	On dry ground and in sand holes	ounces 95	cubic inches 35	inches 10½
<i>Cistudo triunguis</i> , fœm. .	In dry woods, under leaves	19	17¾	6¾
<i>Ptychemys rugosa</i> , fœm. .	In water and on land	62	22½	11
<i>Cinosternon pennsylvanicum</i> , fœm. . . . .	In water and mud	8	½	4½
<i>Chelydra serpentina</i> , mas.	In water and mud	65	7	10
<i>Trionyx ferox</i> , fœm .	In water and mud	76	4½	13

<sup>2</sup> CCC. vol. i. p. 284.

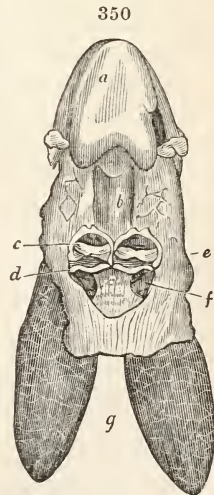
<sup>3</sup> CCCII. quoted in CCC. pp. 277, 284.

<sup>4</sup> Ibid. p. 284.

sending off lateral branches: it then abruptly terminates in a dilated elongated passage, similar to those in which the side-branches open. These passages correspond with the primary divisions of the pulmonary cavity in the Turtle, and the air passes from them by numerous round apertures into the smaller subdivisions forming the cellular structure of the lung.<sup>1</sup>

§ 93. *Larynx of Reptiles.*—In perennibranchial and tailed *Batrachia* the glottis is a simple longitudinal fissure, fig. 346, *a*, in the middle of the ventral walls of the pharynx, each side of which is commonly strengthened by a slender portion of fibro-cartilage (*Amphiuma*), or so divided as to represent an ‘arytenoid’ and a ‘laryngo-tracheal’ cartilage (*Proteus*). The slit opens into a small membranous cavity, usually kept patent by lateral cartilages, from which the lungs diverge directly in *Proteus*, *Amphiuma*, and *Triton*, and with a short trachea intervening in *Siren*, *Axolotes*, *Menopoma*, and *Salamandra*, the trachea being either membranous or with feeble rudiments of cartilaginous rings.

In tailless *Batrachia* the larynx is well developed, especially in the males. There is, in most, an annular thyrocericoid cartilage, which supports in all a pair of large arytenoids, of a triangular shape, the apex forming the upper and lateral boundary of the larynx, fig. 351, *a*: the chordæ vocales stretch transversely from one end of the base to the other, and are wanting only in *Pipa* and *Dactylethra*. Above and below the vocal chords, fig. 350, *c*, there is a mucous pouch; and between the chords there is, in some species, a cartilage. The muscles are a ‘dilator’ and a ‘constrictor rimæ glottidis,’ and a ‘compressor glottidis,’ arising from the cerato-branchials, fig. 74, p. 91, and inserted into the posterior angle of the arytenoid: by bending this angle outward, it stretches the vocal chords, and, both muscles acting, they compress the larynx. This is an influential muscle in regard to the voice or croak, and varies with its quality in different species; it is wanting in the mute *Pipa*. In *Bombinator igneus* and *Hyla verrucosa* the arytenoids are obtuse-angled and nearly equilateral triangles. In *Bufo cinereus*

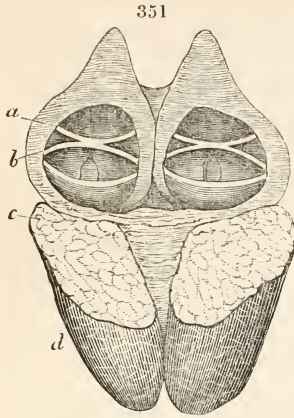


Tongue, larynx, and lungs,  
male Frog, *Rana temporaria*.  
CCCXX.

<sup>1</sup> xx. vol. ii. p. 97, prep. no. 1118.



they are more acute-angled and directed backward. In the Toad (*Bufo*) the chordæ vocales are thin elastic membranes, and in two pairs, fig. 351, *a* and *b*: the sacculi are seen to be lodged in the large arytenoid cartilages. The males of the common and edible Frogs (*Rana*) have two submandibular sacs, the male Tree-Frog (*Hyla*) has one such sac, opening by a straight canal into the larynx, and susceptible of considerable distension by air during the croak. All these diversities of laryngeal structure affect the loudness, deepness, or sharpness of the peculiar vocal notes of Frogs and Toads. The air passes to the lungs, fig. 350, *g*, 351, *c*, *d*, by short bronchi, fig. 350, *f*, save in the



Larynx and lungs (*c*, *d*) Toad, *Bufo*.  
CCCXX.

*Pipa*, in which the bronchial tubes are long, especially in the female.

The glottis in Serpents can be drawn forward and protruded from the mouth by the action of the *geniotracheales* muscles, fig. 147, *y*, p. 229. In marine serpents the glottis is situated very near the forepart of the mouth, and the air can be inspired at the surface without exposure of the jaws. The upper rings of the trachea coalesce to form a cricothyroid cartilage, sending forward two processes which represent the arytenoids in many *Ophidia*; but which are freely articulated therewith in the great constrictors. The 'processus epiglotticus' is subquadrate in *Boa*. True 'chordæ vocales' are absent; and the voice is reduced to a hissing sound produced by the action of the expired air upon the margins of the glottis. The rings of the trachea are entire, and the trachea varies in length in different serpents before it reaches the lung. Along this it continues, of decreasing breadth, with portions of the rings, as if incrustated in the pulmonary parietes, for an extent varying in different serpents.

In Lacertians a cricothyroid cartilage supports a pair of arytenoid cartilages: in most there is a cartilaginous or osseous 'processus epiglotticus,' which, in a few, coexists with an incomplete epiglottis. The mucous membrane of the glottis is reflected over the arytenoids, forming a depression beneath them, and folds with free margins: these 'vocal chords' are broad in the Chameleon and Gecko, and stretch from the base of the arytenoid to the

inner surface of the cricothyroid. In *Iacerta* and *Ascalabotes* the corresponding fold is very narrow, and the chirping call-note of the Gecko may depend rather on the vibration of the margins of the glottis than on the vocal folds, which cannot be brought into contact or be made tense. In the Chameleon, the lining membrane of the larynx is produced between the cricothyroid and first tracheal ring into a pouch. In the *Stellio* of the Levant the tracheal rings are osseous: in most Lizards they are cartilaginous. The trachea is remarkable for its width in *Platydictylus guttatus*, but the diameter is reduced to one half in *Platydictylus vittatus*. In the Chameleon and most other Lacertians it is still narrower.

Amongst the *Chelonia* the Hawksbill Turtle (*Chelone imbricata*) shows a glottis undefended by retroverted papillæ, or by an epiglottis, but capable of being accurately closed by its constrictors. The thyroid cartilage in all *Chelonia* is distinct from the cricoid: the arytenoids are triangular, and their inner facet is large in *Emys* and *Testudo*. The ordinary sound produced by the larynx of the *Chelonia* is a sort of hiss. The European fresh-water Tortoise emits a low piping note, and Agassiz records the same fact in regard to some North American Emydians.<sup>1</sup> In *Chelone mydas* the 'rima glottidis' supports on each side a mucous fold, which serves to produce a low grunt or bark at certain seasons. In some Tortoises (*Testudo tabulata*, *T. elephantopus*) a triangular membrane ascends from the base of the larynx to the 'rima,' dividing it into two parts. The rings of the trachea are entire and cartilaginous: in some species the trachea bifurcates half way towards the lungs, the bronchi being of great length, and one of them usually describing a large curve: in *Testudo græca* the left bronchus is three fourths longer than the tracheal trunk; but in *Testudo couei* the trachea is one fourth longer than the bronchi. The production of the snout in the *Trionycidæ* enables the terminal nostrils to be raised above the surface of the water, to respire, without exposure of the animal.

In the Nilotic Crocodile the mucous membrane is produced into a fold on each side the 'rima glottidis:' the folds deepen as they extend backward, and are produced into a pair of pointed processes above the arytenoids. The broad cartilaginous plate of the basihyal rises in front of the glottis like an epiglottis. On divaricating the rimal folds they are seen to bound a wide pouch anterior to and above the true 'aditus laryngis,' which is much shorter than the 'rima.' The thyroid and cricoid coalesce to form one annular cartilage supporting the pair of arytenoids. The

<sup>1</sup> ccc. vol. i. p. 284.

membrane covering these forms a wide depression anterior to and below them, before being continued as chordæ vocales, along the posterior half of each side the 'aditus laryngis.' These 'chordæ' operate in producing the 'bellow' of the Crocodile, a loud sound, between barking and roaring.

The trachea in the Nilotic and some other kinds of Crocodile forms a bend or loop before dividing into the bronchi: this loop is not found in the Alligator or Gavial. The erectile structure of the single tegumentary nostril in the Gavial, serves, like the short proboscis of the *Trionyx*, to enable the aquatic reptile to breathe the air with more safety.

§ 94. *Respiratory actions of Reptiles.*—The lungs in *Batrachia* being suspended in a common thoracic-abdominal cavity, without the costal or diaphragmatic mechanism of expansion, are filled with air by acts of deglutition.

The hyoid, fig. 350, *b*, is depressed; the pharynx, *ib. e*, is dilated: the air enters by the nostrils, and its return is prevented by their internal valvular folds, and by the application of the tongue, *ib. a*, against their palatal openings. The contraction of the throat-muscles and retraction of the eyeballs send the air backward, the gullet contracts, the glottis opens, and the air is driven through the bronchi, *f*, into the lungs, *g*. If the mouth of a Frog be kept forcibly open it is soon asphyxiated, the essential respiratory acts being prevented: if a breach be made in the abdominal walls, and the act of deglutition can be performed, the lungs are inflated. Expiration is performed by the elasticity of the pulmonary parietes, which is such as to quite empty the lung and reduce it to the size of a small pea, the abdomen being opened.

The lungs of *Chelonia* being lodged in a cavity, the capacity of which is only affected by the retraction and protrusion of the limbs and tail, appear, also, to be filled with air, chiefly by acts of deglutition. These are so habitual that 'the working of the throat' continues when the Turtle is immersed in water; and Hunter was led by observing this circumstance, to relinquish the idea of its being a respiratory act. It is, in fact, in the *Chelonia* in which the plastron remains unfixed by bone to the carapace (*Chelone*, *Trionyx*) that respiratory acts due to movements of the thoracic-abdominal walls are most conspicuous. 'If a Turtle be thrown upon its back, and makes an inspiration, we may observe that its four fins are, as it were, erected; the breast-bone is pushed forward, and the cavity swells out wherever the parts are soft. All this is done, I conceive, by the muscles of the extremities moving

their respective bones in an inverted order: instead of their moving the extremity, the extremity becomes the fixed point: the bones answering to the clavicles are moved forward, and the bones of the pelvis at the lower part are pushed against the inside of the breast-bone, so that the whole bone is pushed out. They appear to draw in their breath but once in twenty minutes or half-an-hour, and often at a much longer interval.<sup>1</sup>

It is probable that such respiratory actions could not be performed by the animal when swimming and diving; and it is certain that such actions of the limb-muscles could not effect any motion of the breast-bone in the great proportion of the Chelonian order, in which the plastron is fixed. The capacity of the thoracic-abdominal cavity may be slightly affected by the movements of the limbs acting on the soft walls at its fore and and back parts, fig. 149, p. 233; the diaphragmatic muscles, figs. 150, 151, 42, may cooperate; but respiration goes on when the limbs are motionless, and apparently by acts of deglutition, as indicated by the 'working of the throat.'

In *Ophidia*, *Lacertilia*, and *Crocodylia*, respiration is performed by the expansion and contraction of the more movable parts of the parietes of the cavity containing the lungs: for this being dilated the air rushes in by the only available passage, viz. the glottis and windpipe, to the lungs. The articulations of the ribs in serpents allow of their rotation forward and backward, and even of a slight divarication of the two ribs of each pair. This mechanism and the muscles concerned in working it are described, pp. 55, 56, 224, figs. 143, 144. To whatever degree the visceral cavity may be so expanded, the air enters by the nostrils or glottis, if they be open and free; and a general expansile or inspiratory movement may then be noticed.<sup>2</sup> But the great length of the thoracic-abdominal cavity and the numbers of pairs of moveable ribs—in some serpents three hundred pairs—are associated with partial enlargements and contractions of the cavity, effecting corresponding changes in the long pulmonary bag, without affecting the total volume of air in it, if the glottis be not in communication with the outward air, either directly or through the medium of the nostrils. Schlegel has observed about thirty such partial dilatations of the trunk and lung between two inspirations.<sup>3</sup> When the Constrictors swallow their prey the glottis is protruded from the mouth: this may be a consequence of the pressure exercised on the parietes of the greatly distended mouth, and may not relate to the necessity of directly receiving

<sup>1</sup> CCXXXVI. vol. ii. p. 348.<sup>2</sup> CCLXXXV.<sup>3</sup> CCXXXIV. tom. i. p. 53.



air during the period occupied by the rotatory transit of the prey to the gullet: it is more probable that at this time the trachea is squeezed flat, and the air in the hinder reservoir of the largest lung may serve to keep up the small amount of respiration needed during the passage of the prey to the stomach, the snake being then at rest and almost torpid.

In Lizards and Crocodiles certain pairs of vertebral ribs (pleurapophyses) at the forepart of the thoracic-abdominal cavity articulate with sternal ribs (hæmapophyses), the bony arches being completed by the sternum below. The pleurapophysis, fig. 49, *f* (p. 57), forms an angle directed backward at the joint with the hæmapophysis, *ib.* 6, the muscles raising or drawing outward and forward the upper rib open the angle between it and the lower one; and the head of the rib being fixed to the vertebra, the sternum yields, is depressed, and both the vertical and transverse diameters of the cavity containing the lungs are increased. Consequently the air enters the pulmonary cavities. By the contrary actions, the thoracic-abdominal cavity is contracted, and, the elasticity of the pulmonary parietes aiding, the air is expelled.

In the Crocodile the increase in the number of the complete sterno-costal arches, fig. 56, 1, 2, 3, &c. (p. 68), gives greater effect to their respiratory movements: and the muscular fibres attached to the midriff-like sheets expanded upon the hepatic lobes, may aid in making the general expansion of the thoracic-abdominal cavity tell more directly upon the lungs.

Almost all the Lacertilia and Batrachia have the peculiarity of inflating their lungs, when they are under the influence of fear or of some other excitement: in the Chamæleon, as well as in Polychrus and many other Iguanoids, the expansion of the trunk consequent thereon aids in producing the remarkable change of colours to which we shall recur in the chapter on the integuments.

## CHAPTER VIII.

## URINARY SYSTEM OF HEMATOCRYA.

§ 95. *Kidneys of Fishes.*—In all Vertebrates an excretory organ is very early developed in the form of a tube, extending from each side of the cloaca forward, along the dorsal region of the abdomen, close to the spine, where it communicates with a number of slender blind tubes placed at right angles to it; the longitudinal trunk-tube serving as the excretory duct of the shorter transverse secerning cæca. These glands are transitory in the air-breathing Vertebrates and are called, from their discoverer, ‘corpora Wolffiana;’ they are persistent in fishes<sup>1</sup> and are called ‘kidneys,’ fig. 352, *n*: in both they are renal organs and secrete urine.

A slightly opaque, slender, elongated glandular body, in the situation marked *h* in fig. 169, may represent the renal organ in *Branchiostoma*. The structure of this organ is more obvious in the Myxinoids: it is double: each long duct, fig. 353, 1, *a*, as it extends from the cloaca through the abdominal cavity, sends off, at regular but distant intervals from its outer side, a short wide tube, *ib. b*, which communicates by a narrow opening with a blind sac, *ib. d*. At the bottom of this sac or cæcum there is a small vaso-ganglion, fig. 353, 2, *D*, free on all sides save that by which the vessels, *ib. a*, enter, and *ib. b*,<sup>2</sup> quit it: there are no uriniferous tubes in this vaso-ganglion: the contents of the cæcum must react through its thin parietes and those of the capillaries with which it is in contact upon the blood in those capillaries, and extract therefrom the azotised uric principle. Analogous vascular bodies, formed chiefly by convoluted tufts of arterial capillaries, are present in the Wolffian bodies of Mammals, and in the persistent renal organs of all Vertebrates. They are called, after their discoverer, ‘Malpighian corpuscles,’ and the uriniferous tubes take their rise by a sacciform blind beginning applied over the vascular tuft or ganglion.<sup>3</sup>

The combined secerning cæca and vaso-ganglia form in the

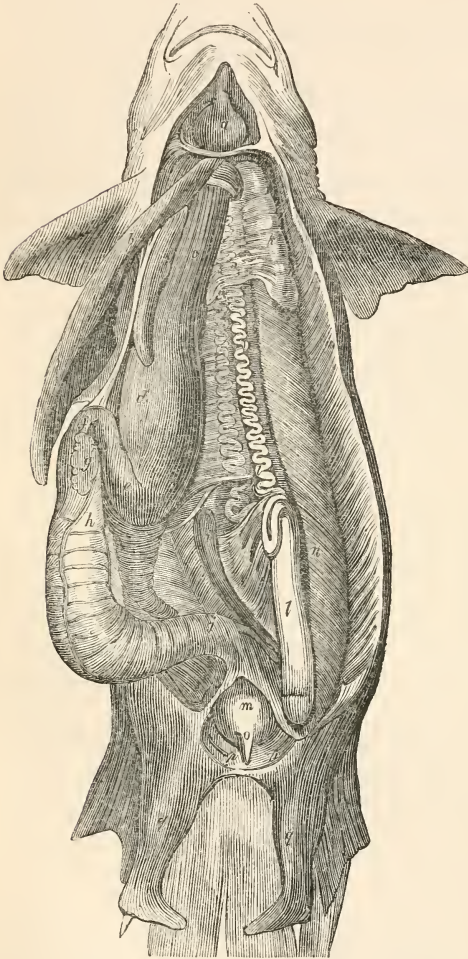
<sup>1</sup> cxxx. ii. p. 314.

<sup>2</sup> xxi. p. 13.

<sup>3</sup> cxxxvii.

Lampreys<sup>1</sup> a continuous narrow elongated gland, which extends in their young or Ammocete condition throughout the abdomen, but in the full-grown fish (*Petromyzon*) along the posterior two thirds: in

352



Viscera of male Shark, showing kidneys, *n*, *in situ*

both being confined to the dorsal part of the cavity, fig. 354, *g*. The ureters, *ib. e*, open into the short canal leading to the papillary production of the peritoneal outlets close to the anus.<sup>2</sup>

In most Osseous Fishes the kidneys are long and narrow, and extend through the whole or a great part of the dorsal region of the abdomen, firmly attached to the vertebral column; they are usually broadest and thickest anteriorly, where they sometimes present a lobulated surface; they contract, approximate, and frequently blend together as they extend backwards (*Cyclopterus*); sometimes penetrating the hæmal canal in the tail. In the Gymnotus the kidneys are distinct and thickest at their posterior ends, as they are in the Gurnard, fig. 379, *k*, and in most Sharks. The kidneys have not a well-defined capsule in Osseous Fishes, but

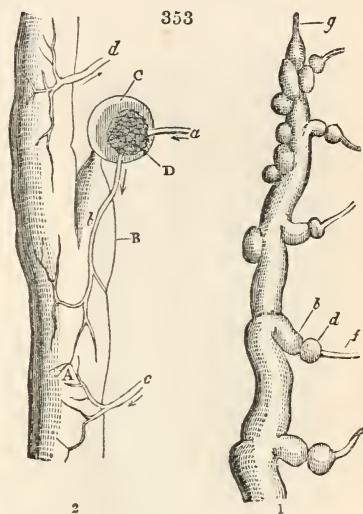
their ventral surface is immediately covered by an aponeurotic membrane, against which the peritoneum, and the air-bladder when present, are applied. The renal tissue is soft and spongy,

<sup>1</sup> In *Petromyzon marinus* the diameter of the tubuli uriniferi is  $\frac{1}{284}$ th of an inch, that of the capillaries of the kidneys being  $\frac{1}{1800}$ th of an inch. <sup>2</sup> XX. iv. pl. 56, fig. 1, e.

firmest at the fore-part of the gland; usually of a reddish-brown colour; sometimes soaked, as it were, with dark pigment.<sup>1</sup> It is supplied by numerous small arteries from the abdominal aorta,<sup>2</sup> which form Malpighian corpuscles; but these are fewer in number and less complex than in the true kidneys of higher Vertebrates. The primary branches of the tubuli uriniferi, given off from the long ureter, are extremely numerous; their divisions in the renal substance are comparatively few; they are in most fishes convoluted and of equal diameter, extending through the whole renal substance, which shows no distinction of cortical and medullary parts, and has neither 'pelvis' nor 'mammillæ:' they are lined by a ciliated epithelium. Sometimes a single common ureter quits the coalesced hinder ends of the kidneys, as in the Pike, and terminates in a urinary bladder. More frequently the essentially duplex nature of the kidneys is manifested by the emergence of two ureters from the ventral surface of their posterior ends when these have coalesced: in some fishes the ureters unite together after quitting the kidneys, and terminate by

a common gradually widening canal in the urinary bladder; sometimes they enter the urinary bladder separately, as in the Wolf-fish, where they both terminate on its left side, half an inch above the cervix: rarely are any smaller accessory ureters seen, as e.g. in the Stickleback, to terminate also, separately, in the bladder. This, in aquatic animals apparently needless, receptacle of a fluid excretion is, nevertheless, rarely absent in Osseous Fishes; the Pilchard, the Herring, and the Loach are among the few instances where it is not developed. In the Loach a very short, in the Herring a long, common ureter terminates behind the anus. In the Gymnotus the common ureter is so wide as to serve as a receptacle, and it is directed forward to reach its termination immediately behind the advanced vent.

The urinary bladder is sometimes round, fig. 379, *b*, sometimes



1. The anterior extremity of the kidney, *Bdellostoma*. XXI. 2. Malpighian body and its blood-vessels, *Bdellostoma*. XXI.

<sup>1</sup> As in *Lepidosiren*, xxxiii. p. 349.

<sup>2</sup> Hunter, vii. vol. ii. p. 112.

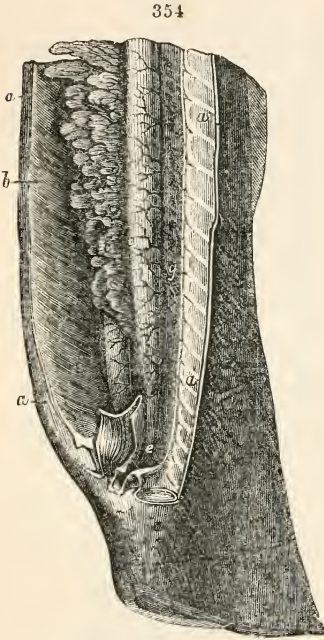


oval or pyriform, often bifid at its fundus, or two-horned; it is largest in those fishes, as the *Pleuronectidæ*, *Lophius*, *Orthogoriscus*, and *Cyclopterus*, in which the air-bladder is absent. In *Callynymus* the bifid urinary bladder extends the whole length of the abdomen. It always lies behind the rectum, generally receives the ureter or ureters nearer its fundus than its cervix, and the latter is prolonged usually into a prominent papilla behind the vent. The long cervix vesicæ in the Salmon is surrounded by a venous

plexus. In the Sturgeon the wide ureters extend along the outer borders of the kidneys, and receive the vasa deferentia or the oviducts in their course towards the cloaca, where they unite into a short duct which forms the common outlet of the urinary and generative products.

The kidneys are long, narrow, but distinct from each other in all the Ganoid Fishes and in the Lepidosiren. In the *Lophius* the kidneys present a more compact form, and are situated wide apart, far forwards in the abdomen, in depressions on either side of the origins of the 'retractores palati.' The kidneys of the Plagiostomes are also of a more compact form than in Osseous Fishes, and are always distinct, and generally show a cerebriform convoluted or lobulated exterior: the primary

branches of the uriniferous tubes are fewer, and their dichotomous ramifications more numerous:<sup>1</sup> the ureteric trunk becomes superficial along the inner and fore-part of the hinder half of each kidney; after quitting which it dilates in the Grey Shark (*Galeus*) into a kind of receptacle, fig. 352, *m*, behind each oviduct or vas deferens, and communicating with its fellow near the cloaca, terminates by a single urethral canal upon a kind of penis or clitoris, ib. *o*, at the back of the anus, within a large common cloaca. In the Torpedo, the ureters terminate on the cloacal papilla by two dis-



Kidney and generative organs, Lamprey (*Petromyzon marinus*). XX.

<sup>1</sup> In the Ray, the diameter of the terminal branches of the tubuli uriniferi are  $\frac{1}{151}$ th of an inch, that of the capillary renal arteries being  $\frac{1}{1650}$ th of an inch.

inct orifices.<sup>1</sup> In the Skate and Thornback each ureter terminates in the neck of a short bifid bladder: these open by a common urethra upon the cloacal papilla. The Lepidosiren has a small urinary bladder situated behind the rectum and in front of the oviducts: the ureters do not communicate directly with it, but terminate separately on small papillæ in the oviducal compartment of the cloaca.<sup>2</sup>

With regard to the circulation in the kidney of those Fishes, as e. g. the Plagiostomes, the Lophius, and the Lepidosiren, in which the organ is best defined, the vein on the outer side of the kidney which receives blood from the tail, the abdominal parietes, and the generative organs has so far the aspect of a 'portal' or inferent vessel, that a second and larger vein, whose roots take their rise in part from the renal substance, extends from the inner and forepart of the kidney to convey its blood to the postcaval vein. The exterior vein is not, however, completely expended in the kidney, but is also continued forward from the anterior end to join the veins from the anterior abdominal parietes, and sometimes those from the pectoral fins. In all Fishes the kidneys maintain the same relations with the cardinal veins that their transitory homologues the 'Wolffian bodies' do in the embryo of higher Vertebrates.

§ 96. *Kidneys of Reptiles.*—In this class the kidneys are always a distinct pair, and are more circumscribed in form, and more compact in structure than in Fishes; but, as in them, the renal tissue is uniform, not divided into 'cortical' and 'medullary' parts.

In the *Siren* each kidney is a long, oval, subcompressed body, tapering anteriorly to a point situated in the hind part of the abdomen, dorsad of the rectum, with an entire investment of peritoneum reflected upon their inner edges, where they receive small arteries. The ureters enter the back part of the cloaca, from the fore part of which is developed a small allantoid or urinary bladder. The kidneys of *Amphiuma* resemble those of *Siren*. In the *Menopoma* the kidneys are relatively longer, extending nearly the whole length of the abdomen on each side of the vertebral bodies.

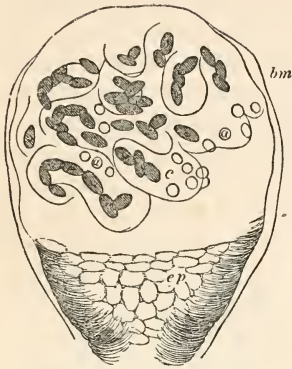
In the Newt the kidneys are less elongate, and their forepart becomes so thin and transparent that it lends itself favourably to microscopical examination. The ciliated epithelium continued from the uriniferous tubule, terminates abruptly shortly after entering the Malpighian capsule, fig 355, *ep*: the basilemma of the capsule, *bm*, beyond the termination of the ciliated epithelium, appears to be unclothed: it is a homogenous, transparent, structureless substance, perforated by the inferent and efferent vessels, and not reflected over them. The inferent

<sup>1</sup> CXXXVI.

<sup>2</sup> XXXIII. pl. 27.

vessel dilates on entering, forms a few coils, again contracts, and

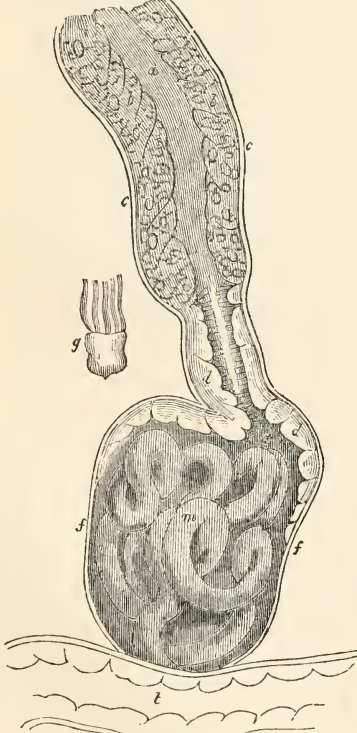
355



Malpighian body, Newt. CCLXXXVI.

meters, the part where the

356



Malpighian body, Frog. CXXXVII.

<sup>1</sup> CXXXVII.

becomes the efferent vessel.<sup>1</sup> In the Frog the kidneys present a more compact form; they are flattened, subelongate, with a convex outer border and a nearly straight inner one, fig. 331, *κ, h*. They are situated at the pelvic end of the abdominal cavity behind the rectum and allantoic bladder: the peritoneum covering only their sternal surface. The renal capillaries, derived from the reniportal vein, *ib. κ*, ramify through the gland to reach the Malpighian capsule, fig. 356, *f*: in the specimen figured, by Bowman,<sup>2</sup> under the magnifying power of 320 dia-

ameters, the part where the capillaries enter (near *t*) is obscured by an uriniferous tube. On entering, the capillary enlarges and forms a few coils, *m*, which lie bare in the capsular cavity. The lemma begins to receive an epithelial lining at *f, f*, which increases in thickness to the neck of the tubule, *d, d*, and is covered by cilia: these may maintain their motions hours after the death of the Frog. The uriniferous tubules form by successive unions the ureter, which opens into the urogenital compartment of the cloaca, opposite the orifice of the large bifid allantoic bladder, the contents of which are mainly water.

In Serpents the kidneys, fig. 357, *t, t*, partake of the usual elongated form of the viscera, and are subdivided into numerous flattened, overlapping lobes, so as readily to accommodate themselves to the flexuosities of the part of the trunk in which they

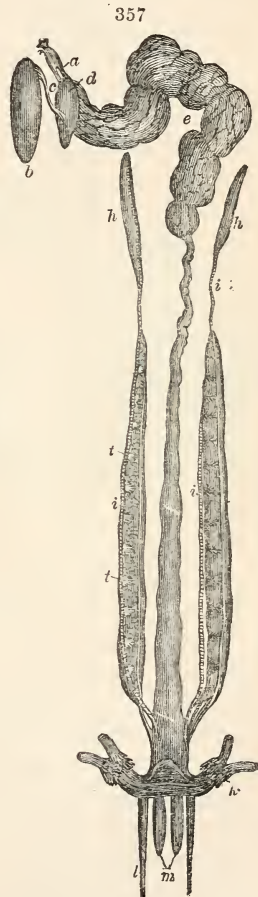
<sup>2</sup> *Ib.*



are lodged. In most Serpents they are unsymmetrically situated; the left in *Coluber natrix*, e.g., being one-fourth of its length nearer the cloaca than the right kidney; and they are loosely attached to the dorsal abdominal walls. Each renal lobe is so distinct that it may be regarded as a separate kidney or renule: it is reniform in *Python* and *Boa*, and is principally composed of the ramifications of the renal artery, the reniportal and renal veins, and the uriniferous tubules with their initial (Malpighian) capsules. The artery of the renule, entering at the notch or 'hilum,' representing the pelvis, distributes its branches fanwise through the middle of the substance: each branch, fig. 358, *a*, sends twigs to the Malpighian capsule which form within it the dilated plexus, analogous to that in fig. 356, whence the blood is returned by the efferent vessel, in the direction of the arrow, to the branch of the reniportal vein, fig. 358, *p, v*: these branches being distributed fan-wise over both surfaces of the flattened renule. In this course they communicate with, or help to form, a rich venous plexus, *ib. p*, surrounding the tubuli uriniferi, *ib. t*, and communicating with the branch of the renal or emulgent vein, *ib. e, v*, which accompanies the artery, in the mid-substance of the renule.

The tubuli, *ib. t*, continued, as in fig. 356, from the capsule of the 'Malpighian body,' after some convolutions, pass to the surface next which the 'body' is placed, and terminate in a branch of the ureter, *ur*, there situated: these superficial branches are dispersed fan-wise, converging to the 'hilum,' and are often seen injected, as it were, by the opake white pultaceous urinary excretion. The Malpighian bodies diminish in size and the tubuli in length, towards the thin edge of the renule.

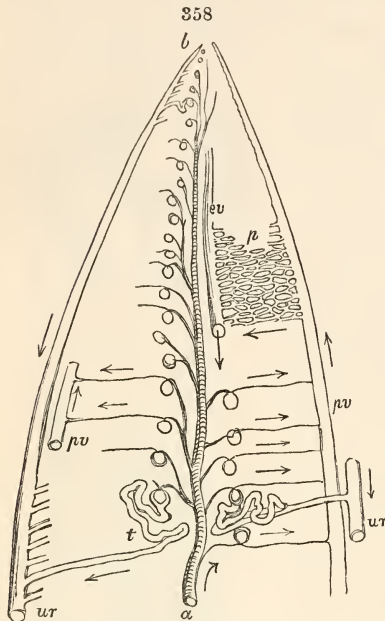
Thus, on each superficies of the flattened renule are the radiating ramuli of the ureters, *ur*, and reni-portal veins, *pv*; whilst along



Kidneys and small organs, Rattlesnake (*Crotalus*). CCL.



the plane, midway between these surfaces, are the similarly disposed branches of the renal artery, *a*, and renal vein, *v*. The material of the urinary excretion thrown by the epithelial cells or bags from the inner surface into the cavity of the uriniferous



Plan of disposition of blood-vessels and tubuli in the renule of Boa. CXXXVII.

tubules, *t*, is derived from the rich venous plexus, *p*, everywhere in contact with their outer surface: the serosity exuded from the dilated arterial plexus in the Malpighian capsule, propelled by the ciliary action, dilutes and washes out the excretion from the tubuli, whence it is conveyed by the superficial branches of the ureters to the trunk, or ureter, common to the several renules, and, by the ureters, is discharged into the cloaca.<sup>1</sup> There is no urinary or allantoid bladder in Serpents.

The kidneys in Lacertians, fig. 301, *h*, fig. 332, are shorter, broader, and less subdivided than in Serpents; situated close to the verte-

bral bodies at the hinder part of the abdominal cavity; they are usually pointed at their forepart (*Cyclodus*). In the Iguana they are of an oblong, subdepressed form: their structure is essentially that above described in the Boa. The ureter runs superficially, as it collects its tributaries, along the free or ventral surface of the kidney, and terminates in a slight eminence, papilla or ridge, close to the genital orifice, in the urogenital compartment of the cloaca, behind or dorsad of the anus. Anterior to, or sternad of, the terminal orifice of the rectum, is that of the urinary or allantoid bladder, of large size in the Iguana. In this reptile Hunter found the bladder 'filled with a white fluid,' and 'there were small calculi in it.'<sup>2</sup> In the same reptile he records the presence of 'one brown calculus in each ureter, almost filling the duct.'<sup>3</sup>

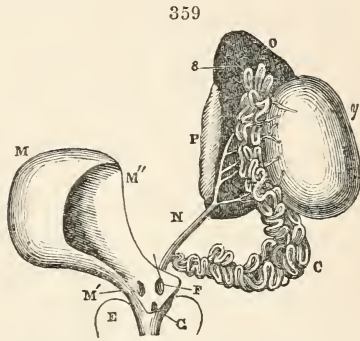
<sup>1</sup> The ingenious and lucid explanation of the functions of the minute structures given by their discoverer, Mr. Bowman, in CXXXVII.

<sup>2</sup> CXXXVI. vol. ii. p. 367.

<sup>3</sup> Ibid.

The fatty appendages which are attached to the kidneys or urinary bladder in *Batrachia*, *Ophidia*, and *Lacertilia*, attain a remarkable size in some members of the latter order; in the *Iguana tuberculata* they are attached by a narrow process to the sides of the bladder, near its neck.<sup>1</sup>

In the *Chelonia* the kidneys present a more compact form, and their surface is convoluted through the disposition of the component lobes. They have the same low pelvic position as in Lizards, but are smaller in proportion, and are outside the peritoneum. In the Tortoise (*Testudo tabulata*) they are oblong, broad, thick, subtrihedral bodies: in the Turtle (*Chelone mydas*) they are flattened anteriorly, or towards the abdominal cavity, convex where they rest upon the dorsal wall. In *Emys*, figs. 307 and 359, o, they are semioval. The tubuli uriniferi pass to the superficies of the lobules and there form the branches of the ureter, which unite towards the mesial border with the beginning of the main duct, ib. n; this is short, and terminates, with the spermduct, c, in the male, in the urogenital cavity at f. The rectal orifice intervenes between this



Male organs of generation, and kidney of *Emys europæa*. XXXVIII.

and the wide opening of the urinary bladder, ib. m, m''. This receptacle is proportionally smallest in the marine *Chelonia* (*Chelone*, *Trionyx*): in its contracted state it presents, in *Chelone mydas*, thick muscular parietes and a corrugated internal surface. In terrestrial and fresh-water *Chelonia* the bladder is relatively much larger, and with thinner walls. In many it is bifid. In Emydians, besides the ordinary bladder, fig. 304, u, a pair of other bladders, ib. u', u'', communicate by wide orifices, behind the ureters, with the cloaca (p. 447).

In the *Crocodylia* the kidneys are of an oblong oval form; the forepart is thickest or largest, and is sternal of the psoas muscle, the hind part extends into the side of the pelvis; they are in contact with each other at the mid-line. The surface is convoluted, like the brain, but with smaller and more numerous gyræ; the colour of the kidney is usually a deep brown. The ureters terminate in low papillæ, in the urogenital compartment of the

<sup>1</sup> xx. vol. iii. p. 221, prep. no. 1820 A.

cloaca behind the genital orifices; the forepart of the cloaca is slightly dilated, and the rectum opens therein by a valvular protrusion.

The formation and disposition of the reniportal and renal or emulgent veins have been previously described.

§ 97. *Adrenals of Hæmatocrya.*—The bodies called ‘suprarenal capsules,’ ‘renes succenturiatæ,’ ‘capsulæ atrabiliaræ,’ &c., in Man, may be represented in the lowest Vertebrates, e.g. the Myxinoids, in the form of a pair of small oval lobulated bodies situated in advance of the kidneys, and close or adherent to the portal sinus. In the lamprey a glandular body lies between the aorta and cardinal vein, adhering to the coats of the latter; but it has not the characteristic structure of the adrenals in higher Vertebrates. In ordinary Osseous Fishes the adrenals have been recognised as roundish bodies of a light grey colour; commonly two, rarely three or more in number, situated sometimes near the middle, oftener at the hinder ends of the kidneys, at or near the entry of the hæmal canal; but in the Eel they are found where the two kidneys unite. They are commonly symmetrical in position; but in the genus *Scomber* one adrenal is in advance of the other; and in *Pleuronectidæ* they lie both on the same side of the body. Sometimes they lie free, sometimes they are imbedded in the renal tissue: they usually possess a proper capsule, and present a minutely granular texture without distinction of cortical and medullary parts. Their surface is smooth in some Fishes, irregular in others; in large and old Pike three adrenals have been seen; but in the young (‘Jack,’ one foot long), the kidney has been found to be beset with a number of small adrenals.<sup>1</sup> The yellowish adrenals of the Sturgeon occur as numerous small glandular bodies studding the dorsal surface of the kidney. Four or five similar bodies are sometimes found in the Skate; but more commonly in Plagiostomes, the adrenals are represented by a single elongated narrow yellowish and lobulate body, situated behind the kidney, and sometimes extending behind the dilated ureter.<sup>2</sup> The adrenal in Fishes, whether compacted or subdivided, consists of an aggregate of lobules, with proper capsules, connected by looser connective tissue: each lobule consists of cells of about  $\frac{1}{4000}$ th of an inch in diameter, containing nuclei, fat-globules, and molecular particles, the latter being mostly aggregated about the nucleus. Processes from the lobular capsule pass inward and insulate the multinucleate cells. In the young Pike the molecular-clothed nuclei acquire a cell-wall, become liberated, and converted into

<sup>1</sup> CCLXXXVII.

<sup>2</sup> CXXI.

new multinucleate cells. In old Pike this multiplication is arrested: the connective tissue increases in quantity and density, and the multinucleate cells are more separated from each other. The connective tissue and the capsules which it forms for the adrenal and its subdivisions, are richly supplied with blood-vessels.

The structure of the adrenals, however, is subject to great variation within the limits of one and the same species in the piscine class. The following modifications have been observed in the Cod-fish<sup>1</sup>: 1. Very rarely the adrenals are entirely absent. 2. They are semifluid, very vascular, not encased in a capsule, and without defined form; the blood-corpuscles are extremely numerous, aggregated in small lumps, and in various stages of transmutation. 3. They possess a proper capsule, being more or less vascular. 4. They are shrunk, with but a few, or without any blood-vessels. 5. Not rarely a part of an adrenal is composed of cells and lobules, whilst another part is a formless conglomeration of molecular particles, fat-globules, &c.

Adrenals are entirely absent in the Herring and in the Launce (*Ammodytes Tobiannus*).

The fish-like Batrachia resemble some Fishes in the subdivided condition of the adrenals; twenty or more lobules, showing the above-described structure, may be found partly imbedded in the substance of the kidney, at its mesial border, partly between the kidney and the renal and postcaval veins, surrounding the coats of the efferent veins (*Siren*, *Triton*). In the Frog and Toad the adrenals appear as a yellow streak on the sternal aspect of the kidney, arching from about one line from the fore end to within two lines of the hind end of the gland; it shows a lobular structure, and surrounds the efferent emulgent veins, closely adhering to or imbedded in the coats, as they leave the kidney to join or form the postcaval vein. The lobules consist of groups of multinuclear cells, containing a greater proportion of oil-globules than in Fishes: but both the free nuclei and granules are present, the former sometimes showing stages of development into nucleate cells. The blood is supplied chiefly by branches of the reniportal vein.

In the *Ophidia* the adrenals are long, slender, lobulate bodies, closely adherent to the coats of the emulgent veins, in advance of the kidneys: in a Python of ten feet in length they measure nearly one inch. The adrenals are rather less elongated in *Anguis fragilis*. The adrenals are supplied by minute branches from the

<sup>1</sup> cccxxxi. 'Fische,' p. 258.



aorta, and more abundantly by vessels sent to them from the plexus venosus of the neural canal; both kind of vessels ramify in their substance, forming a fine capillary network upon the capsules of the multinucleate cells. The blood is returned from the right adrenal directly to the postcaval vein, and from the left adrenal to the corresponding emulgent vein. In *Lacerta ocellata*, each adrenal is about one sixth of an inch in length, and one-eighth of an inch in breadth, adherent to the emulgent vein, where it forms the postcaval: upon which the right and usually the larger adrenal sometimes lies. In the male Lizard it is situated between the vein and the vas deferens: in the female, between the vein and the ovary. The adrenals are lobulated, and well supplied with blood; their minute structure is essentially the same as that in *Ophidia* and *Batrachia*.

Hunter left preparations of two glandular bodies, with a convolutè exterior surface, and a homogenous parenchyme, similarly disposed, which he called 'supra-renal glands' of a Tortoise;<sup>1</sup> and, in his 'Anatomy of a Land-Tortoise,' he writes, 'The capsula renalis is large and flat, situated above the kidneys: it looks like a pancreas, being conglomerated, but, when cut into, appears to be all of the same substance.'<sup>2</sup> Bojanus regarded two long bodies, situated at the inner margin of the kidneys of *Emys europæa* as the adrenals; but, according to Ecker, the adrenals of *Testudo græca* lie on the abdominal (sternal) surface of the kidney, imbedded in its substance, extending almost the whole length of the gland, as in the Frog.<sup>3</sup> Under the microscope they appeared as aggregates of yellow granules, each inclosed by a proper capsule, and containing nuclei, oil-globules, and molecular particles.

Hunter describes the adrenals in the Crocodile as 'two oblong bodies, darker on their exterior surface than internally, and in some places little yellow bodies are to be seen upon them, as in the kidney; and on the outer edge is a very small yellow thread passing down, which is continued along the broad ligament its whole length towards the anus.'<sup>4</sup> This might be the remnant of the duct of the primordial kidney.

<sup>1</sup> xx. vol. iii. p. 130, preps. nos. 1277, 1278.

<sup>3</sup> cclxxxvii.

<sup>2</sup> ccxxxvi. vol. ii. p. 364.

<sup>4</sup> ccxxxvi. vol. ii. p. 340.

## CHAPTER IX.

## TEGUMENTARY SYSTEM OF HÆMATOCRYA.

§ 98. *Composition of Tegument.*—The tegumentary organs of Vertebrates, where they do not happen, as in exceptional instances or parts of the body, to blend with the periosteum of the endoskeleton, are defined from subjacent structures by loose or yielding connective tissue: hence the facility with which Vertebrates of all classes can be ‘skinned.’ The part so removed is the ‘tegument,’ and constitutes the outermost of the organs differentiated in the course of embryonal development from what has been termed the ‘serous’ or ‘animal’ layer of the blastoderm.

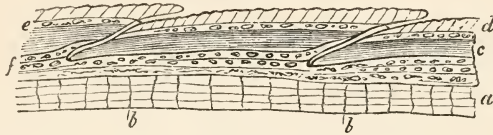
Tegument mainly consists of an outer epithelial layer, called ‘epiderm,’ and an inner fibrous or areolar layer, called ‘derm.’ The tissue of the derm includes ‘white fibres’ and ‘yellow fibres.’ The white element forms bands of unequal thickness, striated longitudinally, but irregularly, and breaking up into fibrils of different width, the finest being too minute for micrometry. The white bands interlace in various directions, with a wavy course, frequently subdividing, and joining those near them. The yellow fibres are solitary, very elastic, disposed to curl, branching at intervals of variable length, and the branches, usually as large as the trunk, uniting with contiguous ones. A drop of acetic acid, which instantly swells the white bands and makes them transparent, produces no change on the yellow filaments.<sup>1</sup> Into the derm enter bloodvessels, absorbents, and nerves: it never contains fat. Epiderm consists of epithelial cells of every form—caudate, tessellate, rarely ciliate—and in all stages of development, increasing in density, horizontality, and overlappingness as they approach the outer surface of the skin, and blended with pigment-cells and pigment-particles in proportion as they are near the derm: but many other parts are specialised in the tegumentary area of the blastoderm than those which, from their greater abundance and constancy, give the character to the two best defined layers.

Bulbs or pulps of hairs and feathers, bony scutes, and fish-scales

<sup>1</sup> CCXC. i. p. 491.

—sebaceous, sudoriparous, and mucous follicles—may be developed in or from the derm: the epiderm may be condensed into nails, claws, hoofs, horns and horny scales. The warm-blooded are distinguished from the cold-blooded classes by the non-conducting or heat-retaining nature of the superficial covering of the tegument.

360

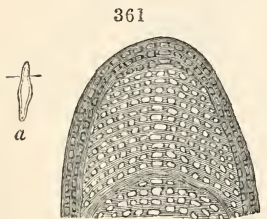


Diagrammatic section of skin of fish.

§ 99. *Teguments of Fishes.*—The skin in fishes is more tensely stretched over the body, and often more closely united to the subjacent fascia or flesh, than in other Vertebrates: consequently it enjoys less mobility. The constituent fibres of the derm or corium are so disposed as to give it a laminated structure, fig. 360, *a*; the horizontal layers being connected by vertical sub-elastic fibres,<sup>1</sup> *ib. b*. The numerous papillæ or processes from the skin of the under part of the head of the Sole (*Solea vulgaris*) give it a villous character: other instances where the derm develops tactile papillæ in fishes are indicated at pp. 326, 411.

In the Lancelet the dermal fibres are minute, and compacted into two planes, one nearly at right angles to the other. In the Lamprey the derm consists of two layers of flattened fibres crossing each other at right angles. The epiderm exhibits numerous large stellate pigment-cells. In the Eel, the epiderm is soft and thick, consisting of many layers of cells, caudate and tessellate, those next the derm showing pigment in stellar masses: the

granular pigment-cells look like black spots in the epiderm. On removing this, narrow oblong scales, two lines to three lines long, fig. 361, *a*, are seen imbedded in depressions of the derm. They consist of a finely reticulate cartilage, the long axis of the meshes, which may be cells with confluent walls, running nearly parallel to the contour of the scale, as shown in the

Scale of Eel: *a*, nat. size, and portion magn. CCXCIII.

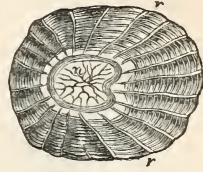
magnified section taken at the line marked in fig. 361, *a*. In the Blenny (*Zoarces*) the skin presents circular depressions which are

<sup>1</sup> 'Arctuous bands' of Clark (CCXCII, p. 148), who well distinguishes them from the gland-ducts perforating the skin in certain fishes, e. g., *muraena*.

due to the presence of small round scales, about  $\frac{1}{12}$ th in. diameter, with concentric and radiating lines: they are set deep in the derm. In the Sand-eel (*Ammodytes*), the scales are proportionally larger, and one margin rises from the derm and pushes outward the portion of epiderm covering it: the dermal depression is limited to the opposite margin, and is deeper than in the Eel. The free part of the scale retains the reticular structure; in the imbedded part the areolæ are obliterated in the direction from the centre to the circumference; the radiating lines preserve their distance, but, being united by cross fibres close set, the structure appears to be laminated. The majority of flexible scales present the same pattern of concentric and radiating lines: the concentric lines are the finest, most numerous, and constant; they repeat the contour of the scale, and with most regularity at the anterior imbedded and covered part, where growth chiefly takes place, the stages of which are marked by these lines. The 'nucleus' or beginning of the scale is usually excentric, fig. 362, *n*. The radiating lines, fig. 362 and 363, *r, r*, are larger and fewer: they are most numerous in the Loach (*Cobitis*), are sometimes confined to the forepart of the scale, fig. 363, or may be absent (*Salmo*): they are furrows. The parts of the scale-margin between the ends of the radiating lines usually project in different degrees from a slight convexity, as in figs. 362, 363, to the form of processes. The latter are most common at the anterior implanted border of the scale (*Esox*): in many fishes the opposite or free border has numerous tooth-like processes, and similar parts may project from the adjacent periphery of the scale in two or more rows. Such scales with a comb-like free border, fig. 363, *t*, characterise the fishes thence called 'ctenoid:' where the free border of the scale is rounded or simply undulated, fig. 362, it characterises the 'cycloid' fishes of Agassiz.<sup>1</sup>

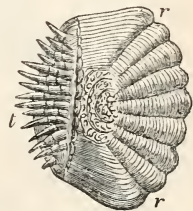
The seat of chief vascularity and greatest activity and variety of development is at the periphery of the derm, between it and the epiderm. Here are formed the scales, constituting an imbricate covering of the body in most fishes; but, in a few, contiguous or scattered. According to their structure and shape, scales are

362



Cycloid scale. XXII.

363

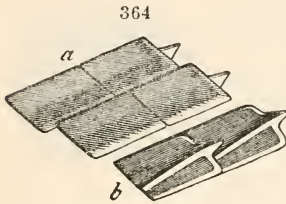


Ctenoid scale. XXII.

<sup>1</sup> XXII.

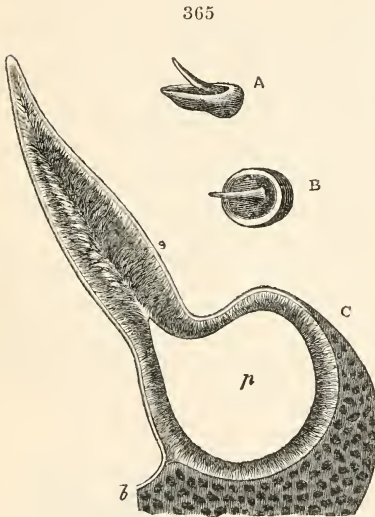


termed 'placoid,' fig. 365, 'ganoid,' fig. 364, 'cycloid,' fig. 362, 'ctenoid,' fig. 363. In the first and second kinds bone-earth predominates, and the scales are as hard as teeth; in the two latter kinds the earth is in less quantity, so that the scale is flexible: it is rarely wanting. The kinds of scale graduate into each other. Most flexible scales present two structures: one next the derm is composed of gristly laminae, usually firm and elastic, fig. 360, *c*; the superficial portion, *ib. d*, is laminated and hardened by inter-



Ganoid scales, *Amblypterus*.

mellar calcareous granules.<sup>1</sup> In the posterior or exposed part of the scale of a Carp there is a peripheral osseous layer, developing the outer markings or projections of the scale, fig. 360, *d*; a



Placoid scale A, B, nat. size; C, magn. section. XXII.

a middle laminated layer, with calcareous granules, *ib. e*; and the internal layer of laminae of structureless cartilage, *ib. c*.

In the Tunny (*Thynnus vulgaris*) the scales are composed of fine, partially ossified, laminae, between which are elongated 'lacunae' or bone-cells: the scale is cancellous at its middle part.<sup>2</sup> In *Lepidosteus* the scale is thicker, is composed of very thin ossified layers, fig. 366, *a*, perforated by vertical tubes about  $\frac{1}{8000}$  th in. diameter, and having numerous lacunae in their interspaces,<sup>3</sup> the radiating canals of which communicate

with a more minute series of vertical branched tubules, called 'Lepidine' by their describer.<sup>4</sup> These, in most ganoid fishes, have a less general distribution through the scale than the larger and less branched series, which, from their analogy to dentinal tubes, I have called 'plasmatic,' conceiving them to relate to the nutrition and vitality of the scale, as doubtless also do the 'lepidine' tubules in

<sup>1</sup> 'Corpuscles of Mandl,' ccciii.: 'Lenticular bodies' of Williamson, ccxcii.

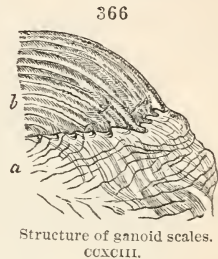
<sup>2</sup> cccxciii. vol. ii. p. 70.

<sup>3</sup> v. p. 14.

<sup>4</sup> ccxcvi. p. 439.

the parts of the scale to which they are limited. The peripheral surface of the scale is coated by a layer of hard transparent laminated substance, *ib. b*<sup>1</sup> ('*émail*,' *Ag.*; '*ganoin*,' '*Wilk.*'<sup>2</sup>). In *Lepidosteus* and *Polypterus* the ganoin is usually confined to two-thirds of the outer surface of the scale. In both existing Ganoids the scale is perforated vertically by a few larger tubes, analogous to the '*vascular canals*' of bone, and conveying blood from the *derm* to the delicate layer of membrane extending from the scale-pit, *fig. 360, f*, upon the ganoin. In the scales of extinct *Ganoidei* a portion of the deeper layer of ganoin traversed by minute branching tubuli, and devoid of lacunæ, has received the name of '*kosmin*.'<sup>3</sup> This tissue constitutes the chief part of the tooth-shaped bodies of the '*shagreen*' of the Dog-fish and many other Placoids; in which it cannot be histologically distinguished from hard dentine.<sup>4</sup> In *fig. 365* are given a side view, *A*, and upper view, *B*, of one of the '*placoid scales*,' or spiny tubercles of the Thornback (*Raia clavata*): *c* is a magnified section of the scale. The substance of the spine consists of superimposed conical lamellæ, having, in the Thornback, a widely open pulp-cavity, *ib. p*, from which proceed vascular canals, resolving into plasmatic tubes, radiating and ramifying through the substance as in ordinary teeth. The base of the spine-bearing scale, *ib. b*, is imbedded in the *derm*; and, as the '*haversian canals*' of the jaw pass into the '*medullary canals*' of the teeth thereto anchylosed, so do the capillaries of the *derm* pass directly into the '*vascular*' canals and pulp-cavity of the dermal dentine in all the various forms of placoid scales, many of which have a coating of true '*ganoin*' over the fine-tubed dentine or '*kosmin*.' Other modifications of the dermoskeleton, such as the placoganoïd and acanthoganoïd, are noticed at pp. 193-198, and illustrated in *figs. 124-127*.

The calcification of scales, as of teeth, *fig. 242*, and bone, *fig. 15*, takes place in layers of the organic basis successively formed: but the primitive lamellate condition is most conspicuous in fish-scales. The idea of excretion, or the throwing out of such layers from a secreting surface, is, however, as inadequate to represent the facts of the formation and structure of the exoskeleton as of the endoskeleton of fishes.<sup>5</sup>



Structure of ganoid scales.  
CCXCIII.

<sup>1</sup> xxii vol. i. p. 74.

<sup>2</sup> ccxci. p. 438.

<sup>3</sup> *Ib.* p. 444.

<sup>4</sup> v. p. 14.

<sup>5</sup> The microscopical observations on the structures of recent and fossil teeth, with incidental notices of corresponding organisation in ossified scales, communicated by

The varied and often brilliant colours of fishes are due to pigment-cells at different depths of the skin, but chiefly in the active or differentiating area: those of silvery and golden lustre are mostly on the surface of the scales: the silvery pigment, called 'argentine,' is an article of commerce, used for the colouring of factitious pearls, and offers a crystalline character under the microscope. The blue, red, green, or other bright-coloured pigment is usually associated with fine oil, and occupies areolæ favouring accumulation at, or retreat from, the superficies, and thus effecting changes in the colours of the fish, harmonising their exterior with the hue of the bottom of their haunt.<sup>1</sup>

The surface of the body is lubricated in most Fishes by mucus, sometimes, as in the Eel and Burbot, forming a thick layer. The skin of the Eel is perforated by numerous ducts or follicles, which contribute to this excretion.<sup>2</sup> In the Pike the scattered ducts notch the border of the scales, near their termination: one series of follicles represents the lateral line, as in the Eel. In most Fishes the follicles of the lateral row are connected by a longitudinal canal, of which they appear to be branches; more particularly so in those species (Dory, Opah) in which the follicles are produced into secondary tubes, and open at some distance from, usually beneath, the lateral canal. In the *Mugil cephalus* there are several lateral canals, giving off the follicles which tunnel the scales in their outward course. The lateral canal itself so marks the scales along which it runs, its follicular outlets perforating them. The 'nervus lateralis' sends a filament to each scale-follicle or tunnel;<sup>3</sup> the cephalic system of well-nerved mucous canals excavates oddly superficial bones of the head in many *Teleostomi*:<sup>4</sup> this system is noticed in *Plagiostomi*, at p. 225. The nervous structure connected with the system of the lateral line suggests a stimulus to active excretion from emotional causes, as in the skin-glands of *Batrachia*.

§ 100. *Teguments of Reptiles*.—The derm in *Batrachia* presents

me to the meeting of the British Association in August 1838, and to the Academy of Sciences, Institute of France, December 1839, established the 'conversion-theory,' and compel any one attempting to revive the 'excretion theory' to substitute a definition of the process wholly different from that to which De Blainville and other supporters of the theory held in 1838-9. Prof. Williamson, who has pursued microscopical investigations into the scales of recent and fossil fishes with perseverance and success, affirms the facts which he brought forward (ccxci. p. 437) 'to be, at least, sufficiently conclusive to settle the question, by showing that, whilst the scales are formed, as originally stated by M. Agassiz, by the apposition of successive layers, these layers are not generated by any process of secretion, but by the calcification of an organised basis, resembling that of bones and teeth, as asserted by Prof. Owen.'

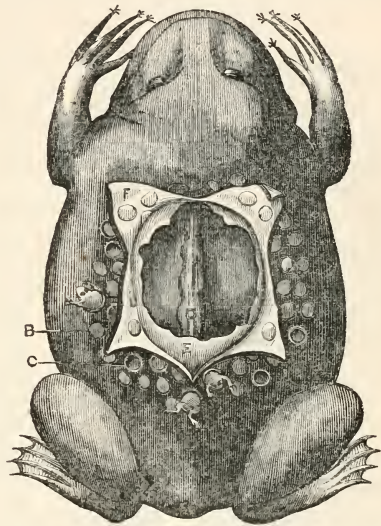
<sup>1</sup> ccxciv. p. 327.    <sup>2</sup> ccxciv.    <sup>3</sup> Leydig (cclxxvii. p. 203, fig. 108) describes it as ending in a kind of ganglion.    <sup>4</sup> ccxiv. p. 171.



a lamellate structure, fig. 368, *g*, like that of Fishes, but with the direction of the fibres, in succeeding layers, more regularly alternating. In most parts of the trunk of the Anoura the skin is separated by wide lymphatic lacunæ, fig. 367, *F*, from the subcutaneous fascia, *ib. E*. Marsupial pouches, one for each larva, *ib. B, C*, are temporarily developed in the skin of the back of the female *Pipa*: a common dorsal pouch for eggs and larvæ is present in the female *Nototrema marsupiatum*, Gnth., and in *Opisthodelphys*. The epiderm in Perennibranchiates resembles that of muraenoid Fishes: in most *Anoura* the constituent nucleate cells are more condensed, fig. 368, *b*: in many Toads the epiderm is tuberculate; rarely are scales, and scutes never, present in the existing *Batrachia*. In *Cecilia* the skin is ringed by transverse rugæ. In the American Newts, of the genus *Plestiodon*, the small scales present a reticulate structure.

In *Bufo tuberosus* the epiderm forms on the dorsal tubercles a horny spine in the centre, surrounded by a ring of smaller spines: *Bufo asper* has conical spine-bearing tubercles on the back and sides of the trunk: those on the upper eyelids of certain Toads have earned for them the generic name *Ceratophrys* (*Rana cornuta*, Linn.). In *Salamandra unguiculata*, and in *Dactylethra* among the Toads, the epiderm is condensed into a claw at the end of some of the digits: in *D. Mülleri* it also forms a spur at the base of the first hind-toe. In *Pipa* the skin is produced at the end of each fore-toe into a 3- or 4-forked appendage, fig. 367. As a rule, the *Batrachia* are without claws. Pigment-cells, fig. 368, *a*, are developed in various degrees, and of diverse shades of colour, commonly of a dull and neutral or mixed tint, but giving to parts of the skin of the land Salamander a yellow or orange hue, and painting the surface of the Tree-Frog (*Hyla*) a bright polished green.

367

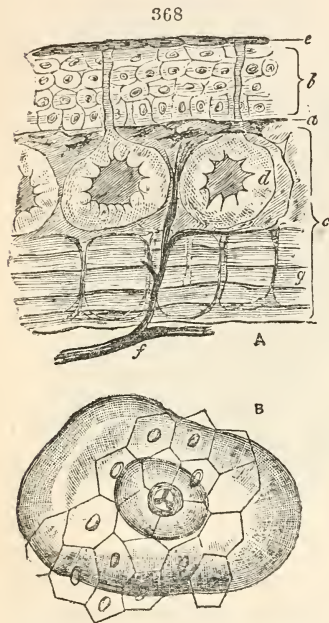
Female *Pipa*, or Surinam Toad.



Mucous follicles abound in the skin of all the *Batrachia*: they are found in linear rows in parts of the Siren:<sup>1</sup> are more generally diffused in the Axolotl.<sup>2</sup> In the Frog they are spheroidal,<sup>3</sup> fig. 368, *d*, or subdepressed,<sup>4</sup> situated in the superficies of the derm, *e*; their ducts perforate the epiderm, *b*, and terminate by rounded<sup>5</sup> or triradiate<sup>6</sup> orifices, *ib. b*. Like the lateral canals of Fishes, they usually contain a clear fluid, which they expel on irritation of their nerve, *ib. f*.<sup>7</sup> This fluid, in the Newts and Toads,

appears to possess an acid or irritating property. A stork will swallow a frog, but rejects a toad, if picked up by mistake. The cutaneous follicles are more localised in the land Salamander, and their secretion is whitish and opaque, of an acrid nature, and poured out abundantly when the animal is alarmed or irritated. The cutaneous follicles are numerous and close-set in the American Newts of the genera *Ambystoma* and *Plethodon*, in which they exude a milky fluid.<sup>8</sup>

Special aggregates of cutaneous follicles occur in most *Batrachia*. In the land Salamander they form a porous tubercle behind each eye. In many Anoura the homologous glandular tubercles ('parotoids' of Günther<sup>9</sup>) are conspicuous



Section of tegument and cutaneous glands of the Frog, magnified. ccxcv.

above the tympanum (*Alytidae*, *Bufo**nidae*): they are enormous in *Bufo aqua*, and are situated on each side of the neck in *Uperoliidae*. In *Bufo calamita*, besides the ordinary parotoids, there is a similar glandular tubercle on the upper side of the legs. The skin of the back in *Kalophrynus* is thick and glandular, like a parotoid. In *Hylarana* the skin has two glandular folds, one on each side of the back, usually of a white colour. *Platymantis plicifera* has several pairs of such longitudinal folds or ridges.<sup>10</sup> In *Polypedates*

<sup>1</sup> xx. vol. iii. p. 277, prep. no. 2108.    <sup>2</sup> cclxxxix. tav. ii. fig. 7.    <sup>3</sup> ccxcv. taf. ii. fig. 10.    <sup>4</sup> *Ib.* fig. 7.    <sup>5</sup> *Ib.* fig. 2.    <sup>6</sup> *Ib.* fig. 3.    <sup>7</sup> *Ib.* (6841), p. clvi.    <sup>8</sup> ccxcvi. p. 281.    <sup>9</sup> Printed by mistake 'paratoid' in his excellent Catalogue.    <sup>10</sup> clxxv. p. 96, pl. viii. fig. b.

a glandular fold curves from above the tympanum to the axilla or shoulder.

The skin takes an important share in respiration in the Anourous Batrachia,<sup>1</sup> and there is a relation of 'supply and demand' between the cutaneous follicles and the large allantoic bladder: the latter would seem to receive water directly by the cloaca, when the Frog may be in that element, and to serve as a reservoir for the supply of cutaneous transpiration when the batrachian is on dry land.<sup>2</sup>

The epiderm is periodically shed in *Batrachia*. It comes away in shreds in the aquatic kinds. In the Toad the old epiderm splits along the middle line of both back and belly, and each lateral half is wriggled off in folds towards the sides. It is then, by contortions of the trunk and limbs, loosened from the hind-limbs, and removed from them by the animal bringing first one and then the other leg forward under the arm, when, by withdrawing the hind-leg, its cuticle is left under the fore-leg. The two portions are now pushed forward to the mouth, by the help of which the anterior extremities are also divested of their cuticle. The whole mass is finally pushed by the hands into the mouth, and swallowed at a single gulp. The new cuticle is bright, soft, and covered with a colourless mucus.<sup>3</sup>

In Serpents the epiderm is shed, usually entire, and the animal, partially blindfolded by the opacity of the layer passing over the cornea, fig. 220, *c*, seeks an obscure retreat; but I have watched the process of exuviation in a captive snake. It rubs the front and sides of the mouth against its prison wall, thus detaching and reflecting the cuticle from the oral margin, until it is turned back from over the whole head: the snake then brings forward its tail and coils it transversely round the head, and by pushing the head through the coil turns the cuticle back upon the neck; then tightening the coil and renewing the forward movement, threading the body, as it were, through the caudal ring, the cuticle is pushed further and further back until the eversion has been carried so near the end of the tail as prevents the further action of the coil; the animal finally glides along dragging behind the whole of the loosened epiderm, and a few wriggling actions of the tail serve to completely detach it. Thus, the entire outer skin of the snake may be found shed and turned inside out, the process of exuviation being like the turning off a stocking from the leg and foot. The whole of the exuviable epiderm in *Ophidia* has been condensed into the form of scales: these are small and pretty

<sup>1</sup> CCXCVII.<sup>2</sup> Ib.<sup>3</sup> CCXCVIII. vol i. p. 102.

regular in size and shape along the back and sides of the body; but are large and transversely extended across the under part, forming what are termed the 'ventral scutes,' 'scuta ventralia,' the use of which in locomotion is explained at p. 259. All or most of the scutes below the tail ('scuta sub-caudalia') are single in *Crotalus*, *Bungarus*, *Boa*; in *Python*, the *Colubridæ*, and most other serpents they are 'paired,' or divided along the middle line. In most sea-snakes the abdomen is compressed and keeled below; in *Pelamys* the keel is bordered by two rows of scales; in *Hydrophys* it is formed by large bituberculate scales; *Platurus* has the venter scutate, with the caudal scales in pairs. Larger scales occur in the head of most serpents, and serve as zoological characters, being defined as 'scuta marginalia labii superioris seu inferioris,' 'scutum labiale medium,' 'scuta mentalia,' 'scuta ocularia,' 'scuta frenalia,' 'scuta nasalia,' &c. The scales of serpents may be smooth or carinate, they are rarely tuberculate (dorsal scales of *Xenodermus*); and in their disposition they may be either 'contiguous,' or 'imbricate.'

The epiderm is condensed into claws or hooks ('calcaria') upon the rudiments of hind limbs that border the vent: these are best seen in *Boa*, *Python*, *Eryx*, *Tortrix*; it is developed into small horns above the eyes in *Vipera cerastes*. In the Rattlesnake the epiderm forms a series of hard moveable rings at the end of the tail, twenty to thirty in number in full-grown specimens, decreasing in size to the end of the series. The terminal (3 to 8) caudal vertebræ coalesce into a long conical bone, covered by thick, soft, vascular derm, divided by two deep annular grooves into three transverse swellings: the basal ring of one joint grasps the projecting second ring of the preceding joint, and this incloses the third ring of the joint next but one in advance. Since the second rounded annular portion of each joint is thus securely grasped by the first rounded annular portion of the piece behind it, and the third by the second, and yet all of them so loosely as to leave room for motion, it has been supposed that when the foremost piece has been completed, and a new piece in advance is about to be formed, the skin which is to secrete it is so modified that its first swelling, which secreted the first projection of the former piece, assumes that shape and size which are accommodated to the shape and size of the second projection of the new piece, whilst the second swelling which secreted the second projection of the piece takes the dimensions suited to the third projection of the future new ring. The basal projections of the successive rings are chiefly visible externally, only the first

ring has a vital connection with the derm: it is caused to vibrate by the muscles of the tail, and its vibration communicates a quivering motion, accompanied by a rattling noise, to the dry horny pieces behind it.<sup>1</sup>

The pigment-cells are mostly combined with the epidermal ones to form the deeper layers of the scales, and ornament the skin of snakes with various and sometimes brilliant colours. The poisonous serpents are mostly of a sombre hue. The periphery of the derm is modelled according to the pattern, contiguous or imbricate, of the epiderm, the scales of which are evolved thereupon. The blood-vessels form a beautiful and regular network, the area corresponding with the shape of the scales, being lozenge-shaped, e. g. in *Coluber natrix*,<sup>2</sup> with the uniting angle at the centre of each scale.

The skin of the snout develops tentacular appendages in *Herpeton tentaculatum*. The integument in the Cobras (*Naja*) expands into a broad fold on each side the neck: the folds are supported by correspondingly elongated ribs, p. 55, fig. 46, *pl.*; when these are drawn forward an oval disc of skin is caused, surpassing the head in breadth, and usually rendered more conspicuous by well-defined tracts of pigment. The name of 'spectacle-snake' refers to the pair of circular spots connected by a curved streak on the hood of the *Naia tripudians*.

The secreting follicles of the skin in Serpents are chiefly confined to certain depressions or inverted folds of the derm. These in *Crotalus* and *Trigonocephalus* constitute a pit between the nostril and eye on each side of the head. The hinder scutes of the lower lip have pits in *Python Schlegelii*; as have those of both lips in *Python amethystinus*. In *Amphisbæna alba* and in *Chirotes* there is a row of pores in front of the vent.

The skin in most Lacertians resembles that of Serpents: the scales are thickened epiderm or horn; in most imbricate, in a few (*Zonosaurus*, V. der H.) verticillate; usually smooth, but in some carinate, and in some tuberculate or gibbous: in a few they support a spine at certain parts of the body, as, e. g. the caudal scales of *Zonurus*, both dorsal and caudal scales of *Tribolonotus*, the circumtympanic scales of *Agama*, the occipital scales of *Phrynosoma*, and scattered dorsal and lateral scales in the Australian *Lacerta muricata* of White. Bone is developed at the base of the scale forming part thereof, or combining scute and scale, in *Ophisaurus*, *Tribolonotus*, *Trachysaurus*. In the Chameleons the scales are small and thin, like grains. The

<sup>1</sup> CCXCIX. p. 294, pl. xii.

<sup>2</sup> XX. vol. iii. p. 241.



pigmental system of the skin is remarkably developed in this family: it is of various colours—red, blue, yellow, brown; each colour is lodged in contractile areolar spaces, and can be accumulated near or withdrawn from the surface. When the Chameleon is kept long in a cold dark place all the pigment subsides into the derm, the superficial pale grey colour of which appears through the thin epiderm. When brought into the light and warmth the pigments flow to the surface, in harmony with the colour of that on which the animal rests, which usually in this arboreal reptile is green. If, however, the Chameleon be irritated, the colour may change to a vinous red, or deepen almost to black: commonly the surface is more or less mottled, grey, yellow and green. These phenomena, which have made a proverb of the Chameleon, are manifested in a minor degree by some other Reptiles, by most Fishes, and by Cephalopods.

The integument, besides covering the surface of the body, extends, in many Lacertians, from various parts, in different forms and degrees. In *Basiliscus* and *Histiurus calotes* it forms a compressed fold or crest along the midline of the back and tail. In *Crocodylus* the tail has a double crest above: in *Phyllurus platurus* the lateral expansions of the skin of the short tail give it a leaf-shape. In *Hoplurus* and *Tropidurus cyclura* the skin of the throat is folded transversely: in *Agama* the transverse fold is associated with a longitudinal fold beneath the under jaw. The jugular fold is longitudinal and pendulous, like a dewlap, in *Iguana*, *Corythophanes*, and *Semiophorus*. In *Chlamydosaurus* a very broad transverse fold of skin extends from above each tympanum across the lower part of the neck: it is partly supported and moved by much elongated cerato- and thyro-hyals, and can be expanded and brought forward or erected, so as to give a formidable aspect to this Lizard, when it is attacked or alarmed.

In the small insectivorous *Draco volans* of Linnæus a broad fold of skin, on each side of the body, fig. 163, is supported by five pairs of slender elongated free ribs, fig. 50, by the movement of which the folds can be expanded into a sort of parachute, as explained at p. 265. The special modification of the tegument of the toes in the Geckos is described at p. 263, fig. 162. In the extinct Pterodactyles still more extensive duplicatures of skin were supported on a much elongated digit, and constituted true wings, as in the Bats, p. 265, fig. 111, A. In many Lizards, on the inside of the thigh, there is a row of tuberculate perforated scales, beneath each of which lies a pedunculate gland, studded with marginal follicles: the presence and position of these ‘pori

femorales' afford generic characters. They are wanting in the Chameleons. Certain male Geckos have both femoral and sub-anal pores. In *Pygopus lepidopodus* the subanal pores are disposed in a single series, but in *Lialis* in pairs, on each side.

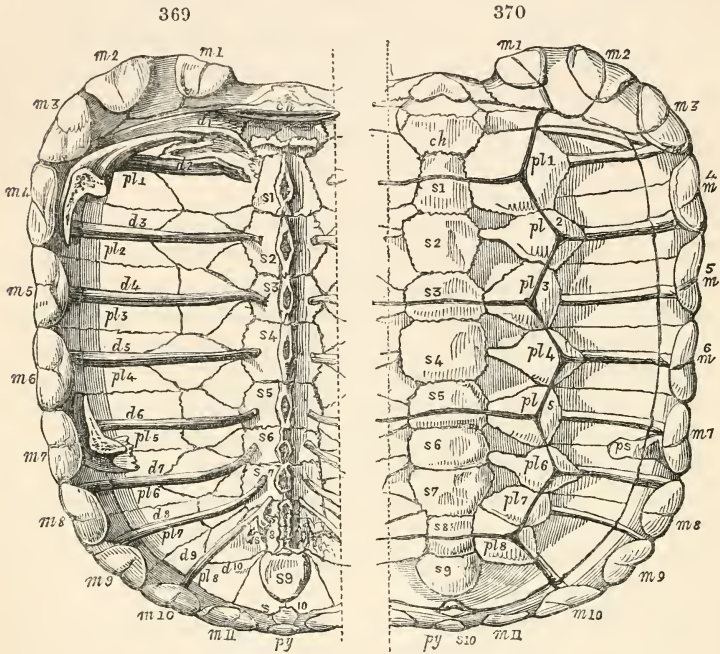
In the *Crocodylia* the conversion of parts of the integument into bone is constant, and the osseous structure shows interlaced or crossing fibres, like that of the derm in and from which the scutes are developed. The arrangements and forms of these scutes in different genera of recent and fossil *Crocodylia* are described at pp. 198, 199. As in Fishes, the dermoskeleton was most developed in the extinct secondary species. In modern Crocodiles a serrated crest extends above the tail, which divides at the base of that organ.

A section of the dorsal integument of *Trionyx ferox* shows a thin epiderm, then a thicker layer of elastic fibres, next many layers of fibres crossing each other regularly, and producing seeming layers of the derm. In *Sphargis* a superficial portion of the derm is ossified, so as to form a kind of girdle to the trunk, beneath which is a felt of soft corium, and under this the endoskeleton. In all other *Chelonia* the derm adheres to the periosteum of certain neural spines and pairs of pleur- and hæm-apophyses, whence ossification extends in different degrees into the substance of the derm. In most *Chelonia* a series of bones are developed independently in the derm, at the circumference of the trunk, and also above certain neural spines, with which they may or may not become anchylosed.<sup>1</sup>

The dermal bones connate with neural spines are those above the nine dorsal vertebræ, figs. 370, 371, *ch*, *s*<sub>1</sub>-*s*<sub>8</sub>: they are termed 'neural plates.' The dermal bones connate with pleura-pophyses are those which take ossification from near the heads of the second to the ninth, inclusive of the dorsal ribs, *ib. pl*<sub>1</sub>-*pl*<sub>8</sub>. The dermal bones connate with hæmapophyses are those which start from the sternal or abdominal ribs, or coalesced groups of ribs, figs. 372, 373, called hyosternal, *hs*, hyposternal, *ps*, and xiphisternal, *xs*. Occasionally, ossification extends into the skin from the entosternal, *s* (*Emyda ceylonensis*), and from the episternals, *es* (*Cryptopus Petersii*). The dermal bones are least developed in the *Trionycidæ*, and are not covered by horny epiderm. 'Neural' and 'costal' plates are present in all. One pair of dermal bones is developed from the hyosternals in *Trionyx subplanus*; in *Trionyx niloticus* and some other species dermal bones are developed from the hyo-, hypo- and xiphi-sternals, the

<sup>1</sup> CLXII. p. 165.

hypo- and hypo-sternal plates on each side being naturally united together; in *Emyda ceylonensis* dermal bones are developed from the epi-, hypo- and xiphi-sternals, and from the entosternal or sternum proper, forming seven pieces: the skin of the hinder margin of the broad depressed trunk is strengthened in *Emyda*



Inner surface, Carapace, young Tortoise.

Outer surface, Carapace, young Tortoise.

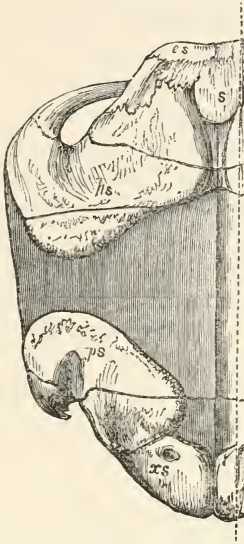
by a few dermal ossicles; much of the skin of the trunk, where not ossified, in *Trionycida*, has the dermal tissue of cartilaginous hardness.

In the Turtles, or marine *Chelonia*, besides the eight connate neural plates, fig. 52, s1-s8 (p. 61), dermal bones are developed in advance of and behind them, and are commonly unattached to the subjacent vertebræ. The anterior one, ib. *ch*, is the 'nuchal' plate: the posterior one, ib. *py*, is the 'pygal' plate; the costal plates, *pl1-pl8*, articulate suturally with the neural plates, but do not extend to the end of the ribs; the marginal plates, *m1-m12*, are articulated with each other and with the nuchal and pygal plates suturally, and eight on each side receive the ends of the eight ribs supporting the costal plates. Two



pairs of dermal bones are developed from the hypo- and hyposternals, fig. 53, *hs* and *ps*: but these do not articulate with the marginal series. In Freshwater and Land Tortoises the dermal ossifications spread further, uniting all the parts of the plastron

371



Outer surface, plastron, young Tortoise.

372



Inner surface, plastron, young Tortoise.

into one more or less flat floor, and all the parts of the carapace into one more or less convex roof, fig. 51; side-walls being likewise now formed by the union of the hypo- and hyposternals with the coextensive marginal plates. In all Chelonia, save the *Trionycidæ* and *Sphargis*, the epiderm of the trunk is condensed into large horny scales, usually contiguous, more rarely imbricate, and then only on the carapace. They may be keeled, or rugous, or scabrous, but are commonly smooth and polished, or marked only by concentric lines of growth. Their growing margins indent the dermal bones supporting them, forming the triradiate grooves, e. g. upon the beginnings of the costal plates in the young Tortoise, fig. 370, *ph*, and those marked *s1-s5* on the neural and costal plates in the Turtle, fig. 52. The large epidermal plates of the carapace and plastron are termed 'shields' and 'tortoise-shell': most of them have special names in Zoology, as they afford useful characters in the discrimination of genera and species; whilst the impressions they leave upon the subjacent bones give similar light in the interpretation of fossil remains,



after the horny shields themselves have perished. The epiderm is disposed upon the head in various forms: in most freshwater *Chelonia* it is a continuous thin hard layer on the top and sides of the head: in marine and terrestrial *Chelonia* it is usually in the form of large plates, leaving marginal impressions on the skull, and distinguished by special names: they are more symmetrical in *Chelone* than in *Testudo*. The skin of the neck and of the limbs is covered by small contiguous scales: some of these are of larger size on parts of the feet. The epiderm is thickened and condensed into a beak in all *Chelonia*, and into claws in most. In *Sphargis*, however, the claws are replaced by small coriaceous scales: in *Chelone* only one digit on each foot supports a claw: in *Caretta* two digits, and in *Trionycidæ* three digits, support claws: in some Tortoises (*Testudo*) there are four claws on each foot: in most Tortoises and Terrapins (*Emys*) there is an additional claw on the fore-foot: in the heavy Land Tortoises the claws assume the form of hoofs. The epiderm of the tail is usually wrinkled, and covered only by small scales: in the Snapper (*Chelydra*) it supports a row of hard compressed tubercles; in some Tortoises the end of the tail has a thick epidermal sheath, which, in the male *Cinosternon*, is armed with a pointed tip.

The large imbricate plates of the carapace of *Chelone* have their fore border imbedded in a matrix of the derm, and here receive their chief increase, the older parts moving backward, and being worn off. The plates with contiguous borders receive increase at their under surface and entire circumference; the concentric lines of growth may be marks of annual increment:<sup>1</sup> but these usually show a greater ratio of growth at the front and sides than at the back. The old and dull superficial layer is worn away, or thrown off from time to time, leaving the rest of the epidermal shield of a bright colour: the smooth or scaly epiderm of the limbs and neck is usually shed entire.

The skin of the neck developes fimbriate processes and caruncles in *Chelys fimbriata*: that of the nose is produced into a short snout in most *Trionycidæ*.

The deeper stratum of soft, usually imbricate, epithelial cells of the epiderm are intermixed with pigmental cells, mostly dark brown or black; abundant pigment-particles are also suspended in an oily fluid, occupying areolar spaces of the deep epiderm, and usually of the brighter yellow, red, or green colours. Such

<sup>1</sup> As conjectured by Agassiz, ccc. vol. i. pt. ii. p. 259.

pigmental cells are blended with the tissue of the shields and scales, and may ornament the former with well-marked patterns, e.g. in *Testudo areolata*, *Emys ornata*, *Emys picta*, &c.

Cutaneous glands or follicles open between the warts of the skin in *Chelydra*, and probably occasion their musky odour: but this, in other *Chelonia*, appears to be due to larger, more compact, and more localised glands. Beneath the epiderm of the skin of the under part of the body, in the Soft-Turtles, is an extensive network of vessels, spreading into dendritic ramifications, too numerous and large for the mere nutritive purposes of the skin or supply of epithelial cells, and therefore probably<sup>1</sup> subservient to respiration.

Viewing the integuments in their relations to the external influences from which they defend the body, and by which they are themselves affected, we may remark that most of the house-bearing Reptiles which have the surface of their abode habitually in contact with air or water have the epiderm hard and thick, whilst those living in ooze or mud have it soft and thin. In the sea the horny scutes may be partially loosened, and grow over one another: in the air they condense upon the surface with the margins in contact: in the mud the skin is lubricous: the only known scaleless species of marine habits (*Sphargis coriacea*) has the tegument tough and leathery. In the most vagrant and widely diffused Turtle (*Chelone imbricata*) the separation of the scales takes place at a part of their circumference, which makes the direction of imbrication the most favourable to their aquatic movements. Growing and projecting from before backward, the one in front overlapping the next behind, the polished shields offer no resistance to the forward movement impressed upon the body by the oar-shaped limbs; whilst the scutal interspaces, widening as the trunk tends to recede during the preparation for the next stroke, oppose the backward slipping, and take hold, so to speak, upon the wave, retaining the advantage of one stroke until the next is played.

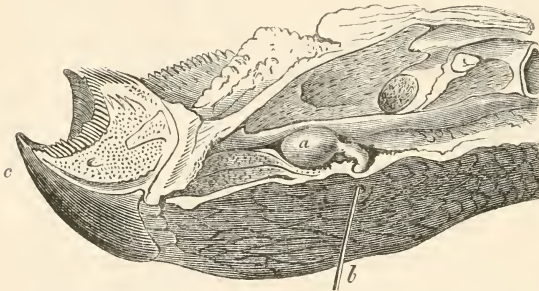
<sup>1</sup> As conjectured by Agassiz, ccc. vol. i. pt. ii. p. 284.

## CHAPTER X.

## PECULIAR AND DUCTLESS GLANDS.

§ 101. *Scent-glands of Reptiles.*—The Chelonia, like most Reptiles, have scent-glands, with periodical access of activity, enabling and exciting, as it seems, the sexes to find each other at the pairing season. In Tortoises the gland, fig. 373, *a*, is situated beneath the skin of the mentum; its duct, *b*, in a *Testudo indica* of two feet long, opens about an inch and a half behind the symphysis of the mandible, and about half an inch from the

373



Section of mandible showing the scent-gland. *Testudo indica*.

mesial line. In the Turtle the glands excrete at the base of the neck; in the Kinosternon a gland is situated near the fore and hind margins of the side-walls, uniting the carapace and plastron: the duct perforates the bone, and opens by a fine slit in the wall.

In the *Crocodylia* a small sinus is formed by an inward fold of integument near the inner side of the mandibular ramus, into which sinus opens the dilated duct of a gland, which is surrounded by a muscle, detached from the back part of the pharynx, and proceeding along the outer side of the ceratohyal to expand upon the gland and reservoir.<sup>1</sup> Cuvier<sup>2</sup> describes its contents as being unctuous, of a dark grey colour, with a strong musky odour.

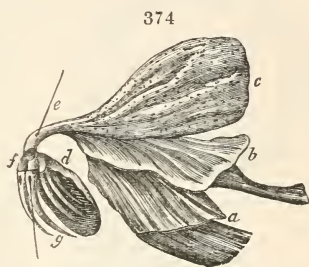
<sup>1</sup> xx. vol. iii. p. 272; prep. no. 2106.

<sup>2</sup> xii. tom. v. p. 252 (1805).

The Crocodiles have glandular follicles, which open at the anus. Hunter preserved 'a section of the skin of a Turtle (*Chelone*), to show a gland situated near its anus.'<sup>1</sup> There is a glandular fossa which opens into the dorsal part of the cloaca, close to the termination of the rectum in most Emydians.

The anal bags in Serpents are two in number, of an elongate form, fig. 357, *m*: they are lodged in the base of the tail, and open into the back part of the cloaca: their excretion has a strong, disagreeable, nauseating odour.

§ 102. *Poison-glands of Reptiles*.—The gland which secretes the poison in ordinary venomous Serpents is situated on each side the head, anterior to the tympanic pedicle, inclosed in a strong capsule, fig. 145, *a* (p. 227), and partly covered by the muscle analogous to the masseter, ib. *e*, some of the fibres of which, fig. 374, *a*, are attached to the capsule, ib. *b*. On reflecting these, as in fig. 374, the gland, ib. *c*, is seen composed of a series of elongated narrow lobes, extending from the main duct at the lower border of the gland upward and backward. Each lobe gives off a series of lobules, which are again subdivided into smaller cæca. Their secretion is collected into the dilated beginning of the duct which conveys it to the base of the poison-fang, *f*; the bristle *e* passes from the duct into the poison-canal of the fang, the structure of which is described, pp. 396-398: the gum-capsule, *d*, of the reserve-fangs, *g*, is laid open. In *Hydrophis* the poison-gland is of smaller size, narrow, elongate, broadest behind, and extended upon the maxillary and ectopterygoid bones, in advance of the masseter: its capsule is attached to the tendinous tract (p. 228) detached from the digastricus and ectopterygoid: its duct enters the foremost of the series of four to six small fangs attached to the maxillary. The bite of these inferiorly endowed venomous Sea-Snakes has proved fatal: they are said to occasionally climb along the hawser into ships at anchor; and as they may be drawn in, adhering to it by their prehensile tail, or be caught in the fishing-net and hauled on board, it is well that their dangerous property should be known.



Poison apparatus of the Viper (*Vipera Berus*). CXVI.

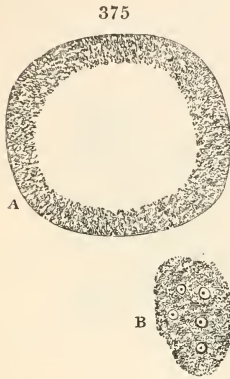
The secretion of the poison-gland is a tasteless fluid, drying under exposure to air into small scales: it is soluble in water,

<sup>1</sup> xx. vol. iii. p. 279, prep. no. 2130.



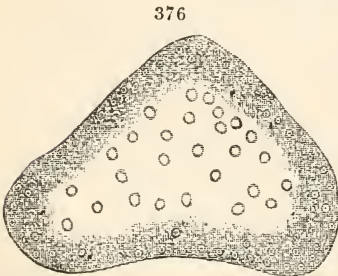
insoluble in alcohol, and slightly reddens litmus paper: it long retains its noxious property. Against this the mucous surface of the alimentary tract is proof: the poison, to take effect, must enter the current of the blood. Here it is ordinarily introduced by the puncture of the poison-fang, but it takes effect by application to an abraded surface. The poison affects the nervous system; death is usually preceded by spasmodic convulsions, and followed by speedy putrefaction.

§ 103. *The Thyroid Body or Gland of Hæmatoerya.*—In the Skate (*Raia*) the body which seems to have best claim to be regarded as a thyroid is situated sternad of the terminal division of the branchial artery, of a reddish-grey colour and conglomerate exterior. It consists of numerous, mostly subspherical, vesicles, of from  $\frac{1}{67}$  to  $\frac{1}{112}$  inch diameter, fig. 375, having a structureless tunic, A, lined by a thick stratum of epithelial substance, consisting of nuclei and granular matter, B. Dr. Handfield Jones, who has given the above result of microscopical investigation of this ductless gland, also found, in the Skate, ‘at some distance behind it, just at the junction of the branchial arches anteriorly, a small light reddish mass, which was



Vesicle from thyroid of Skate.  
CCLXXXIX.

covered by a thin fascia, and by mucous membrane.’<sup>1</sup> It consisted ‘of vesicles about  $\frac{1}{100}$  to  $\frac{1}{150}$  inch diameter,’ fig. 376, ‘formed by a structureless “limitary” tunic, thickly lined by epithelial substance, and containing abundance of nuclei and granular matter, with a few cells. The pseudo-branchia, situated on the anterior wall of the spiracular canal, is manifestly of entirely different structure to the organs described. It consists of small plicæ of mucous membrane, covered by a kind of pavement epithelium.’<sup>2</sup>



Vesicle from accessory thyroid of Skate, diam.  $\frac{1}{99}$  in. CCLXXXIX.

In the Menobranchus the thyroid is represented by two symmetrical bodies, situated at the sides of the basibranchials.

<sup>1</sup> CCLXXXIX. p. 1110.

<sup>2</sup> *Ib.*, and see CXLV. p. 270, with reference to the non-thyroid nature of the pseudo-branchiæ in other fishes.

In the Frog they lie on the carotids, also close to the basi-branchials, or thyrohyals.

In a *Python* of ten feet in length the thyroid was an oval body, ten lines by six lines in the two diameters, lodged in the fork made by the divergence of the large and small carotids, and having the smaller thymus bodies, one on each side.

In the true Lizards (*Lacerta*) the thyroid is single, but broader than it is long; in the Monitor it is double: it is single in Geckos, Skinks, and Chameleons, but has a more advanced position in the latter, where it is underlapped, or covered, by the laryngeal pouch.

In *Chelonia* the thyroid, as in Serpents, lies between the two carotids, but is usually covered by the pericardial part of the thymus. The constituent vesicles are from  $\frac{1}{50}$  to  $\frac{1}{84}$  inch diameter, closely aggregated: the epithelial lining contains a row of nuclei imbedded in the granular substance, fig.

278. Among the contents of the vesicles were found, in most, 'one to three yellowish, coarsely granular globules,  $\frac{1}{500}$  to  $\frac{1}{1000}$  inch diameter.' 'A fine large octohedral crystal was also seen in one of the cavities.'

377



Portion of the wall of a vesicle from the thyroid of a Tortoise. CCLXXXIX

§ 104. *The Thymus Body or Gland of Reptiles.*—The ductless gland-like tubulo-vesicular body to which the name 'thymus' can, with any homological probability, be given makes its first appearance in the Vertebrate series with the establishment of lungs as the main or exclusive respiratory organ.<sup>2</sup> Thus in *Siren* and *Proteus* the thymus is wanting, as in all Fishes: in tailed *Batrachia* (*Menopoma*, *Triton*) it is represented by a pair of bodies situated, one on each side, near the origin of the pulmonary artery. They make their appearance near the same part, but rather more in advance of the pericardium, in the larvæ of anourous *Batrachia*, and often degenerate into fat in the old Frog or Toad. In most *Ophidia* the thymus lies on each side of the carotid, of elongate form and unequal size: sometimes in two or more distinct parts: usually associated with, and concealed by, fatty matter. In a *Python* of ten feet in length I found the thymus in two bodies, each about the size of a pea, of a yellowish colour, one situated on the termination of the right jugular, the other between the origin of the larger carotid and the left jugular. Between the thymus bodies was the much larger single thyroid. In the *Psammosaur* and *Iguana* the thymus is broad and flat, covers sternally the thyroid, extends along the common trunk of

<sup>1</sup> CCLXXIX. p. 1100.

<sup>2</sup> CXVIII.

the carotids, and divides to accompany them a short distance. In the young Crocodile<sup>1</sup> the thymus is relatively larger, thicker, subtrihedral, extending backward upon the pericardium, as well as forward along the carotids to the basis cranii. In young *Chelonia* an elongate body, of a yellowish white colour, lies between the carotid and axillary trunks on each side: it presents lateral cavities, defined by limitary membrane, and containing nuclei, oil-drops, and fine molecular matter. In older *Chelonia* it seems to degenerate into fat.

§ 105. *Reproducible Parts in Hæmatocrya*.—One effect of life is the reproduction of the parts of the body as they pass away through unfitness for the required actions: this mainly takes place molecularly and invisibly; but parts of the integument, hairs, teeth, antlers, may be cast off *en masse*, and reproduced on a scale which catches the ordinary attention as a new growth. Certain animals have the faculty of reproducing organs and compound parts of the body which may have been removed by violence: amongst Vertebrates the property is greatest in the cold-blooded series; and here, so far as experiment yet shows, is most conspicuous in the tailed species and larvæ of the batrachian order. In the Newt (*Triton*) the tail, amputated at any distance from the base, is reproduced: the same with respect to the fore-limb and hind-limb, the reproduced member having the digits, but with diminished power of movement. The same member has been, in young Newts, removed and restored four times successively. In the experiments recorded by Bonnet,<sup>2</sup> it was found that warmth promoted, and cold retarded, the regeneration of the part. An eyeball of a Newt was extirpated, and, in the course of a year, it was restored with the usual organisation. Duméril cut off about three-fourths of the head of a *Triton marmoratus*, and deposited the animal at the bottom of a large vessel, having half an inch depth of water, which was constantly renewed. The Newt continued to live, and to move slowly. The nostrils, the tongue, the eyes, and the ears were gone, and the senses reduced to that of touch. It crept slowly, and Duméril imagines cautiously, about, occasionally raising the neck to the surface, as if to breathe. The process of cicatrisation at length completely closed the aperture of respiration and deglutition; and so it survived for three months after the operation, when it died from accidental neglect. This experiment exemplifies chiefly the power of endurance of mutilation, and, collaterally, the respiratory function of the skin. In

<sup>1</sup> I have not had an opportunity of examining this structure in a full-grown specimen of Crocodilian.

<sup>2</sup> CCCI. tom. xi. pp. 62-179.

the young larvæ of *Rana temporaria* and *Bombinator igneus*, Dr. Günther cut off the tail, and it was reproduced before the time when its absorption normally commences: it was transparent and colourless, a small quantity of pigment being deposited at its root only. 'Larvæ from fourteen to twenty days old did not survive the loss of the entire tail, probably because they are disabled from obtaining the requisite food; but if only a portion of the tail be cut off, it is more or less completely reproduced until its growth is arrested by the commencement of the last stage of metamorphosis. If a hind limb be cut off when the larva is about two lines long it is reproduced. No part of an Anourous Batrachian is reproducible after completion of the metamorphosis, not even the interdigital web.'<sup>1</sup>

In *Reptilia* the power of local reproduction has been exemplified chiefly in respect of the tails of Lizards. Hunter's preparations, nos. 2208-2223, are all from this order, and include species of *Ameiva*, *Gecko*, and true *Lacerta*. No instance of the restored tail shows ossified vertebræ, and some exemplify the tendency to greater abnormality in the reproduced part. A structure of the normal caudal vertebræ, related apparently to this property, is noticed at p. 59: the caudal muscles, by their proportions and interlocking arrangement, seem likewise to favour the rupture of the tail. When it is cast off, it continues to writhe for some time, and, when these motions have ceased, exemplifies the reflex function on being pricked or otherwise irritated.

The degree in which the reproduction of parts is exemplified in Fishes awaits the results of experiments. Van der Hoeven<sup>2</sup> affirms that parts of the fins are restored after amputation, and that the power is limited to this extent. Amputation of the small adipose dorsal fin has, however, served to mark an individual Salmon from its 'parr' state to that of the 'grilse';<sup>3</sup> and it appears that only the peripheral (dermoneural or dermohæmal) rays are reproducible, and to this the hard ones in Acanthopterans form an exception. 'The modified dermoneurals forming the cephalic tentacles of *Lophius* and *Antennarius* are as frequently reproduced as they are injured, to meet the particular use which these angling fishes make of them: they may be observed in every stage of growth. Lost parts of fins appear to be more easily reproduced in young than in old fishes.'<sup>4</sup>

<sup>1</sup> MS. Notes by Dr. A. Günther.

<sup>2</sup> cccv. vol. ii. p. 52.

<sup>3</sup> cccxxxiv. 'The wound caused by marking was covered with skin, and in some a coating of scales had formed part.' Page 5.

<sup>4</sup> MS. Notes by Dr. A. Günther.



## CHAPTER XI.

## GENERATIVE SYSTEM OF HEMATOCRYA.

§ 106. *Male Organs of Fishes.*—All Fishes are diceious, or of distinct sex. The male parts of generation present a progressive gradation of complexity from the essential gland, or testis, as a single organ distinguishable only by microscopic examination of its contents from an ovarium, to a more definite and concentrated form of testis with complete bipartition; then to the development of a proper duct or ‘vas deferens,’ next of a vesicula seminalis and prostate, afterwards of an intromittent organ, and finally of superadded ‘claspers,’ or mechanical instruments for retention of the female *in coitu*. In *Petromyzon marinus* the testis is a long thin plate, disposed in the form of a series of folds, closely attached by a duplicature of the peritoneum to the median line of the back of the abdomen, between the kidneys; the extension of the overlapping oblique folds to the right and left of the line of attachment feebly indicates the duplex character of the gland.<sup>1</sup> Its tissue consists of small spherical cells filled with spermatozoa, fig. 402. These escape, by dehiscence of the cells and rupture of the peritoneal covering, into the abdominal cavity, and are expelled by reciprocal pressure of the intertwined sexes from the peritoneal outlets at the cloaca. The Eel closely resembles the Lamprey in the general form and condition of the male organs; but the right and left sides of the plicated testis are more distinct, and the spermatic cells are more numerous and minute.

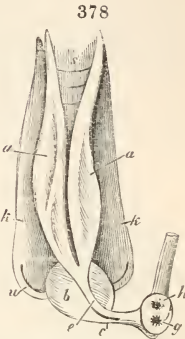
The Sand-Eel (*Ammodytes*)<sup>2</sup> has a single testis, compacted into an elongated triedral form, and impressed by a median longitudinal fissure: it usually inclines a little to the right side. In the Perch the single testis inclines to the left: in the Blenny and the Loach it lies in the middle line. In these osseous fishes the glandular part of the testis is inclosed in a proper fibrous capsule, which is continued from the posterior end of the gland, with its serous covering, into a short and simple sperm-duct, or ‘vas deferens,’ which opens usually into, or receives, the urethral prolongation of the urinary bladder. In the Gurnard the testes, fig. 378, *a*,

<sup>1</sup> xx. vol. iv. p. 48, prep. no. 2373.

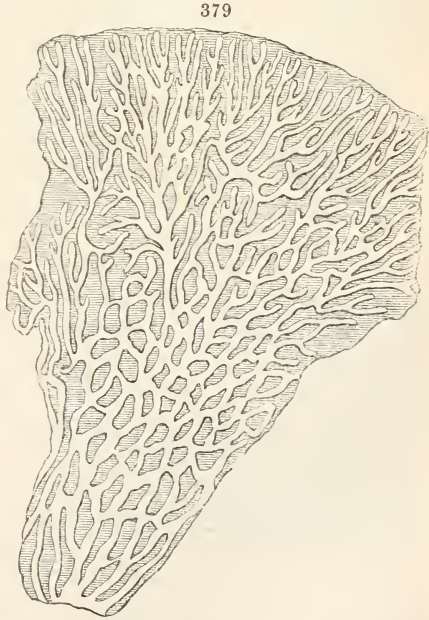
<sup>2</sup> Ib. p. 49, prep. no. 2378.

are distinct from each other, but their 'vasa deferentia' almost immediately unite into a common duct, *e*, which joins the urethra, *c*, behind the rectum, *h*, and terminates at the outlet, *g*. In the Salmon and the Herring the 'vasa deferentia' do not unite together until near their termination in the urethra. In the Cod and the Bull-head (*Cottus*) the common portion of the efferent duct is much dilated: it forms a saccular seminal reservoir in the Sole. The canal common to the ureter and vas deferens is of great length in the Sturgeon: a valve prevents the regurgitation of the urine into the spermatic duct. The urethra is usually produced into a papilla, which projects conspicuously from the back part of the cloaca in the viviparous Pœcilia, Anableps, and Blenny: it is large also in the Lump-fish. The testes are almost

entirely extra-abdominal in the Flounder and some other *Pleuronectidæ*, extending backward into a kind of concealed scrotum between the integuments and muscles on each side above the anal fin. The testes differ much in form in different Osseous Fishes, but are remarkable in all for their enormous seasonal increase: when fully developed, they are commonly known as the 'milt' or 'soft roe.' In *Gymnotus* they are two oblong triedral bodies, attenuated at both ends. In the Pipe-fishes (*Syngnathi*) they present the form of two simple elongated straight tubes, fig. 427, *g* 3.<sup>1</sup> In the Lump-fishes (*Cyclopteri*) they are divided by incisions into lobes: in the Cod a vast extent of the glandular surface of the glandular substance is packed into a small com-



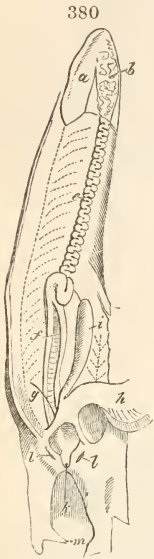
Renal and male organs :  
*Trigla lyra*, Carus



Structure of the testis in *Clupea Alosa*. CXXII.

<sup>1</sup> xx. vol. iv. p. 48, prep. no. 2375.

pass, by being disposed in convolutions upon the edge of the 'mesorchium.' The primitive spermatie cells, which are persistent in the Cyclostomes, have coalesced into tubes (tubuli seminiferi) in Osseous Fishes; the tubes open at one end in the wide and sometimes saccular commencement of the vas deferens, and terminate at the other, either by blind free extremities or by reticulate anastomoses.<sup>1</sup> In the Herring, Shad, and other Clupeoids, the discerning tubes ramify and anastomose in the substance of the testicle, and from this plexus, fig. 379, the initial caeca are prolonged to the surface of the gland, where their obtuse blind ends give a granulated appearance to the exterior.



Male organs, left side:  
*Spinax.*

In the Plagiostomes the testes, figs. 352, *h*, 380, *a*, are always distinct from one another, and usually of a circumscribed compact form, situated far forward in the abdominal cavity. They have a proper capsule, or 'tunica albuginea,' and a peritoneal covering; the capsule sends many 'septa' into the substance of the gland, and the lobes thus formed consist chiefly of the tubuli testis, and their expanded cell-like extremities, filled with the spermatozoa: the convolutions of the 'tubuli' are plainly discernible in the portion of the testis of the Basking Shark (*Selache maxima*) preserved in the Hunterian Museum, London, prep. no. 2396, A.<sup>2</sup> Numerous 'vasa efferentia' convey

the 'semen' to the beginning of the 'vas deferens,'<sup>3</sup> which forms a large 'epididymis,' fig. 380, *b*, by its manifold convolutions. These gradually decrease as the duct, *ib. e*, approaches the cloaca, when it becomes straight, and expands into an elongated reservoir, *ib. f*, the mucous surface of which is commonly increased by numerous transverse plicæ, as in *Spinax* and *Selache*. Behind the termination of the rectum the 'vasa deferentia' suddenly diminish, approximate, communicate with the ureters, and terminate upon the cloacal penis, fig. 352, *o*. This is hardly visible, and the testes are very small, except at the breeding season, in the Piked Dog-fish (*Spinax*).

The claspers are present in the Chimæroid Fishes as well as in the Plagiostomes. They project backward, as appendages to the bases of the anal fins, and are sometimes bent inward at their free extremities, figs. 352, *g*, 380, *m*. Near this part may be

<sup>1</sup> cxxii. p. 105.

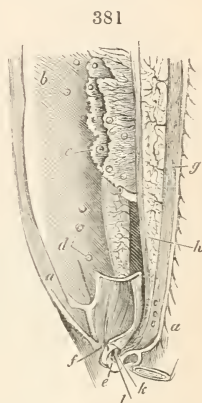
<sup>2</sup> xx. vol. iv. p. 52.

<sup>3</sup> cxxxiv.

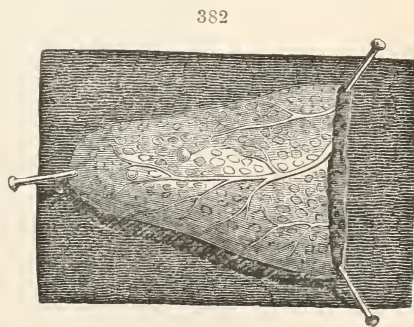
discerned a fissure, which is the outlet of a blind sac, extending forward from the base of the clasper, beneath the muscles and skin, at the sides of the cloaca. The inner surface of the cavity is smooth, and lubricated by a fluid mucus: the attached vascular surface is richly supplied with vessels, especially with veins: in the Rays a glandular body adds its secretion to that of the surface of the cavity.

§ 107. *Female Organs of Fishes.*—The gradations of structure of the female organs correspond very closely with those of the male. In the young Lamprey the ovarium is a simple longitudinal membranous plate, fig. 381, *c*, suspended by a fold of the peritoneum (mesoarium) along the under part of the vertebral column: it increases in breadth and thickness as the ova are developed in it, and still more so in length, being accommodated to its locality by numerous folds, fig. 382. But no superadditions are made to this primitive structure: the ova, *d*, escape by rupture of their capsules into the abdomen, *b*, and are excluded by the peritoneal aperture, *ib. l*. In all other Fishes in which vasa deferentia are absent in the male, oviducts are absent in the female. But it does not always happen, where vasa deferentia are developed in the male, that the homotypal ducts exist in the female: the Salmon is an example in which the ova are discharged by dehiscence into the abdominal cavity, and escape by peritoneal outlets, as in the Eel and Lamprey.

With this exception, the parallelism of the male and female organs is very close. Thus the ovarium is single in those bony Fishes, as the Perch, the Blenny, the Loach, and the Ammodyte,<sup>1</sup> in which the testis is single: the median cleft of the ovary of the Ammodyte is deeper than that of the testis, but the continuity of the two seemingly distinct glands is obvious at the upper and lower ends. In



Renal and female organs  
*Petromyzon*. xx.

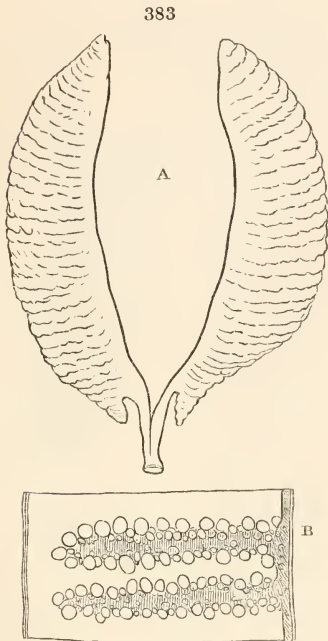


An ovarian fold of the Lamprey.

<sup>1</sup> xx. vol. iv. p. 133, prep. no. 2675, A.



most Osseous Fishes the ovaria, fig. 383, A, form two elongated sacs of mucous membrane, with a thin fibrous tunic and a peritoneal covering, closed anteriorly, but produced posteriorly into a short, straight, and commonly wide oviduct, terminating behind the anus, and commonly before the urethra, fig. 281, *i*. In the



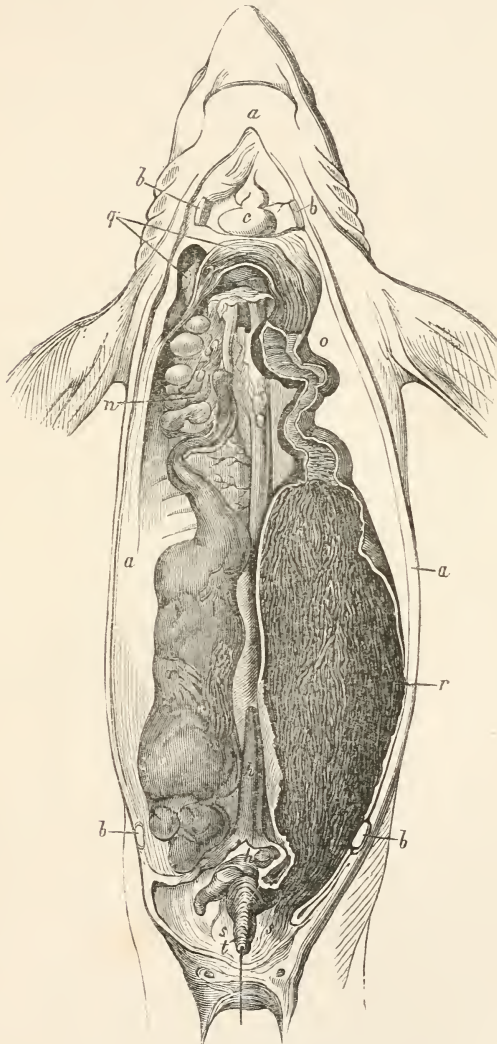
Ovaries and oviduct of an Osseous Fish.

Pipe-fishes the oviducts continue distinct to the cloaca. In most Fishes the oviducts coalesce, after a brief course, as in the Herring, or after a longer course, into a single tube before arriving at the cloaca: the common terminal portion becomes much dilated in the Cod-fish, the Lump-fish, and some others. The 'stroma,' or cellular tissue, which is the seat of development of the ova, is interposed between the mucous and fibrous tunics of the ovarian sac: it sometimes, though rarely, is coextensive with the mucous membrane. In the *Lophius* the two ovaria are long and large plicated tubes, flattened when empty, cylindrical when inflated, with the ovigerous stroma lining, as it were, only the ventral half

of the walls of the cylinder, and terminating where the oviducal portions of each sac unite together to form the common short efferent canal. The inner surface of the 'stroma' is beset with small tubercles, arranged in interrupted linear series, each tubercle supporting four or five papilliform ovisacs. In the Pike the stroma forms a longitudinal strip, in short transverse plaits, along the median side of the long ovarian sacs: fig. 383, B, shows two of the ovarian plaits, from which the developed ova hang in subpedunculate ovisacs. In the Wolf-fish the stroma extends over the whole of the internal surface of the ovary, into the cavity of which it projects in the form of numerous oval compressed processes. In general, its superficies is extended by being plaited into numerous folds, which are transverse in the Cod and Salmon, oblique in the Mackerel, and longitudinal in some other Fishes.

In the Salmon the free surface of the stroma is exposed. In the Osseous Fishes that retain and hatch their ova the stroma does not extend to the posterior part of the ovarian sac, but this

384



Viscera of female Shark. xx.

serves as a kind of uterus, and contains an abundant albuminous secretion at the season of the internal incubation. The viviparous

Blenny (*Zoarces*), the Anableps, the Pœcilia, and Embiotoca<sup>1</sup> are examples of ovo-viviparous Osseous Fishes, and at the same time manifest naturally, what occurs as a rare abnormality in higher Vertebrates, viz. ovarian gestation. In the Plaice and other Pleuronectidæ the parallelism between the male and female organs is so close that the ovaria also escape from the abdomen, and become lodged in greater or less proportion in subcutaneous scrotal cavities above the basis of the anal fin.<sup>2</sup>

In the Lamprey the short and narrow lateral infundibuliform passages behind the rectum, into which the ureters open, and which terminate in the peritoneal outlets, fig. 381, *e, l*, have been compared to short oviducts. In the Sturgeon actual oviducts are continued from the ureters forward, which open by wide infundibular apertures, comparable to the 'morsus diaboli' of anthropotomy, into the general peritoneal cavity, and receive the ripe ova as they burst from the ovarium. The urine is prevented from regurgitation into the serous cavity through the same passage by a valve which only allows the passage of the ova backward into the common urogenital duct.

The higher grade of the sexual organisation of the female Plagiostome, as compared with the cartilaginous Ganoid fish, is manifested chiefly by modification of the oviducts: they are always two in number, fig. 384, *q, r*, and distinct from one end to the other, but they are brought into close proximity, or coalesce at both ends: they are always distinct from the ureters, which terminate on the prominent urethral clitoris, *ib. t*, between the oviducal outlets, *ib. s, s*. Different parts of the oviducts are modified, moreover, for special functions, superadded to that of effecting the safe transit of the generative product. The ovaria of Plagiostomes, fig. 384, *n*, are relatively much smaller than in other Fishes, of a more compact form, and confined to the fore part of the abdominal cavity: they are sometimes blended into a single body. The stroma is not spread over the walls of a cavity, but is collected into a loose cellular mass, circumscribed by a fibrous membrane, and suspended by a duplicature of peritoneum to the dorsal parietes of the abdomen, at the sides of the œsophagus. The ova are much fewer in number than in the 'roe' of Osseous Fishes, and are seen in different stages of growth, being developed more consecutively. The approximate or confluent abdominal apertures of the oviduct, *ib. q*, are anterior to the ovarium, between the liver and the pericardial septum; they form together a heart-shaped opening, with entire margins,

<sup>1</sup> CCCXXXV<sup>2</sup> XLIII. v. pl. 4, fig. 1.

attached by two diverging ligaments to the abdominal walls. If a little powdered charcoal be sprinkled on the ovarian orifices and ligaments exposed by opening the abdomen in a fresh caught female Dog-fish, the particles will be seen to move towards and enter the common oviducal aperture, indicative of a ciliated epithelium in the serous membrane, which may aid in the transport of the ova to that aperture. The oviducts, narrow, and with thin tunics at their commencement, diverge from each other, arching over the fore part of the ovaria, and then descend along the ventral surface of the kidneys, to terminate at the lateral and posterior parts of the cloaca, *ib. s.* A glandular body, *ib. o.*, is developed in their coats, after the first, fifth, or sixth part of their extent, and their terminal half or third part, *ib. r.*, is dilated; the sizes of the glandular and of the uterine parts of the oviduct are usually in inverse proportion: in the oviparous Plagiostomes the gland is large, the uterus small, and the reverse obtains in the viviparous species, *fig. 384.* The inner surface of the Fallopian portion of the oviduct presents longitudinal or very oblique folds of the delicate mucous membrane: but near the aperture the folds resolve themselves into minute compressed villi. The glandular part varies in structure as well as in size in different species. In the viviparous Dog-fish (*Spinax acanthias*) it consists of two elliptic flattened lobes, of laminated structure, the free surface presenting minute transverse striæ, beset with pores, the orifices of discerning tubes, the aggregate of which composes the layer of glandular substance. In the oviparous Homelyn (*Raia maculata*) the lobes of the large rudimental glands are reniform, and consist of close-set layers of discerning tubes. In the Tope (*Galeus*) the lobes of the gland present the same essential structure, but are conical, subspiral, and hollow. The uterine part of the oviduct in the viviparous Dog-fish, *fig. 384, r.*, has the lining membrane produced into longitudinal folds, with wavy margins, each of which contains a single vessel following its sinuosities, and sending off branches to the parietes of the oviduct: the folds gradually subside at the outlet of the oviduct. In the oviparous Dog-fish (*Scyllium*) the folds of the lining membrane of the corresponding part of the oviduct are oblique, and their vessels are derived from trunks in the walls of the oviduct, and are distributed in minute and tortuous ramifications on the folds.<sup>1</sup> The uterus of the Smooth Dog-fish (*Scoliodon*, M.; *Emissole lisse*, Cuv.) shows several uterine

<sup>1</sup> xx. vol. iv. p. 136.



cotyledons developed from the internal surface of the dilated part of the oviduct: corresponding fœtal cotyledons are developed from the vitellicle of the embryo.

Thus the various forms of the generative organs of Fishes resolve themselves into four well-marked grades of complexity. First, the essential gland, testis or ovarium, without excretory canal. Second, the same, with a simple duct, continuous with testis or ovarium. Third, a partial oviduct, not continuous with the ovarium, and not separated from the ureter. Fourth, testis or ovarium, of a more compact form, each with a long and complex duct, distinct from the ureter; the beginning of the vas deferens convoluted into an epididymis, and its end dilated into a seminal reservoir, with a plicated glandular inner surface; the oviduct not continuous with the ovarium, but with a nidamental gland near its commencement, and dilating into a receptacle, with a plicated surface, at its terminal half. Besides the 'claspers' of the Plagiostomes, there are other accessory organs of generation, viz. the subcaudal marsupial tegumentary folds in the male of some species of *Syngnathus*, fig. 427, *o*,<sup>1</sup> and the subabdominal marsupial pouch in the male Hippocamps.<sup>2</sup>

§ 108. *Male Organs of Batrachians*.—These consist of testes, their ducts and appendages, the seminal reservoir, and the common excretory canal and terminal papilla: there is no intromittent organ.

The testes, though in some Batrachia subdivided, resemble in their relative size and compactness of form and tissue those of the Plagiostomes. In the *Proteus anguinus* the testis is long, cylindrical, with obtuse ends, slightly fissured lengthwise by the insertion of the suspensory ligament: they sometimes show inequality of size, and the right is usually about three vertebræ in advance of the left. In *Amphiuma* the testis is subcylindrical, and tapers at both extremities: adipose appendages project from their free or ventral surface. In the Axolotl the 'mesorchium,' or suspensory duplicature of peritoneum, is broader, and permits the vessels and ducts to be readily seen as they traverse it transversely. The adipose appendages are branched. In the Menopome the testes are rather broader than in the Amphiume, approaching the oval shape. This is likewise the case with one or both testes of the great Japan Newt (*Sieboldtia* or *Cryptobranchus*), which are suspended by a broad mesorchium on each side of the aorta and narrow remnants of the Wolffian bodies, between the ends of the lungs and the beginnings of the kidneys.

<sup>1</sup> xx. vol. v. p. 67, preps. nos. 3226–3228.

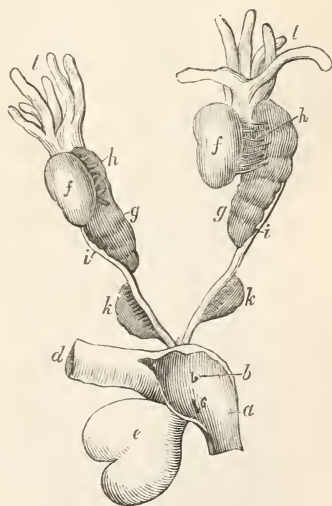
<sup>2</sup> Ib. p. 68, preps. nos. 3230 and 3231.

In most Newts the testis is divided into two lobes, fig. 387, *a*, one, usually the larger, in advance of the other: I have observed three detached lobes or testes on each side. In the Salamander there may be one or two smaller lobes or accessory testes, besides the two chief divisions of the gland.<sup>1</sup>

In tailless Batrachians the testes, in accordance with the shape of the body, present a full oval form, compact and undivided: they are situated, as shown in the Frog, fig. 385, *f, f*, on the ventral side of the anterior half of the kidneys, *g, g*, having an entire investment of peritoneum, often deeply or brightly coloured by pigmental cells, which forms a broad and short mesorchium, suspending them to the renal glands and supporting the blood-vessels and efferent ducts. Processes of peritoneum, filled with fat, *l, l*, diverge from the fore part of both bodies.

In all Batrachians the testis consists of seminiferous cæca, more elongated than the sperm-follicles of Fishes, shorter and straighter than in higher Reptiles, having their blind ends next the capsule. This consists of a fibrous or 'albugineous' tunic, beneath the serous one: both have been removed to show the tubuli testis in Swammerdam's accurate figure, fig. 386. The semen is conveyed by short transverse efferent ducts, *h*, to a common longitudinal canal, *i*. In the Menopome about ten vasa efferentia quit the elongated testes and enter the common canal, which extends along the anterior three-fourths of the kidney, and at its fore-end is connected with the ligamentous remnant of the duct of the Wolffian body: it is thence reflected back along the outer border of the kidney, receiving in its course toward the cloaca the ureters, which are short transverse or oblique tubes, from ten to twenty in number: the urino-seminal canal, supported by a narrow fold of peritoneum, forms a few slight bends, and gradually expands as it approaches its termination at the back part of the cloaca. In *Sieboldia maxima* the longitudinal canal which receives the short efferent ducts is

385

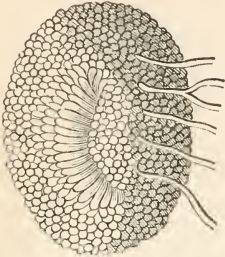


Generative organs of male Frog. CCLXX.

<sup>1</sup> xx. vol. iv. p. 53.

continued forward to the Wolffian ligament, far in advance of the testes, contracting to a point: in its backward course, between

386

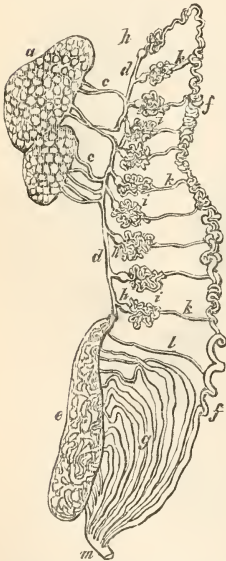


Testis of Frog. CCLXX.

the testis and remnant of the Wolffian gland, it receives a few short transverse ducts therefrom, which come from small masses of convoluted tubes, still pervious to mercurial injection in the male dissected by Dr. J. Van der Hoeven: continuing its descent, the longitudinal duct gradually expands, describing convolutions, and receiving in its course along the outer side of the kidneys the excretory ducts, two or three in number, of those glands. Each urino-seminal canal expands into a simple

oblong reservoir, with thickened glandular coats, at the termination of the rectum, and communicates with the cloaca by a papilliform orifice, a little in advance of the blind end of the reservoir. The slender elongated remnants of the Wolffian glands are direct continuations from the fore part of the kidneys.

387

Male organs, Newt. *Triton taeniatus*. CCCXXII.

In the Newt (*Triton taeniatus*) from four to five efferent tubes, fig. 387, *c, c*, quit each of the two chief divisions of the testis, *ib. a*, and terminate in the common longitudinal canal, *ib. d*, which extends forward to the Wolffian ligament, and backward to the anterior end of the kidney, *ib. e*: in this course it sends off about ten short transverse branches, which, after dilating and convoluting, *ib. i*, severally terminate in the beginning and fore part of the urino-seminal canal, *ib. f*. The small dilatation and larger mass of convolutions on each of the transverse branches of the longitudinal duct are retentions of modified parts of the Wolffian or primordial urogenital gland. The urino-seminal duct, *f*, forms many close coils, like an epididymis, as it approaches

the kidney: it receives directly one or two uriniferous tubes, *ib. l*, and communicates, near its termination, with the orifices of a series of modified ureters, *ib. g*, which receive the rest of

the urine as well as the semen. Each uriniferous duct dilates into a long reservoir, describing a curve external to the kidney, the first or anterior being the longest, the rest successively shorter : they are connected together, eight to ten in number, so as to form, in appearance, a flattened semi-oval 'vesicula seminalis,' and terminate by a short wide canal, *ib. m*, common to them and the vas deferens, in the back part of the cloaca.

In the Frog about six transverse efferent ducts, *fig. 385, h*, enter the longitudinal one, *g*, extending along the inner (mesial) side of the kidney, which is reflected round the fore end of that gland to form the beginning of the urino-seminal canal, *ib. i*, which courses along the outer (lateral) side of the kidney. This canal does not describe convolutions: it enlarges as it progressively receives the ureters, and suddenly expands beyond the kidney into a semi-oval 'vesicula seminalis,' *ib. k*, the outer half of which has folliculo-glandular walls, the inner half being smooth and with the character of a reservoir. A short duct conveys the contents of the vesicle to the back of the cloaca, *ib. b*; at the fore part is the orifice, *c*, of the allantoïd bladder, *e*.

No Batrachian has the intromittent organ, or a vas deferens distinct from an ureter: a stage in the substitution of kidneys for Wolffian bodies is hereby obviously indicated.

§ 109. *Male Organs of Reptiles.*—In the scaled Reptiles the conduits from the kidney and the testes are distinct to the cloaca, and terminate there on separate papillæ. The testes, *fig. 389, b*, are comparatively small and compact: they are always abdominal, with a complete investment of peritoneum, frequently coloured by pigment-cells. They have a strong albugineal tunic, and consist of blind seminiferous tubes, *fig. 388*, much longer and more slender than in Batrachians, and packed up in close convolute folds, in ill-defined loculi of the gland. From these tubes a variable number of efferent canals proceed, which are inclosed in a prolongation of the tunics of the testis for a brief course, and then unite into a vas deferens.

In the Ophidia the testes, *fig. 357, h, h*, are of a more elongate

388



Tubuli seminiferi ; testis of Lizard.



form than in other Reptiles. In the common harmless Snake (*Coluber natrix*) they are oblong, subcompressed, in advance of the kidneys, the right about an inch more forward than the left, corresponding to the difference in the relative position of the kidneys. In the Rattlesnake the testes are more symmetrical in position. The vas deferens, disposed in short undulations, goes along the kidney to the cloaca, the papillæ terminating near the beginning of the urethral groove. The intromittent organs are two in number, and consist of invertible sheaths, or long narrow bags, with a highly vascular papillose lining membrane, bifurcate at their blind end, to which are attached the muscles, fig. 357, *l*, for inverting and keeping them retracted and hidden in the base of the tail. By tumefaction of the vascular portions of the bags, and the action of the 'constrictor basis caudæ' and 'sphincter cloacæ,' they are everted. In the Rattlesnake the blind end of each inverted pouch bifurcates, and the vascular membrane is thickened and produced into many processes near the bifurcation: when eversion with erectile tumefaction of the parts takes place, each penis presents a papillose and bifurcate glans, as in fig. 357, *k*. In *Elaphis quadrilineatus* the body of the penis presents large retroverted papillæ, and the glans is beset with small flattened wrinkled processes.

In the Slow-worm (*Anguis*) the testes are situated a little anterior to the dilated rectum, the right in advance of the left; the sperm-duct simulates a long epididymis by its initial convolutions or transverse folds. The intromittent organs are invertible and evertible pouches, as in Serpents, but are shorter.

In a Scinc-lizard (*Tiliqua*) the right testis is more advanced in position than the left. The body of the penial pouch, when everted, shows transverse rugæ, and the sub-bifurcate glans short retroverted papillæ. In *Lacerta ocellata*, as in *Draco volans*, fig. 389, the testes, *b*, show a similar degree of unsymmetrical position. The sperm-ducts form, by a series of short transverse folds, a long body or band, like an epididymis: but there is no structure properly so called consisting of the convolutions of several efferent tubes prior to their union to form the vas deferens, *ib. c*. In the interspace of the orifices of the ureters a ridge is continued backward, on each side of which is the orifice of the vas deferens, whence is continued the urethral groove extending along the penial sheath to the papillose blind end or glans.

The peritoneal covering of the testes shows in some Lizards

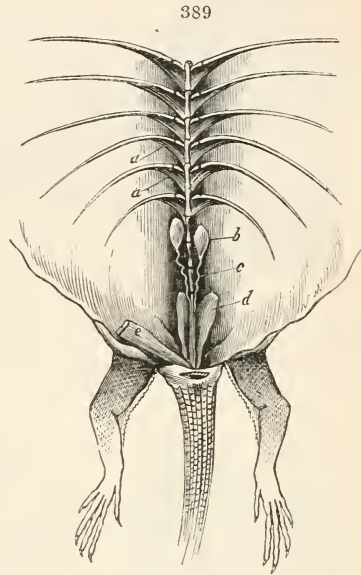
stellate pigment-cells: in the Chameleon they give a black colour to the gland.

The short and outwardly extended legs of Lizards serve for progression, not for support, and the animal rests with its belly on the ground, as in Serpents: hence the necessity not only for the internal position of the testes, but for the mechanism by which the intromittent organs can be inverted, and safely lodged out of sight, in the base of the tail, when not in use.

In the Turtle (*Chelone midas*) each testis is an elongate, cylindrical, slightly bent body, decreasing in size at the end next the cloaca: the efferent tubes leave it near the fore or upper part of its concavity, and soon join the vas deferens, which forms a large and compact body by numerous convolutions, situated between the testis and kidney.

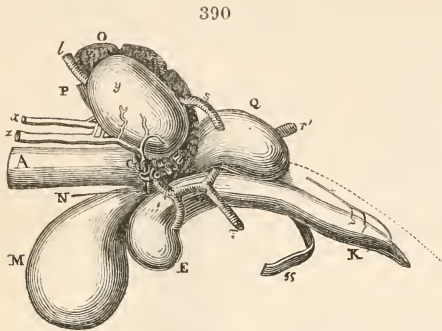
Each vas deferens terminates, with the ureter, in a papilla, the spermatic orifice being nearer the bladder. The penis is short, and is indicated, in the unexcited state, chiefly by the urethral groove; only the glans and the pointed end of the fibrocartilaginous body immediately above it project from the cloacal surface, and these are partly enclosed by a thick duplicature of the cloacal membrane, representing a preputium: in the erection of the organ this fold is everted and obliterated.

In the *Emys europæa* the testes, fig. 390, *y*, and convoluted sperm-duct, *ib. c*, are separated from the kidneys, *ib. o*, by the peritoneum, which, after giving an entire investment to the testes, is simply reflected over the contiguous surface of the kidney: an artery, *l, s*, runs between the two glands. The testis presents a full elliptic figure: its peritoneal covering is usually stained with a dark pigment: *x* is the spermatic artery, *z* the spermatic vein. The sperm-duct opens, close to the ureter, upon a papilla, fig. 391, *F*, at the commencement of the urethral groove, *ib. g*. The penis, in both freshwater and land Chelonia, is longer and



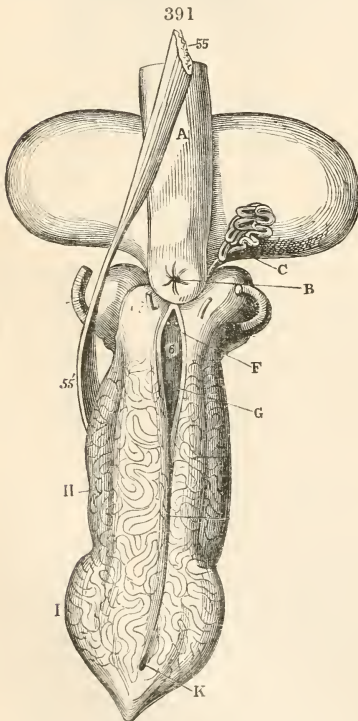
Male organs, *Draco volans*.

larger than in the marine species: it is subcylindrical, with an expanded terminal glans, *ib.* I, usually ending in a point. The



Male organs of *Emys europaea*. XXXVIII.

penis consists of two 'corpora cavernosa,' *ib.* II, which are firm fibrous bodies, cohering mesially and attached to the ventral surface



Penis of *Emys europaea*. XXXVIII.

urethral groove, *ib.* G, extends along the middle of the dorsal surface, and becomes deeper as it approaches the glans: in erection the tumefaction of its borders converts the groove into a temporary canal, and it then appears to end by an orifice, *κ*, which is usually divided by a papillary eminence. The

of the cloaca; and of two median tracts, *fig.* 392, 4, of a more vascular erectile tissue, forming the walls of the median groove, 5, and covered by a soft *quasi*-mucous membrane. Each vascular tract commences by an enlargement, *fig.* 390, E, analogous to the *bulbus urethrae*. The erectile tissue is continued forward, thinly at first, but afterwards increasing in thickness, to the glans, *figs.* 391, I, and 392, which it chiefly constitutes. On each side of the mid-line of the penis is a canal, *fig.* 392, *f*, which at one end communicates with the cavity of the peritoneum, and by the other end is prolonged into the substance of the glans, where it terminates, blindly or by a kind of reticulate sinus.<sup>1</sup> The penis is provided with two retractors, *fig.* 391, 55, *fig.* 392, 55', arising from the

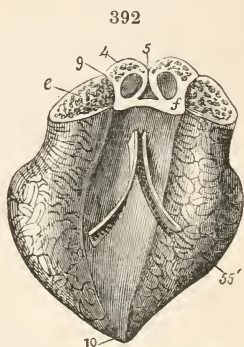
<sup>1</sup> XX. vol. iv. p. 62, prep. no. 2450.

ischium, and extended along the under (ventral) surface of the penis to the glans. This muscle folds up the penis in retracting it within the cloaca, and at the same time closes thereby the orifice of the rectum, fig. 390, A, and that of the allantoic bladder, *ib.* M. Erection is followed by eversion of the cloaca, effected by its 'sphincter.' The development of the penis bears relation to the physical impediments to coitus, caused by shape, extent, and completeness of the shell, and by the medium in which the act takes place: thus the penis is least developed in the marine species, with a flattened carapace and incomplete plastron. The glans penis is trilobate in *Trionyx*.

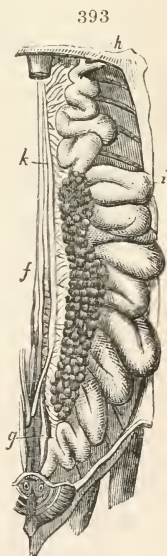
In the Crocodile the testes are longer than in *Chelonia*, and rather more in advance of the kidneys. The penis is single, with a dorsal groove, continued forward on a slender conical process. It consists of a firm fibrous cavernous structure, commencing by two crura, and becoming softer towards the glans, which consist of vascular and erectile tissue: this is prolonged beyond the apex of the corpus cavernosum, so that two points are thus seen, one above the other: these points are united together on each side, and also in the middle, by a vertical septum, which divides the interspace between them into two culs-de-sac. The urethral groove is continued as far as the extremity of the upper point. The peritoneal canals do not penetrate the cavernous structure, but lead to and open outwardly on papillæ, situated on each side the base of the penis, within the cloaca.

As Lizards are allied to Serpents by the double extra-cloacal penis, so Tortoises are allied to Crocodiles by the single intra-cloacal penis: the structure of this organ also presents two types, respectively characterising the scaled and scuted groups of Reptilia.

§ 110. *Female Organs of Reptiles.*—In the Axolotl, fig. 393, and *Siren lacertina*, the ovaries, *ib.* f, are granular elongated bodies, situated on each side of the root of the mesentery. They



Peritoneal canals of penis; *Emys europæa*. XXXVIII.



Female organs; *Axolotl*.



consist of delicate folds of membrane, inclosing stroma studded with ovisacs, of two grades of size, the larger with ova for the present season, the smaller for the following one. In a Siren with enlarged ovaries I observed them bearing impressions of the intestinal convolutions. The oviducts, *ib. i*, are external to the ovaria, and are attached to the sides of the spine, each by a broad duplicature of peritoneum. They commence anteriorly by a simple slit-like aperture, with entire borders, *h*, are attenuated at their commencement, and soon begin to be disposed in short parallel transverse folds, in the Axolotl about twelve, in the Siren twenty, in number, which gradually diminish near the cloaca, where the oviducts open behind the rectum upon small prominences. Above the kidneys, *g*, a linear tract, *k*, indicates the remnant of the Wolffian body.

The foregoing type of female organs is closely followed in all the perennibranchiate Batrachia. In the Newt the ovaries, as they expand, assume a lobulated exterior and greater relative breadth, especially at their hinder end, than in the Axolotl. Each oviduct begins by a simple slit-shaped aperture, between the pericardium and liver, and passes backward in a wavy course, which becomes irregular as it approaches the kidneys: here the oviducts diverge from each other, then approximate at the medial line, and again diverge, describing a regular curve outward, and again converge to their cloacal terminations.

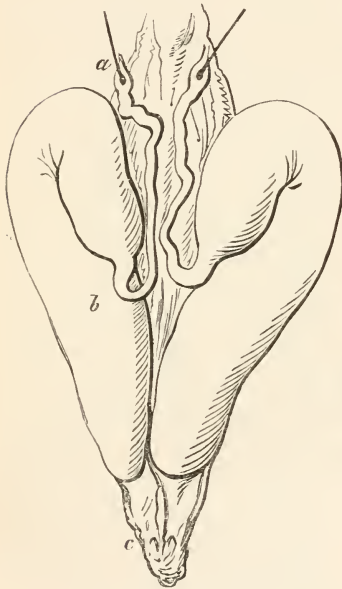
In the Salamander (*Salamandra maculosa*) the oviduct is more definitely divided into an oviducal, or 'fallopian,' and a uterine part: the former, *fig. 394, a*, is slender, and before impregnation is convoluted to within a short distance of the cloaca, where it suddenly expands into the uterine part, *b*: this part curves forward and outward before terminating in the cloaca at *c*. The young are developed in this expanded part of the oviduct, which is much enlarged after impregnation, as in the figure.

In the tailless Batrachia the ovary, in its quiescent state, *fig. 395, o*, has the form of an irregularly plicated membranous sac, with thin and transparent parietes. The initial aperture of the oviduct, *ib. a*, is situated close to the base of the heart: the tube is disposed in many, usually transverse, folds or coils, before its termination in the dilatable terminal part, in which the ova to be impregnated and discharged in the same season are accumulated, as in *fig. 395, b*. In the cloaca the following outlets are seen:—in front, that of the allantoic bladder, behind it that of the rectum, then the oviducal outlets, *ib. c*, and lastly those of the ureters.

In scaled Reptiles there is a clitoris or some representative trace of the intromittent organ of the other sex.

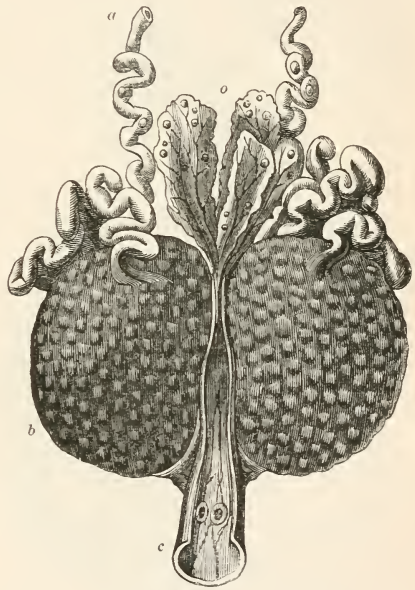
In Ophidia the ovaries, like the testes, are long, slender, and disposed one, usually the right, in advance of the other, and the ovisacs are developed for impregnation, in a single longitudinal series in most species. The ovaries are connected with the beginning of the oviducts by a broad fold of peritoneum. Each oviduct commences by an expanded ostium, with a wide fissure, fig. 396, *a*; its tunics, at first delicate and transparent, increase in thickness as the tube contracts: here its course is slightly wavy, but it soon becomes straight, and, in the viviparous Serpents, expanded, *ib.* *b*:

394



Oviducts and uteri, Salamander.

395



Oviducts and uteri, Frog.

in the Rattlesnake the lining membrane of the oviduct, prior to the expansion, is disposed in minute parallel longitudinal rugæ. The correspondence of the ostia of the oviducts, *a*, with the ovaries in position renders the left shorter than the right, and in viviparous Serpents it usually contains fewer ova or young, as in fig. 396. The cloacal terminations of the oviducts are in a semilunar fissure, behind the orifice of the rectum.

In the Lacertians the ovaria usually manifest a slight want of symmetry in position, the right being a little more advanced than

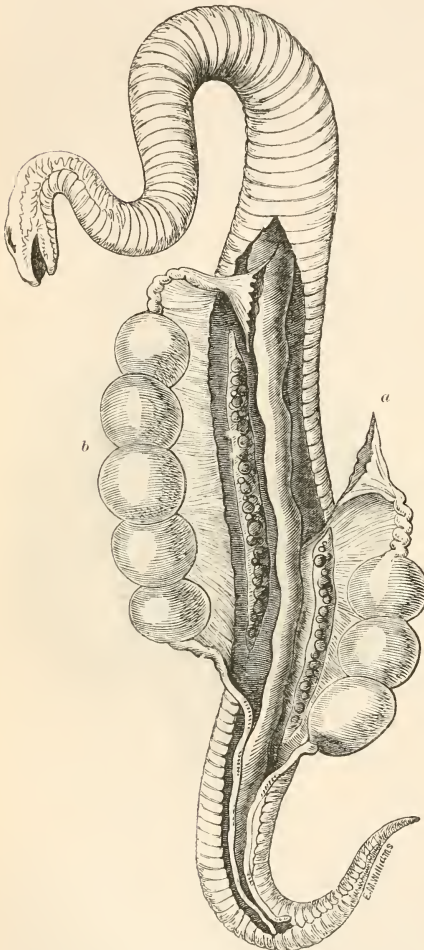
the left. In the *Lacerta bilineata* each ovary shows about a dozen visible ovisacs: the oviducts are plicated throughout their course. In *Agama atra* there are seven or eight equally developed ovisacs in each ovary. In an Iguana the left ovary exceeded the

right in size, and the immature ovisacs appeared as flattened discs overlapping each other. The duplication of peritoneum which connects the oviduct to the side of the vertebræ is continued beyond the canal, and terminates in a free edge. In the ovoviviparous Lizard (*Lacerta* [*Zootoca*] *muralis*) the part of the oviduct in which embryonal development proceeds is very expansile, as in the Viper; in the specimen figured, fig. 397, the right oviduct contained three ova, *ib. e*, the left two ova: the ovaria are shown at *a*, the abdominal aperture of the left oviduct at *c*, the fallopian part of the tube at *d*, the uterine part at *e*, the terminal part at *f*: the peritoneal fold, attaching the oviduct to the ovary and to the spine, is marked *b*, the rectum *g*, and the cloaca *h*.

In *Chelonia* the ovaries are symmetrically disposed, and placed far back in the abdomen. The female organs of the Turtle (*Chelone midas*), in the quiescent

state, show the ovaries in the form of a broad, flattened, variously folded substance, thickly studded with innumerable ovisacs, like white specks: each ovary is attached by a peritoneal fold, 'mesarium,' to the sides of vertebræ, between the rectum and the

396



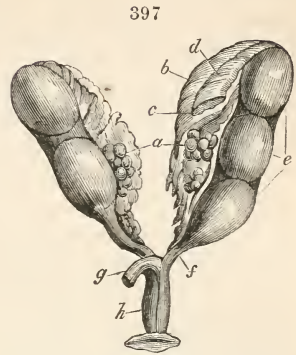
Female organs impregnated, Viper. cccviii.



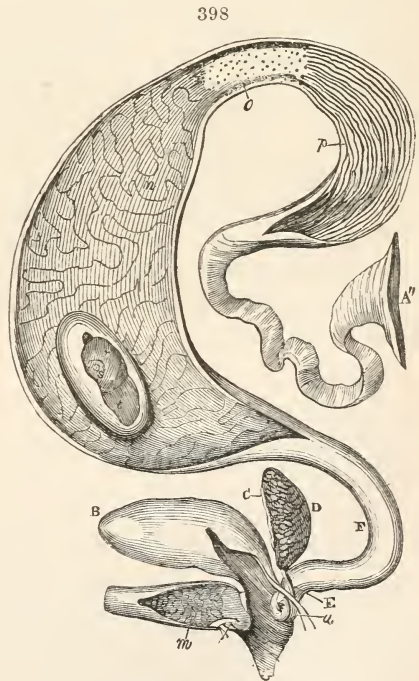
oviducts. The oviduct commences by a simple elongated slit, opening upon the free margin of the mesoary; the duct soon contracts to almost capillary tenuity, and gradually expands as it approaches the cloaca, contracting again before its termination.

In the Snapper (*Chelydra*) the oviduct is disposed in short transverse folds, between the layers of a broad duplicature of peritoneum, gradually diminishing in width, and increasing in the thickness of its parietes as it approaches the cloaca. The inner surface of the initial part of the duct presents a series of oblique folds, which gradually become more produced and more longitudinal.

The oviducts terminate between two diverging folds of the lining membrane of the cloaca, which folds gradually subside as they converge to meet and terminate in the sinus of the 'glans clitoridis.' In the European Freshwater Tortoise the inner surface of the initial, narrow, and thin-walled part of the oviduct, *A''*, *p*, fig. 398, is disposed in fine longitudinal folds, and is lined by ciliate epithelium: beyond these, for a short space, *ib. o*, the walls of the oviduct are glandular: in the expanded part (containing an egg in the example figured) the rugæ of the lining membrane are feeble and sinuous. External to the mucous membrane there is a stratum of muscular fibres, by the contractions of which the ovum is propelled along the oviduct:



Back view of female organs impregnated; *Zootoca*.



Descent of the egg in the oviduct of *Emys*. One oviduct, the cloaca and parts opening therein. XXXVIII.

the ovum is propelled along the oviduct:



at the termination, *F*, where the egg-shell is secreted, the membrane is vascular, and thrown into broad irregular rugæ, which are continued as far as its termination, *n*, in the cloaca. The ureter, *E*, opens behind the oviduct, *a*: the allantoic bladder, *B*, and rectum, *m*, in front.

In *Crocodylia* the ovaria are more advanced in position, and more compact in form and structure, presenting, in the unexcited state, a surface granulated by minute ovisacs. The abdominal orifice of the oviduct has an entire margin; the duct maintains a more uniform diameter, and sooner gets upon the edge of the supporting fold of peritoneum than in *Chelonia*. The lining membrane of the hind part of the oviduct is puckered up into close-set undulating transverse rugæ: but these subside gradually toward the terminal shell-forming segment, where the membrane shows minute longitudinal puckerings. The outlet projects into the cloaca. The clitoris arises by two crura, and is impressed by a longitudinal groove.

Of parts in female Reptiles accessory to generation, the most remarkable are the temporary tegumentary pouches on the back of the female *Pipa*, fig. 367, *B*, *C*, which, receiving the impregnated ova, retain the young until the metamorphosis is complete. In *Nototrema* and *Opisthodelphys* there is a large single pouch in the middle of the back, with the entrance above the vent. It serves for the reception of the ova, which are hatched therein. This pouch is peculiar to the female, which attains nearly to its full size before the pouch is developed. After the reception of the ova, it extends nearly over the whole back of the animal, whilst it is shrunk and scarcely visible when the season of propagation has passed.

## CHAPTER XII.

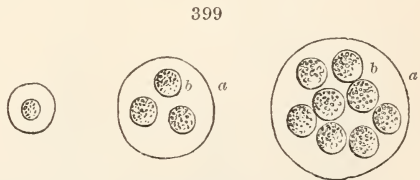
GENERATIVE PRODUCTS AND DEVELOPEMENT OF  
HÆMATOCRYA.

THE functions of the above-described Generative Organs are 'semination,' 'ovulation,' 'fecundation,' and 'exclusion,' to which is added, in some Hæmatocrya, that of 'fœtation.' Semination, or the production of sperm-cells, is peculiar to the testis: ovulation, or the production of germ-cells and vitellus, is peculiar to the ovary: fecundation is the combined act of the male and female. A part of the oviduct is usually modified to add accessory parts to the ovum, or in subserviency to fœtation in the viviparous *Hæmatocrya*: but, in a few instances, the protective and portative functions are relegated to tegumentary wombs or marsupia, which may be developed in either sex. Exclusion of the male generative product is called 'emission,' that of the female generative product 'oviposition:' but if the ovum be arrested for the process of fœtation, the exclusion of the fœtus is then termed 'birth.' Sometimes the male assists in the process of exclusion.

§ 111. *Semination of Hæmatocrya.*—The product of the testis in Fishes consists of 'sperm-cells,' 'spermatoa,' and 'spermatozoa,' with very scanty fluid medium of suspension: the function is seasonal, and attended by rapid increase of the glands.

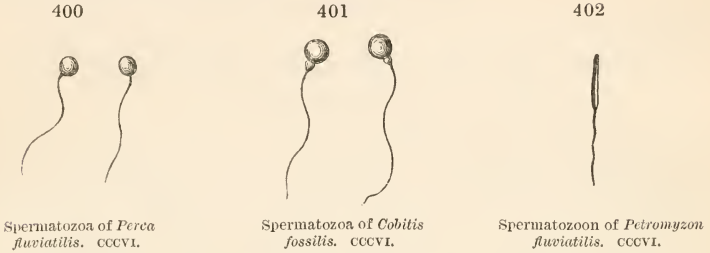
This is greatest in Osseous Fishes, in the testes of which, at the beginning of their enlargement, the sperm-cells (cysts or 'mother-cells') are seen, fig. 399, *a*, containing one or more spermatoa ('cells

of development'), *ib. b*. These usually escape from the sperm-cell as such, and then undergo some change of shape, through the development of the spermatozoa within them. The rupture of the spermatoon gives issue to the extremely fine capillary appendage, or 'tail,' the movements of which extricate the nuclear mass forming the so-called 'body' of the spermatozoon. In most Osseous

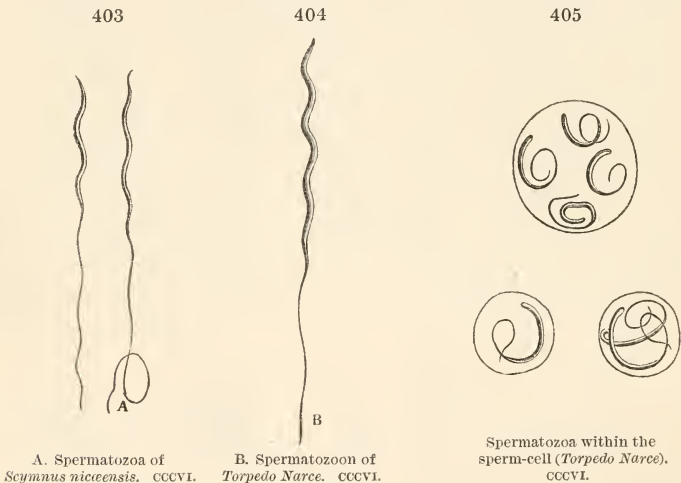


Sperm-cells with spermatoa, Bream. CCCVI.

Fishes the spermatozoa resemble those of the Perch, fig. 400: but in some, e. g. the Loach, there is a small swelling at the insertion of the appendage, as in fig. 401. In a few the 'body' is scarcely indicated, e. g. in the river Lamprey, fig. 402: in the *Petromyzon marinus* the body expands into an egg-shape.



The spermatozoa in the Plagiostomes are very long, with an anterior cylindrical body. This is proportionally shortest in *Chimæra monstrosa*, and is disposed in three spiral coils: in *Scyllium canicula* it is about half the length of the spermatozoon, .



is straight, and tapers at both ends: in *Scymnus niceensis*, fig. 403, it is spirally disposed. In *Spinax acanthias*, the Rays and Torpedos, fig. 404, the spiral coils are rather closer, usually four in number: in *Raia oxyrhynchus* the coils are more numerous, but only affect the anterior half of the body.

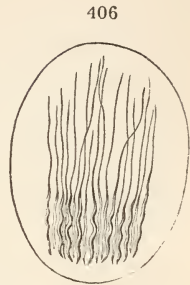
In the Plagiostomes the spermatozoa appear as one or more nuclei within the sperm-cell, like those in fig. 399, *b*: but they are not, as in Osseous Fishes, excluded in that state.<sup>1</sup> In each spermatozoon

<sup>1</sup> CCCVI. vol. iv. p. 484.

a spermatozoon is developed, which escapes by solution of the spermatoal wall into the sperm-cell, as in fig. 405.<sup>1</sup> At this stage the body does not show the spiral disposition. If the sperm-cell has contained numerous spermatoa, the resulting spermatozoa group themselves into a bundle, as in fig. 406: their bodies are contiguous and acquire the spiral form before escaping from the dilated sperm-cell.

The spermatozoa are developed in most *Batrachia* as they are in the *Plagiostomi*; a sperm-cell may contain from ten to twenty spermatoa, in each of which the spermatozoon is developed, as in fig. 407, and through solution of the spermatoal membrane the spermatozoa become free in the cavity of the sperm-cell, where they usually aggregate into a bundle, pressing the sperm-cell into a pear-shape, which bursts at its small end, and liberates either the filamentary appendages, as in the Frog, or the spiral bodies, as in *Pelobates*: in either case the remains of the sperm-cell continue recognisable, for some time, at the non-liberated ends of the spermatozoa, as in fig. 408, *a*.

In the igneous Toad (*Bombinator igneus*) the spermatozoa lie confusedly within the sperm-cell: the remains of the spermatoon long adhere, like a pectinate appendage, to the spermatozoon. When fully developed and liberated, the spermatozoa show a long cylindrical body, attenuated towards the head, which is again slightly enlarged, and more gradually shrinking



406  
Bundle of Spermatozoa within the sperm-cell. *Torpedo Narce*. CCCVI.



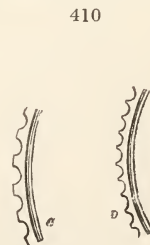
407  
Spermatoon with its contained spermatozoon, from the sperm-cell of a Frog. CCCVII.



408  
Bundle of Spermatozoa, *c*, escaping from the sperm-cell, *a*. *Pelobates*. CCCVI.



409  
Spermatozoa of *Bombinator igneus*.



410  
Part of Spermatozoon of Triton.

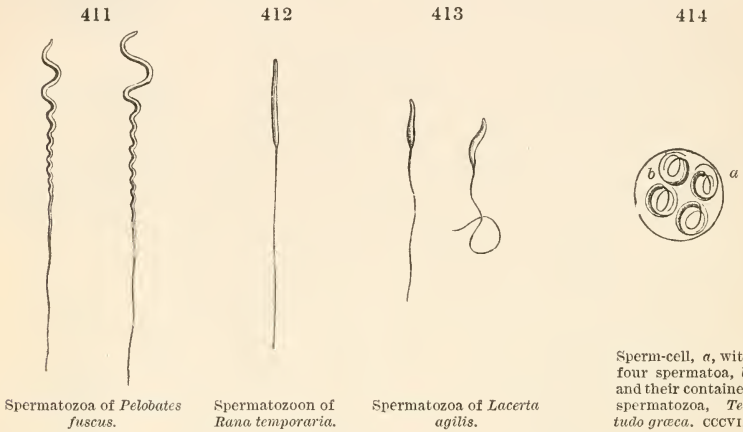
into the filamentary tail, which is reflected and coiled in narrow

<sup>1</sup> "Sometimes the entire nucleus becomes a coil of fibre."—*Barry*, CVII. 1842, pls. V. VI. XI.



spirals about the body, fig. 409. The spermatozoa of the Salamander and Newt have a similar form and disposition, and the coils of the reflected tail present the appearance of a crenate fringe or ridge, as in fig. 410. The fully-developed spermatozoa of *Pelobates fuscus* have a long spirally disposed body, gradually attenuating into the filamentary appendage, fig. 411; the total length is about  $\frac{1}{2}\frac{1}{3}$  of a line: the looser anterior end has a constant vibratile motion.

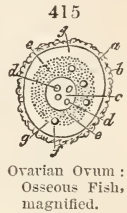
In the Frog, fig. 412, the body of the spermatozoon is long, cylindrical and straight, and is terminated by a straight capillary



appendage. In the *Coluber natrix* the body of the spermatozoon is pointed anteriorly: in Lizards it is shorter and more obtuse, fig. 413. The spermatozoa rarely exceed eight in number in the sperm-cell, from which they usually escape prior to the full development and extrication of the spermatozoa. The same is the case also in *Testudo græca*: but here the sperm-cell, fig. 414,  $a$ , remains longer than in Lizards and Snakes, and spermatozoa,  $ib$ ,  $b$ , with developed spermatozoa, may be observed within it.

§ 112. *Ovulation in Osseous Fishes and Batrachians*.— In Cyclostomous and Teleostomous Fishes, and in Batrachians, the ova are developed almost simultaneously at each breeding season: whilst in Chimæroid and Plagiostomous Fishes, as in scaled Reptiles, the ova are successively developed, or come to perfection at longer or shorter intervals. In Osseous Fishes, however, besides the ova of the present season, there are the germs of those of the next, often studding the ovisacs of the former. In the ovary of the Frog, before pairing-time, three sets of ova are

distinguished: those about to be discharged are large and dark-coloured, those intended for the next season are also of uniform size, but smaller, and partially coloured, and the rest are much smaller, colourless, and varying in minuteness. In Plagiostomes the ova are fewer in number than in the 'roe-fish.' From four to fourteen ova, for example, may be developed at one season in the Torpedo (*T. marmorata*),<sup>1</sup> whilst in the Herring 25,000 ova, in the Lump-fish 155,000 ova, in the Holibut, 3,500,000 ova, have been estimated to fill the enlarged ovarian sacs. In a Lump-fish, the total weight of which was 9 lbs. 8 ounces, or 66,500 grains, the ovaries weighed 3 lbs. 3 ounces, or 22,300 grains: thus they were to the body as 1 to 3. Each ovum weighed one-seventh of a grain.<sup>2</sup>



In all Fishes the ova are formed in chambers of the ovary, called 'ovisacs.'<sup>3</sup> In Osseous Fishes the ovisac consists of a delicate membranous hollow sphere, fig. 415, *a*, lined by epithelial nucleate cells, and surrounded by a thin layer of the proper tissue, or 'stroma,' *b*, of the ovary; which, as it protrudes with the growth of the ovum into the ovarian cavity, carries before it a covering of the delicate mucous membrane lining that cavity. This tunic is not present in Cyclostomes and Plagiostomes. The first-formed and essential part of the ovum is the germ-cell, or 'germinal vesicle,' *c*, which, in Osseous Fishes, shows several nuclei, maculae, or 'germ-spots,' *d*, but in Plagiostomes only a single nucleus. Around the germ-cell there accumulates a collection of minute yolk-corpuscles and albuminous granules, *e*, with oil-like globules, *f*, and in some species (Carp) flat angular corpuscles are added: all are suspended in a clear gelatinous yolk-fluid, and are ultimately circumscribed by a delicate yolk-membrane, *g*, devoid of visible structure. The increase of the ova is due chiefly to the accumulation of the yolk, and its colour to that which the oil-globules acquire as the ova approach maturity. Finally is formed the external tunic, or 'ectosac.'<sup>4</sup> At

<sup>1</sup> CXXXII.

<sup>2</sup> CCCVIII. p. 49. The periodical, but rapid and enormous increase of the hard and soft roes in osseous fishes admits of no rigid cinctures, no unyielding bony hoops around the abdominal cavity, such as would have resulted from a conversion of the pleurapophyses, by their junction with hæmapophyses and a sternum, into 'true ribs.' We see, therefore, in the fecundity of fishes—in this compensation for their limited intelligence and numerous foes—the physiological condition of their free or 'floating' ribs. <sup>3</sup> XX. iv. 1838, p. 131.

<sup>4</sup> As the homology of this tunic is not clearly determinable either with the vitelline membrane of the ovum of the Bird, or with the chorion of that of the Mammal, it is indicated by the above term in the description of the ovum of the Osseous Fish.

this period the ova in Osseous Fishes escape into the cavity of the ovarium, and the ectosac then receives its villi, or appendages for adhesion, in the Fishes possessing them. The ovisac remains behind, and coalesces with the stroma of the ovigerous layer, to form, according to Barry, a 'vesicle analogous to the Graaffian vesicle of Mammals;'<sup>1</sup> but the evacuated ovisacs collapse and speedily disappear, after the discharge of the ova, in the shrunken ovarium of Dermopteri and in the collapsed ovarian bag of Osseous Fishes: they are longer recognisable in the more compact and solid ovaries of the Plagiostomes.

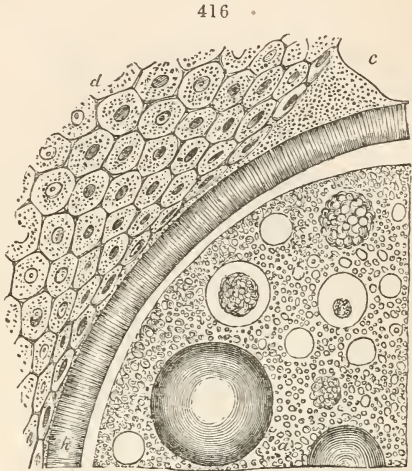
The earlier stages of the development of the ovum within the ovisac are illustrated in figs. 1 A-D (pp. 1 and 2), from Ransom's observations on the Stickleback (*Gasterosteus aculeatus*). In 1 A the ovisac, *c*, has a diameter of  $\frac{1}{40}$  inch: the germinal vesicle, *d*, appears as a gelatinous spheroid, with few 'maculæ' and a scarcely definite wall: a slightly turbid fluid, *a*, fills the space between the vesicle and the ovisac, from the inner surface of which a few delicate epithelial cells, *b*, project. In B, with a diameter of  $\frac{1}{25}$  inch, the maculæ have increased in number, and the germinal vesicle in size: fine yolk-granules have begun to aggregate near the periphery, but there is no vitelline membrane: on the exterior of the ovisac are the nuclei of flattened cells. In C, with a diameter of  $\frac{1}{18}$  inch, the maculæ have become more numerous and distinct: the yolk-granules more abundant and opaque: the yolk-mass is now more circumscribed, and a clear space intervenes between it and the ovisac. In D, with a diameter of  $\frac{1}{14}$  inch, the germinal vesicle has more maculæ, but has ceased to grow: the yolk-granules are much increased in number, and a clear peripheral space indicates the beginning of the formation of the external membrane, *ch*.

The 'roe,' or ova, of Osseous Fishes, being usually shed in or on the sediment of shores, are subject to the action of the flow of streams or break of waves upon their sandy or gravelly bed, and these pellucid and seemingly delicate vesicular spherules are accordingly provided with a very elastic and resisting outer coat, constructed on a principle analogous to that by which a tooth sustains and exerts its pressure. This coat is composed of a close-set series of hollow columns, set perpendicularly to the surface, fig. 416, *h*: the part of the outer surface turned into view, at *c*, shows the pores, or 'lumina,' of the tubules. The yolk, *a*, with its granules, granular and nucleated corpuscles, and oil-globules, now shows its delicate structureless membrane, which is partly

<sup>1</sup> CIX 1st Series, p. 814.

detached from the ectosac, as it becomes after impregnation. Against the ectosac, *h*, are closely applied the flattened epithelial cells, *d*, which line the ovisac and probably contribute to the growth or thickening of the external membrane. In the Perch the ectosaccal tubes have a slightly spiral course, and the peripheral end of each is set in a small hexagonal prism: this outer stratum serves to connect the excluded ova in groups. The ova of the Stickleback have villi developed for this purpose from one part of the exterior, figs. 417 and 421.

The structure of the outer coat of the ova of Fishes relates not only to the accidents of appulse, but to the act of impregnation, which takes place after exclusion and exposure. Besides the pores, or tubular orifices, of the



Part of the ovarian ovum of the Salmon. cccviii.

ectosac, there has been observed, in the ova of *Gasterosteus*,<sup>1</sup> *Salmo*,<sup>2</sup> *Blennius*,<sup>3</sup> *Esox*, *Trigla*,<sup>4</sup> a foramen homologous with the micropyle of the invertebrate ovum. Dr. Ransom, its discoverer, has observed the passage of the spermatozoa through this foramen into the ovum. Fig. 417, A, gives a magnified view of a portion of the surface of a mature ovarian ovum of the Stickleback, showing the funnel-shaped depression leading to the aperture of the micropyle, with a few of the flask-shaped villi of the outer membrane: B represents diagrammatically a section of the ectosac and funnel of the micropyle: C is a portion of the membrane at the apex of the funnel, with the aperture of the micropyle pressed flat, of the Trout's egg, magnified 500 diameters: D is a similar portion, magnified 1,000 diameters, showing the 'lumen' of the ectosaccal tubules, and the hexagonal division of the spaces between them.<sup>5</sup>

In the *Batrachia* (Frog) a greater proportion of the ovarian ova show different states of development, previous to sexual pairing, than in Osseous Fishes, although all those destined for impreg-

<sup>1</sup> CLXXVI.

<sup>2</sup> CCCVIII. and CCCIX. p. (101).

<sup>3</sup> CXXX. pt. ii. p. 4.

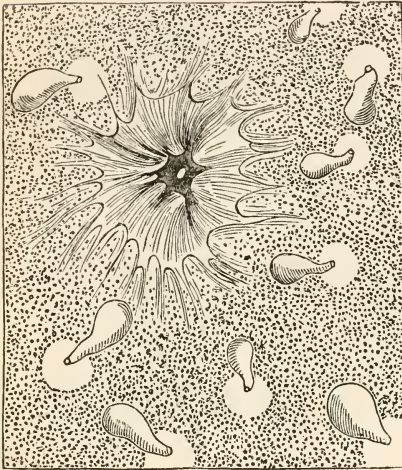
<sup>4</sup> CCCX p. 376, fig. 6.

<sup>5</sup> CCCVIII. p. (101).



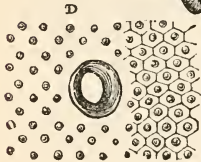
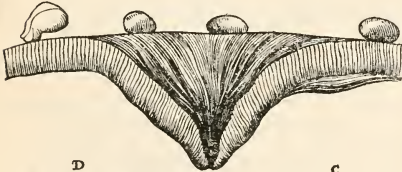
nation at the same season are simultaneously ripened. As soon as the germ-cell is recognisable, it is contained in a delicate ovisac, and speedily exhibits several nuclei, or maculæ, fig. 418, B, *g*: it is

417

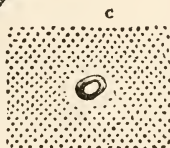


A

B

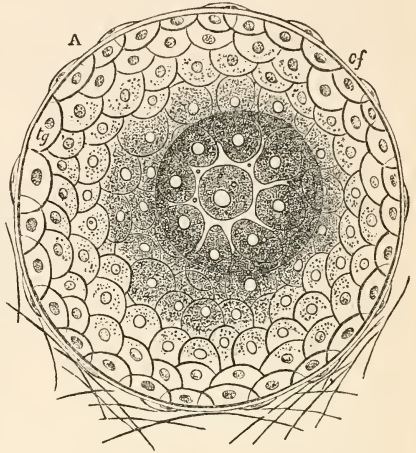


D



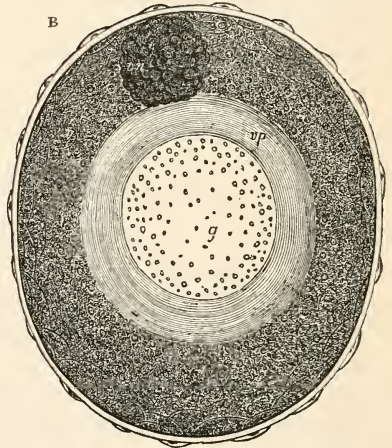
C

418



A

B



Micropyle of the ovum in Osseous Fish. CCCVIII.

Batrachian ovum in the ovisac,  $\frac{1}{100}$ th inch diam. CCCVIII.

surrounded by a clear albuminous yolk fluid, *vp*, which gradually becomes opaque, and about which the yolk-granules accumulate, among which is the opaque or dark aggregate peculiar to *Batrachia*, and called the yolk-nucleus, *ib. vn*. This body disappears as the yolk-mass approaches its mature bulk, and acquires the larger quadrilateral or quadrangular particles. The smooth and well-

defined periphery of the yolk-mass is in close contact with the layer of nucleated cells lining the ovisac, *ib. s*: and at a later stage of development, when the pigment-cells have been applied to the surface of the germinal portion of the yolk, a distinct external membrane is present. In the month of February the maculæ of the germ-cell multiply and form aggregates, with envelopes, representing cells with a granular nucleus, which nucleus finally disappears, and the so-rendered clear cells escape by solution of the coat of the germ-cell into the surrounding yolk-substance, this rupture or disappearance of the germ-cell preceding, as in some Osseous Fishes, the reception of the matter of the spermatozoon. The ripe ovarian ovum of the Frog (*Rana temporaria*) is from  $\frac{1}{12}$  to  $\frac{1}{15}$  inch diameter. The outer membrane (ectosac) of the ovum, after quitting the ovarium, is surrounded and defended, before exclusion, by the gelatinous secretion of the oviduct: it does not show the structure of that of the Fish. If a 'micropyle' exist prior to impregnation, as Prevost and Dumas record,<sup>1</sup> it has escaped the express research of some later observers.<sup>2</sup> The full-sized ovum of the oviduct retains its spherical form, fig. 420, A. In the Newts the ectosac of the ovum is elliptical, fig. 420, B, and a clear albuminous fluid intervenes between it and the yolk. In *Triton cristatus* the yolk is bright yellow: in *Lissotriton punctatus* it is ash-coloured: in the Land-Salamander it is orange. In tailless *Batrachia* the colour is limited to the surface of the yolk, which is grey beneath: in the Toad the pigment is almost black, in the Frog it is dark brown: in both it covers all the surface, save one small round spot; in *Alytes obstetricans* it covers half the yolk: it stains vertically from  $\frac{1}{8}$  to  $\frac{1}{10}$  of the diameter of the yolk: in all it defines the germinal part of the yolk.

§ 113. *Ovulation in Cartilaginous Fishes and Scaled Reptiles.*—If the generative organs and products were exclusively to govern the classification of Animals, the Chimæroids and Plagiostomes would be separated from other Anallantoids, and be combined with scaled Reptiles, with which they agree in the type and grade of their generative organs, and in the more important characters of the structure of the ovum. Its essential constituent, the germ-cell, has a single nucleus, and it becomes surrounded, while in the circumscribed ovary, with a large mass of vitelline substance, consisting in great part of oily and albuminous matter, inclosed in delicate vesicles. Besides these, there is a small proportion of the yolk, consisting of minute

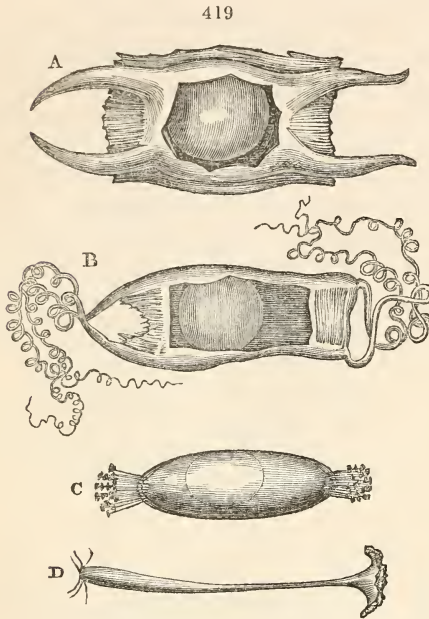
<sup>1</sup> In the centre of the brown hemisphere. CCCXI. p. 104.

<sup>2</sup> CCCXIII.

granules and granular corpuscles, more immediately surrounding the germ-cell; which, moving from the centre to the periphery of the yolk, there forms the 'cicatricula,' the exclusive seat of subsequent development. In the cartilaginous Fishes the impregnating influence is received before the ovum quits the ovarium,

or shortly after. In the egg's passage through the oviduct the yolk is surrounded by fluid albumen, and finally by a case of the denser albuminous secretion of the nidamental gland. The form of the egg when thus invested is remarkable, and different in different genera.

In the Skate, fig. 419, A, it is an oblong quadrangular flattened case, with the angles produced forward and backward, like those of a butcher's tray. In the Spotted Dog-fish, ib. B, the ova are also quadrangular, but longer, and the angles are extended into filamentary



External form of ova of Oviparous Cartilaginous Fishes.  
CCCVIII.

tendrils, which attach themselves to floating bodies, and thus keep the ovum near the surface, where the influence of solar heat and light is greatest. In *Notidanus*, with a similarly shaped cirriferous egg, the anterior and posterior surfaces are crossed by about twenty parallel transverse ridges.<sup>1</sup> In *Cestracion* the egg is pyriform, with a broad ridge, or plate, wound edge-wise round it in five spiral volutions. The eggs of *Callorhynchus* resemble a broad-leaved fucus, in the form of a long depressed ellipse, with a plicated and fringed margin.<sup>2</sup> The ovum of the *Myxine glutinosa*, fig. 419, C, is a long ellipse, terminated at each end by a tassel of slender tubular filaments, twenty-five to thirty in number, expanding at their free end (opposite D) into a funnel-shaped process.<sup>3</sup>

<sup>1</sup> xx. vol. v. p. 70, preps. nos. 3245, 3246.

<sup>2</sup> xx. vol. v. p. 69, preps. nos. 3235, A. and B.

<sup>3</sup> CCCVIII. p. 51.

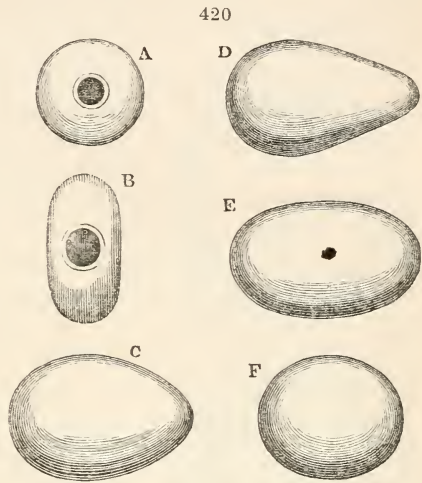


The structure and formation of the ovum in scaled and scuted Reptiles are essentially the same as in the cartilaginous Fishes. The germ-cell, with a single nucleus, is first formed in a delicate ovisac imbedded in the stroma of a solid ovarium. A yolk of large size is added, of which

the greater part consists of large non-nucleated oil-vesicles, and the smaller part of the vitelline granules and cells with a granulated nucleus; these originally surround the germ-cell, then indicate its tract from the centre to the periphery of the yolk, and form with the matter of the germ-cell the eicatricula, or blastoderm. This occupies a much smaller extent of the surface of the yolk than in the small-yolked eggs of Batrachians and Osseous Fishes, and segmentation is limited

thereto, the rest of the yolk being nutritive. The ovum, consisting of the above parts, inclosed in a vitelline membrane, quits the ovary and is received into the oviduct: here it acquires a certain proportion of soft albumen, upon which is condensed a thin tough layer, called 'chorion.' In the ovo-viviparous Snakes (*Vipera*) and Lizards (*Zootoca*) this membrane is thin: in the oviparous species it acquires a crust of calcareous matter before exclusion. This crust is very thin and scanty in most Serpents and Lizards, but is thicker in *Chelonia* and *Crocodilia*, forming a shell. The egg is spherical in some *Chelonia*, spheroidal in others, fig. 420, F, elliptical in *Emys*, fig. 399: in the Crocodiles the egg is a long ellipse, fig. 420, E. In no reptile does it show the oval form which prevails in Birds, ib. C and D.

§ 114. *Fecundation in Fishes.*—Certain changes and peculiar phenomena attend the increase of size of the soft and hard roes during these primary processes of generation. The colours of the fish become more marked and brilliant: the different sexes are often distinguished by peculiar tints, as the male Stickleback by his bright red throat, for example. The cutaneous crest on the head is developed in *Salarias* and many other Bleennioids, e.g.,



External forms of different eggs of Reptiles and Birds.  
CCCVIII.



in the male viviparous Blenny, which, by eversion of the terminations of the sperm-canals, impregnates internally. The claspers in the male Plagiostomes then acquire their full development and force: the basal glands in those of the Rays enlarge. In Osseous Fishes the whole abdomen swells, and the viscera are displaced by the prodigious bulk of the germinal and seminal matter.

As the period of 'fecundation' approaches, the female osseous fish seeks a favourable situation for depositing her spawn, usually in shoal water, where it can be most influenced by solar warmth and light. The marine Herring, Mackerel, and Pilchard approach the shore in shoals: the fluviatile Salmon quits the estuary to ascend the river, overcoming, with astonishing perseverance and force, the rapids or other mechanical difficulties<sup>1</sup> that impede its migration to the shallow sources, whither the sexual instinct impels it as the fit place for oviposition. The female fish is closely pursued by the male, sometimes by two: in the Capelin (*Mallotus*) these swim on each side of her, aiding by their pressure in the expulsion of the spawn, and at the same time impregnating it by diffusing over it the fluid of the milt: thus absorbed in the sexual passion, they have been seen, on the shores of Newfoundland, to rush on land in their spasmodic course over the shallows, which they strew with the fecundated ova. In some genera violent combats take place between the males. Mr. Shaw,<sup>2</sup> a close observer of the habits and development of the Salmon, states:—'On January 10, 1836, I observed a female Salmon of about 16 lbs., and two males of at least 25 lbs., engaged in depositing their spawn. The two males kept up an incessant conflict during the whole day for possession of the female, and, in the course of their struggles, frequently drove each other almost ashore, and were repeatedly on the surface, displaying their dorsal fins and lashing the water with their tails. The female throws herself at intervals of a few minutes upon her side, and, while in that position, by the rapid action of her tail, she digs a receptacle for her ova, a portion of which she deposits, and, again turning upon her side, she covers it up by the renewed action of the tail, thus alternately digging, depositing, and covering the ova, until the process is completed by the laying of the whole mass, an operation which generally occupies three or four days.'

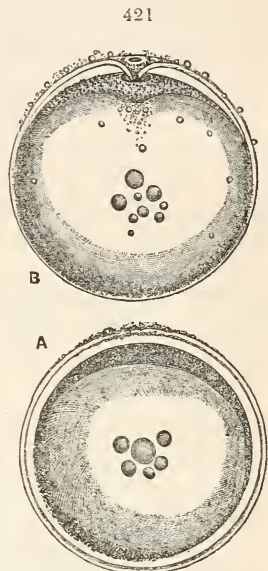
In the ovo-viviparous Osseous Fishes the well-developed cloacal papilla, in which the sperm-ducts terminate, doubtless serves to

<sup>1</sup> Save those erected by stupid cupidity to effectually bar the salmon's progress.

<sup>2</sup> CXXIV. p. 551.

ensure intromission. The superadded claspers in the male Plagiostomes lend more effectual aid in the act of internal impregnation, for in those species that are oviparous the ova are impregnated and covered by a nidamental coat, or 'shell,' prior to exclusion.

In Osseous Fishes, where exclusion usually precedes impregnation, the first change observed in the ovum after entering the water is its imbibition, causing a separation of the outer tunic from that of the yolk, fig. 421, A. Dr. Ransom connects the phenomenon with the passage of the spermatozoa through the micropyle, which he observed in his experiments on the ova of the Stickleback.<sup>1</sup> In these ova, about three minutes after impregnation, the funnel of the micropyle, which had descended into a depression on the upper surface of the germinal part, fig. 421, B, began to be withdrawn by the recession of the external membrane from the surface of the yolk and the formation of the intervening clear space. About ten minutes after impregnation the clear respiratory space is more marked: the germinal layer, with a few large oil-globules, is distinguishable by its opacity from the clearer part of the yolk, *ib.* A. In the Perch it presents a greyish, in the Pike a yellowish, tint. The germinal vesicle, which had previously become filled and obscured by granules and granular corpuscles, breaks up to form, or contribute to form, the germinal layer, which now becomes more circumscribed and distinct: the process of segmentation, which follows that of impregnation, is limited to the germinal portion of the yolk, with which it is co-extensive. In the Perch the ova assume a greenish tint shortly after impregnation. There is reason to suppose that impregnation of the eggs of both Sharks and Rays takes place in the ovarium or the contiguous part of the oviduct, for they become enveloped in the dense albuminous secretion of the nidamental glands after having passed that part, which covering would prevent the subsequent influence of the spermatozoa.

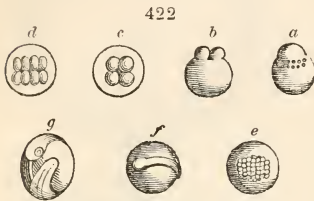


Ovum of the *Gasterosteus* at the time of impregnation.

§ 115. *Development of Fishes.*—The germinal layer consists of

<sup>1</sup> Cited in cccviii. p. 98.

a minutely granular matter, with clear corpuscles, vitelline cells, and oil-particles: it projects from the surface of the yolk, fig. 422, *a*, and becomes transparent: the vitelline and oil-globules, aggregating at its base, buoy it up. The formation of two hyaline centres is followed by the cleavage of the germinal layer into two equal parts, *ib. b*, and these are next cleft at right angles into four, *ib. c*. In the Tench this occurred about half an hour after the rising of the germ-layer. Each of the four divisions undergoes subdivision, but irregularly, *ib. d*: further subdivision gives the surface a mulberry character, *ib. e*, and finally the parts are broken up to such a degree of minuteness that the surface is again made smooth. The hyaline principle, which is the centre and cause of these successive divisions, is thus diffused through, or assimilated by, the whole germinal layer, which has thereby become the 'germ-mass.' It now subsides



First steps in the development of a Tench.  
CXXXI.

to the form of a circular disc, separated by a layer of oil-globules from the yolk. The process occupies about three days in the Salmon, and from fifteen to twenty hours in the Pike:<sup>1</sup> before it is completed in the latter fish the yolk rotates within the ectosac.<sup>2</sup>

A cavity is formed in the centre of the germ-mass, which, as the mass subsides and extends over the yolk, is obliterated by the contact of the outer and inner layers. It clothes half the yolk by about the end of the third day, and when it covers two-thirds or more, the rotation ceases. The margin of the germ-mass encompassing the uninclosed part of the yolk is tumid. No rotation takes place in the ovum of the Perch,<sup>3</sup> and the germ-mass incloses the whole vitellus, as in the Cyprinoids.

The peripheral layer in the Pike begins to rise from the tumid margin of the germ-mass, as from a base, and extends, contracting, towards the opposite pole: this tract of germ-substance is the 'embryonal' or 'primitive trace.' It next sinks in along the median line, forming a furrow, which stops short of the two ends of the trace: that end opposite the point from which the germ began, swells into the head, and the median furrow expands upon it; the cephalic borders are next united by a thin layer of epithelial cells above the furrow, converting it into a cavity or ventricle, and the myelonal furrow is similarly covered by a layer, uniting the lateral columns. The embryonal trace becomes longer, narrower, and bends round

<sup>1</sup> CCCXIX. p. 486.

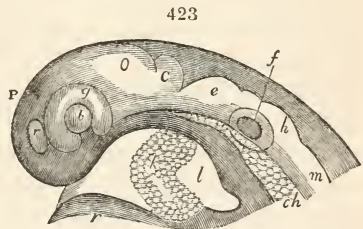
<sup>2</sup> CXXXI.

<sup>3</sup> *Ib.* p. 512.

half the vitellus, fig. 422, *f*. A layer of epithelial cells forms a net-work over the whole dorsal (upper) surface of the embryo. In the germ-mass broadening from the primitive trace oblique striæ appear, indicating its division into segments: these beginnings of aponeurotic septa probably accompany and support nervous productions from the myelonal columns.

Two transverse constrictions begin to divide the cephalic enlargement into three lobes, the second and third of which expand into vesicles: an accumulation of cells at the sides of the middle expansion appears to add greatly to its breadth, but forms the basis of the eyes. A similar accumulation of darkish granular matter on each side of the third enlargement lays the foundation of the acoustic vesicles.

The differentiation and confluence of the cell-constituents of the primitive trace have previously led to the formation of a pair of albuminous chords along the sides of the median furrow, forming the myelon proper; the cells exterior to and above them are converted into muscle and fibrous septa, whilst beneath the columns is the jelly-filled cylinder, with a transversely striate sheath, pointed at both ends, forming the 'notochord,' fig. 423, *ch*: its anterior point passes a little in advance of the acoustic vesicles, *ib. f*. Beneath the notochord and surrounding blastema is stretched the vegetative or mucous layer of cells, in contact with the yolk. Both head and tail of the now cylindrical embryo are liberated from the surface of the yolk. A fold of



Head of embryo Pike. cccxix.

blastema, reflected from the under part of the head, sinks, like a pouch, *ib. l*, into the yolk, and soon includes the rudiment of the heart, like a bent cord, *ib. h*, which begins to oscillate about the seventh day. From the mid-line of the inferior surface of the embryo, or its mucous layer, two longitudinal plates descend, diverging into the yolk-substance, and form the primitive intestinal groove.

The ophthalmic vesicle, *ib. g*, elongates and curves outward, until the two ends almost come into contact: between those ends and beneath the delicate tegumentary layer connecting them the crystalline lens, *ib. b*, is formed. About the same time, the otoliths appear in the acoustic vesicles, *ib. f*, and these have now acquired a cartilaginous case. The cerebral lobes, *p*, begin to



be formed by small folds, rising laterally, and overlapping the fore-part of the second enlargement, *ib. o*, which has expanded to greater breadth. The olfactory cavities appear as small cutaneous depressions or follicles, *ib. r*.

The two myelonal columns, expanding between the ear-sacs, and receding so as to show the notochord beneath, bend upward and inward, and unite, to be continued into the back part of the optic lobes, thus commencing the cerebellar bridge, *ib. c*, across the epencephalic ventricle. The encephalic vacuities have begun to be filled by the granular basis of the cerebral fibre or substance. The intestinal groove begins to be converted into a canal at its two ends, which are closed: beneath the anterior end, and behind the heart, progressively accumulates the cellular basis of the liver. The free caudal end of the embryo grows rapidly; muscular heavings of the body occur before the heart beats, and pulsation begins before the cavity is visible in the cell-mass. The heart appears first as a cylinder of cells, changing in its movements from a straight to a bent fissure, *fig. 423, k*, and propelling only colourless plasma; a canal is next seen, along which the blood-particles traverse the cylinder, from the yolk below to the head above: these blood-particles are spherical or polyhedral, colourless and homogeneous, and are more minute than the germinal cells. The cardiac cylinder is next divided by a constriction into an auricular and a ventricular compartment. The blood, in which the discs soon acquire increased size and a pale red colour,<sup>1</sup> is propelled from the ventricle by channels encompassing the fore part of the alimentary canal into a dorsal trunk, which, after a short course, bends down, and returns as a vein to the vitellus, over which the blood at first courses in undeterminate streams, but which converge to enter the auricular division of the heart. As the abdominal cavity, intestine, and body elongate, a succession of such vertical loops is formed, receding from the first, with corresponding elongation of the aorta and postcaudal, or entero-vitelline, vein. The aorta soon sends off pairs of transverse loops, corresponding with the vertebral segments, the returning channels of which open into or constitute the cardinal vein. The embryo now encompasses the yolk, as in *fig. 422, g*.

In the eye the crystalline, developed from the epithelial layer uniting the two ends of the bent ophthalmic vesicles, sinks deeper

<sup>1</sup> Lereboullet observed in embryo-fishes raised in tanks from artificial impregnation, that the blood-particles were later in formation, and more scanty than in the embryos derived from the free streams: a remark worthy the attention of the breeder of fish. cccxix. 580.

as those ends approximate each other. The choroid appears in the form of an inner cylinder, applied to the sunk back-part of the lens, and its extremities, approximating and uniting, produce the choroidal fissure: the eye is now the most conspicuous part of the embryo, especially in the ovum of the *Salmonidæ*, and is a useful sign to the pisciculturist of the impregnation and vitality of the egg.

The hinder cæcal part of the intestine rapidly elongates, from behind forward, the yolk advancing in position. The anterior cæcum also elongates from before backward: the open part of the intestine, which communicates with the vitelline sac, becomes in the same measure constricted.

When the two divisions of the heart are bent upon one another, the liver shows several small cæca, which rapidly multiply, and become opake: it is situated, fig. 424, *l*, behind the heart and above the yolk, now becoming reduced to a globule of oil, which is long retained in the young Perch.

The primordial kidneys appear as two parallel rows of rounded cells, above the liver, their ducts uniting to form a tube, which runs above the intestine, and dilates above the hinder cæcal end of the gut.

The pectoral fins begin to bud forth: the protocercal membranous fin-fold commences at the middle of the back, borders the tail, and returns along the belly as far as the vitellus. Large pigment-cells are spread over the yolk-sac, which become stellate. Muscular fibres appear in the myocommata as transparent cylinders, without the transverse striæ: they move the tail vigorously, and cause the embryo and its yolk-sac, in the Perch, to rotate in the egg. This has increased in size by imbibition of water, and its external coat is thinned by stretching; it now gives way, and the embryo is extricated, about the tenth day in the Pike and the twelfth day in the Perch. The size and shape of the yolk-sac, fig. 424, *c*, vary in different kinds of Osseous Fishes.<sup>1</sup>

The vitelline vascular network, *ib. d*, is the first respiratory organ of the fish: its divisions carry the blood-discs only in single files. The outer tunic covering the vascular one permits the interchange of gases between the blood and the water outside. This respired or arterial blood is mixed with the venous blood which is returned to the heart by the cardinal veins, and is distributed, so mixed, by the arteries. The vitelline capillaries gradually exchange a reticulate for a parallel longitudinal course, with diminution of

<sup>1</sup> In artificial hatching, young trout, and especially char, show a difficulty in extricating the yolk-sac, and many perish from inability to liberate themselves.

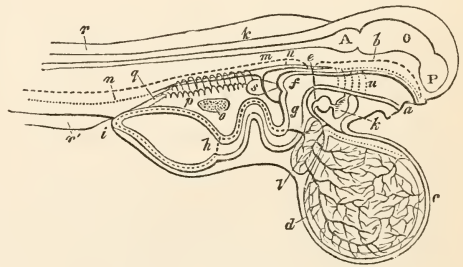
numbers and increase of size: and as the fitness of the vascular surface for respiration decreases, the development of the gills progresses. The branchial arches appear, three in quick succession, from behind forward, and branchial tubercles bud from them in like order. The mouth and the branchial slits being now opened, the arches move rhythmically, so as to produce branchial currents: the blood is yellowish, and the discs begin to show the flat oval shape. As the vitellicle decreases, its circulation is changed, or merged into the portal hepatic system; and now that through the branchial buds begins. The change of the vitelline for the branchial circulation relates, in a general way, to that from the confined to the free state of the young fish: but no such alterations of the circulating or breathing systems attend the escape of the fish from the egg as mark extrication in the Reptile and Bird, or birth in the Mammal. Vitelline respiration, carried on *in ovo* by means of the imbibed water between the outer and vitelline tunics, continues to operate for a longer or shorter period after the little fish is free, according to the species, and also according to the individual constitution in the same species.

Each branchial bud is at first a solid cell-mass, and is excavated to receive the blood with blood-discs in single file: secondary tubercles bud forth at right angles to the primary ones, through which similar blood currents flow: the primary buds become the stems of the leaflets into which the secondary ones are developed, and the cartilaginous axis of the arch and stems next appears. The pseudo-branchia also shows itself behind the eye, in the form of flattened elongated folds, through which the blood courses at first in a few vascular loops. In the *Anabas*, and probably other Labyrinthibranchs, the epibranchial reservoir, fig. 325, retains a comparative degree of simplicity until the fish is full-grown.

The intestinal canal, after the formation of the mouth and vent, retains its uniform diameter, except where it is partly surrounded by a mass of the cells, in which the

liver, fig. 424, *l*, is developed: the gall-bladder appears to be a caecal production from the intestine, independently of the liver. Opposite

424



Fore Part of embryo Osseous Fish.

the liver a tubercle of cells buds out, which elongates, enlarges, and then acquires a cavity: this is the beginning of the air-bladder, *ib. s.* Many Fishes retain the tubular connection with the alimentary canal, and those which ultimately lose the 'ductus pneumaticus' usually retain for a longer or shorter period that evidence of the place and mode of origin of the air-bladder. The posterior compartment of the air-bladder is first developed in the Cyprinoids, which accounts for the connection of the air-duct with that part: the whole posterior compartment disappears with the duct in the Loach. In the Herring the primitive place of its connection with the alimentary canal is retained.

The ureter, *q*, developed from the intestine before the embryo quits the ovum, communicates with the extremities of the transverse parallel tubuli, *p*, formed by confluence of primitive cells in the renal blastema. The cardinal veins traverse or groove the renal organs, as they do the Wolffian bodies in the embryos of higher Vertebrates; and this primitive relation of the vascular to the renal system is not changed in Fishes by the substitution of true kidneys for the primordial renal organs. In many Fishes a caecal process is developed from the fore, or ventral, surface of the termination of the intestine, and extends forward, as a bladder: its growth is arrested at various stages in different species, and it is termed 'urinary bladder,' but it is the homologue or beginning of the allantois.

The intestinal wall is completed, and the fissure behind the liver closed, by the time the yolk is consumed. The vent opens, in the Pike, on the fourth day after extrication: in the Perch coloured particles added to the water were seen to traverse the intestine, and escape 'per anum' on the sixth day.<sup>1</sup> Previously the mucous walls of the gut are in contact, although the peristaltic movements are active. About the eighth day the presence of bile is indicated by the colour of the gall-bladder and ducts. The stomach expands, and divides the œsophagus from the intestine.

After extrication the eye loses the choroidal fissure: the iris acquires the silvery pigment. The ear-sacs assume a triangular form: the two otoliths grow unequally by additional calcareous layers.

The primary enlargements of the encephalon are connected, respectively, with the acoustic, optic, and olfactory nerves: the anterior one, *fig. 424, p*, becomes divided into prosencephalon and rhinencephalon; the second, *o*, rapidly gains superior bulk in connection with the large eyeballs, and its pineal and pituitary appendages appear as vascular membranous canals. The cere-

<sup>1</sup> CCCXIX. p. 483.



bellum is the last part which is formed by reflection upon the upper and fore part of the encephalon,  $\Lambda$ .

The mode of development of the cartilaginous cranium is described at pp. 71-74. In the Perch a layer of cartilage-cells beneath the fore-part of the head is continued down on each side into the front border of the inferior transverse mouth: a second cartilaginous arch extends from the side of the cranium, behind the eyes, and supports the hinder and more prominent border of the mouth: a delicate cartilaginous filament from each side of the occiput seeks an attachment with the basis of the rapidly vibrating pectoral fin, and proceeds to curve beneath the cardiac chamber. Between this basis of the scapular arch and the mandibular arch are discernible several smaller arches, beneath the large ear-sacs, of which three are conspicuous as 'branchial arches,' but the foremost acquires the most decided gristly structure, and is proximally attached to the origins of the mandibular arch: it becomes the hyoid arch. The first and second inferior or hæmal arches, called 'maxillary' and 'mandibular,' rotate forward upon their piers, or points of attachment, and from being vertical become more and more oblique, until the opening of the mouth is brought to the fore-part of the head, and becomes terminal in position: the third, or hyoid, arch, in a minor degree, takes the same forward inclination: the arches between this and the scapular one are monopolised by the branchial organs, which are transitory or undeveloped in the higher Hæmatocrya. Ossification in the proto-cranial cartilage begins in the four pairs of neurapophyses, answering to the four hæmal arches below, and to the four primary divisions of the encephalon: the four vertebral segments composing the head are as instructively illustrated by the development of the skull as by that of the brain.

The scales are formed late in all Osseous Fishes: their integuments remain smooth and lubricous, as in the Dermopteri, some time after the disappearance of the vitellus.

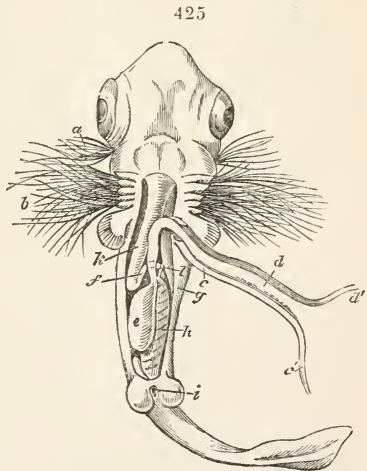
After the formation of the embryonal, continuous fin-fold blastema accumulates in its dorsal, anal, and caudal regions; and, as the rays are here formed, the intervening membrane begins to be absorbed. The fin-rays (dermo-neurals and -hæmals) commence near the free border, and elongate by approaching the neural spines: they there meet the inter-neurals and -hæmals, which grow in the opposite direction. During the formation of the caudal rays, the end of the notochord, in the Pike, Perch and Salmon, bends upward, or 'neurad:' the heterocercal type succeeds the protocercal one, and is followed by the resumption of symmetry under the more advanced 'homocercal' condition.

This, as a rule, is the form and structure acquired by the tail in existing Teleostomous Fishes: but the 'heterocercal' modification does not intervene between the proto- and homo-cercal ones in the *Gadidæ*.

The pectoral fins are developed usually before extrication, and are often of large relative size: in this respect, as well as in the inferior position of the mouth, in the unsymmetrical form of the tail, in the gristly skeleton, and uncovered gill-slits, the embryo Salmon, Pike, Perch, &c., manifest transitory characters which are permanent in Sharks.

The singular productions of the rostrum in most Plagiostomes, like the elongation of the jaws in osseous species, are later phenomena of development. It is interesting to find the broad, depressed, obtuse embryonic form of head common to many of the Fishes of the old red-sandstone. M. Agassiz thus accounts for the extreme rarity of the Ichthyolites of this formation presenting a profile view of the head: it lies in most cases upon the upper or the under surface of the body.

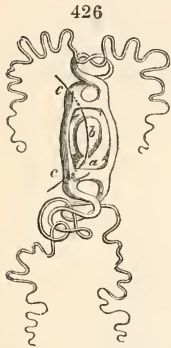
All the Plagiostomes have the external as well as the internal division of the vitellicle, fig. 425; the peduncle of the external one *d*, is longer, in some species considerably so, than in Osseous Fishes, and it is beset with villi in *Carcharias* and *Zygæna*.<sup>1</sup> The tegumentary covering of the outer yolk, *ib. d'*, is denser and more opaque in Plagiostomes: the inner yolk, *ib. e*, is covered only by the proper vitelline tunic, which is thin and transparent: it communicates with the short tract of small intestine which intervenes between the pylorus and the valvular straight gut, *h*: it receives the external yolk, *d'*, as this is progressively squeezed into the abdomen by the contraction and interstitial absorption of its tunics, *e'*: and, as no part of the foetal abdominal appendage is cast off, nor the chord divided, there is no cicatrix—no umbilicus. The arterial vessels of the yolk are derived, not from the mesenteric vein as in Osseous Fishes, but



Embryo Cartilaginous fish, *Scyllium*.

<sup>1</sup> CXXIII. tf. iii.

from ramifications of a branch of the mesenteric artery, and the blood is returned to the mesenteric vein. Hunter's preparations of the embryo *Carcharias* (No. 1061), *Scyllium* (No. 3250), *Spinax* (No. 3255), and *Alopias* (No. 3261)<sup>1</sup>, demonstrate another foetal peculiarity which later researches<sup>2</sup> have shown to be probably common to all Plagiostomes, viz. the external fringe of filaments developed from the branchial surfaces, *b*: a tuft extends out of each aperture, and even from the spiracula, *a*, in the genera with those accessory openings. Each filament contains a single capillary loop: <sup>3</sup> they disappear early, being removed by absorption. The last remnants may be seen in the preparation of the foetal Sawfish (*Pristis*, No. 3263),<sup>4</sup> which is eight inches in length, including the saw, and has the duct of the external vitellicle attached. In



Egg and Embryo; *Scyllium*. One fourth nat. size.

the oviparous Sharks, the branchial filaments react on the streams of water admitted into the egg by the apertures, fig. 426, *c*. In the ovoviviparous Sharks the size and position of the cloacal apertures of the uteri would seem adapted to allow free ingress of sea-water; so that, whilst the vitellicle, *ib. b*, administers to the nutriment of the embryo, *a*, the external branchiæ may perform the respiratory function. In the smooth Emissole (*Mustelus levis*), vascular cotyledons are developed from the vitelline (omphalo-mesenteric) capillaries, which are firmly connected to the uterine cotyledons; so that here the vitellicle, like a true placenta, may perform both the nutrient and respiratory functions: the external branchiæ disappear some time before the exclusion of the embryo and the absorption of the yolk. In the *Lepidosiren annectens*<sup>5</sup> three small external branchial filaments project from the single opercular aperture on each side, and are long retained.

Some of the Plagiostomous Fishes are oviparous, but not as in the majority of Osseous Fishes; a remarkable transposition in the times of the processes of fecundation and exclusion marks the distinction. In the oviparous Osseous Fishes the ova are first excluded, then impregnated: in the oviparous Plagiostomes impregnation is internal, and precedes oviposition. The eggs are much fewer in number, but their impregnation is more certain than in the scattered indiscriminate act of spawning of the Osseous Fishes, where the countless numbers of the ova seem to

<sup>1</sup> xx. vols. ii. and v.

<sup>2</sup> Rudolphi, LXXVI.; Rathke, CXI.; Leuckart, CXXV.; J. Davy, LXXXII.

<sup>3</sup> A. Thompson, CXI.      <sup>4</sup> xx. vol. v.      <sup>5</sup> Jardine, CXXXV.; Peters, CXXXVI.

compensate for the chances that may intervene to prevent the contact of the milt.

§ 116. *Growth and Nests of Fishes.*—When developement has stamped the Fish with its specific characters, growth proceeds at various rates and to different degrees, according to the species—viz., from the size of the Stickleback to that of the Shark of thirty-five feet long (*Selache maxima*). Carp, Pike, and some other Fishes, which may live in ponds or lakes under circumstances favourable for continuous observation of the same individual, show that growth is not definitely arrested as an adult character; few Fishes, perhaps, can be called ‘full-grown’ in the sense in which the term is applied to warm-blooded Vertebrates: but, after attaining the average size characteristic of the species, individuals under favourable circumstances continue to increase, though very slowly, in size. Growth is accompanied in many species by changes of colour, in some by a greater proportional size of the head, or by elongation or curvature of the mandible, or by increased length of a rostral prolongation—sword or saw: other special weapons, as the dorsal spines of Cestracionts, File-fish, and Dog-fish, and both dorsal and pectoral spines of Sheat-fish, acquire length and hardness, or dentate borders, in the course of growth. External sexual characters are assumed, as shown in the form and structure of the ventral fins in some Osseous Fishes<sup>1</sup>, in the growth of the ‘claspers’ of Plagiostomes, and of the marsupial folds or pouches of Lophobranchs. In the Dolphin (*Coryphæna*), the cranial crest and fore-part of the dorsal fin gain so much proportional height that young individuals of even two feet in length were referred by Cuvier to a distinct genus (*Lampugus*).<sup>2</sup>

In a few instances the changes accompanying growth amount to a metamorphosis. The edentulous state of the young Lamprey, and the semicircular form of the upper lip, are exchanged for the suctorial multidentate mouth, shown in fig. 277. The external branchial apertures enlarge, and the furrow in which they at first open disappears. The perfect form of the Lamprey is not attained until the fourth year. During half or two thirds of that time, the growing *Petromyzon* presents a form which passes as that of a distinct genus of Cyclostomes (*Ammocetes*).<sup>3</sup> The *Leptocephali* are probably larvæ of some larger known fish: they have never been observed with roe or milt: the same may prove to be the case with *Branchiostoma*.

‘In almost all the Teleostomes the body of the young is more

<sup>1</sup> CCCXXVIII.

<sup>2</sup> CLXXIV. ii. p. 405.

<sup>3</sup> CCCXXVII. p. 323.



slender than that of the mature fish, or the height of the body is less in comparison with its length. The eye ceases to grow long before the individual has attained its full size; so that old fishes have comparatively smaller eyes than young ones. The form of Fishes is altered by changes in the shape of fins, by the development or by the loss of spines belonging to the opercular apparatus or to the fins; as in the following examples.

‘*a.* Some of the fin-rays are prolonged with age into long filaments: species of *Anthias*, *Pagrus*, *Ephippus*, *Callionymus*.

‘*b.* Some of the fin-rays are prolonged in young individuals, but the filaments are worn off with age: *Lophius*, *Echeneis*, *Trachynotus*.

‘*c.* *Cephalacanthus* is merely the young of *Dactylopterus*; the pectoral fins are short in the young, and become with age so long as to serve for an organ of flying in the adult (*Dactylopterus*).

‘*d.* In some species of *Thyrsites* and *Gempylus* the ventral fin is reduced to a very small spine, which in the young is very long, nearly half as long as the head. Sometimes the young has ventral fins, whilst they are entirely absent in the adult: *Stromateus*.

‘*e.* The young of almost all the *Carangidæ* have the præoperculum armed, like a Percoid: this bone is entirely smooth in the mature fishes. The same in *Labrus*.

‘*f.* Some fish have no visible, or but a rudimentary, spinous dorsal fin; this fin is very distinct in the young: *Brama*, *Platax*, *Stromateus*.

‘*g.* Large prominences of the skin are developed, which are absent in the young: *Cyclopterus*.

‘*h.* Many of the well-armed *Siluroids* have the osseous carapace on the head and neck more or less covered with skin in early age: the dorsal and pectoral spines are more feeble in the young than in the old.’<sup>1</sup>

There are few fields of Natural History that return more material reward for scientific labour than that relating to the generation and growth of Fishes. The mercantile value of the Salmon, and the necessity for basing laws that are to operate in its preservation upon a knowledge of its natural history, have led to interesting observations on its growth and migrations.

Mr. Shaw,<sup>2</sup> observing ova spawned on January 10th, noticed dark eye-specks and some movement of the embryo in

<sup>1</sup> For the above examples I am indebted to my colleague, Dr. A. Günther.

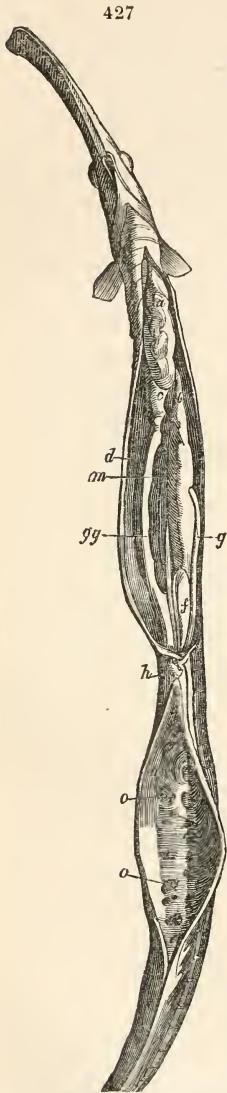
<sup>2</sup> CXXIV.

the ovum on February 26th, that is, forty-eight days after being deposited; and on April 8th, or ninety days after impregnation of the ova, the young were excluded. They measured  $\frac{2}{8}$ ths of an inch in length; the vitellicle being  $\frac{2}{8}$ ths of an inch in length, oblong in form, and of a light red colour: the tail was margined like that of the tadpole, with a continuous fin running from the dorsal above to the anal beneath. The vitelline sac and its contents were absorbed by May 30th, or in about fifty days, until which time the young fish did not leave the gravel of the hatching-pond. This quiescent state in their place of concealment, from the period of exclusion to the absorption of the yolk, seems to be common to Osseous Fishes; but the time varies in different species: it is much shorter in the Tench, Perch, or Pike, for example, than in the Salmon. When the young Salmon measures an inch in length, the vertical fin begins to divide itself into the dorsal, adipose, caudal and anal fins; and the transverse bars on the sides of the body make their appearance. It is very active, and continues in the shallows of its native stream till the following spring, when it has attained the length of from three to four inches, and is called the 'May-parr.' In this state the 'parr' descend into deeper parts of the river, and are believed by Mr. Shaw to remain there over the second winter. The weaker ones do so, but the stronger fish proceed to the estuary at once. In April, the caudal, pectoral, and dorsal fins assume a dusky margin; the lateral bars begin to be concealed by a silvery pigment; and the migratory dress, characteristic of the stage called 'smolt,' is assumed. Such fish begin in April and May to congregate in shoals and to migrate seaward: they return in July and August, of a size proportionate to the length of their stay in the estuary. A smolt may not exceed two ounces in weight when it goes to sea: after a few months there it may have grown to a 'grilse' of eight or ten pounds' weight: 'at two years and eight months old it becomes a Salmon of from twelve to fifteen pounds' weight.'<sup>1</sup> It may subsequently acquire a bulk of forty pounds' weight, and upwards.

In the *Syngnathus acus* the sexes come together in the month of April, and the ova pass from the female and are transferred into the subcaudal pouch of the male, fig. 426, *n*, being fecundated *in transitu*, and the valves of the pouch immediately close over them. In the month of July the young, *ib. o, o*, are hatched and quit the pouch; but they follow their father, and return for shelter

<sup>1</sup> cccxxv. p. 120. Experiments on marked fish have proved this extraordinary rate of growth. cccxxxiv. p. 57.

into their nursery when danger threatens.<sup>1</sup> In *Syngnathus ophidion* the male carries the eggs under the flat abdomen in cells placed lengthwise in three rows.<sup>2</sup> In the male Hippocamp the marsupium is subcaudal, opening by a vertical fissure just below the vent.<sup>3</sup> In the *Holconoti* the young acquire full development, perfect gills, and a size one third that of the parent, before quitting the ovarian marsupium.<sup>4</sup>



Marsupial pouch of *Syngnathus acus*.

Both Salmon and Trout excavate the gravelly bed which they select for spawning; and the ova may be found from one to two feet deep in this stony nest. The Stickleback (*Gasterosteus aculeatus*) fabricates a more artificial nest. Aristotle signalises the *Phycis*, since recognised as a Mediterranean species of *Gobius*, as the only sea-fish that makes a nest and deposits its spawn therein. Olivi confirmed the statement, and describes the nest as being composed of sea-weeds (algæ and zosteræ), adding that the male fish guards the female during the act of oviposition, and the young fry during their development.<sup>5</sup>

Dr. Hancock has observed similar habits in certain fresh-water Siluroid Fishes of Demerara called 'Hassars,' which belong to the genus *Callichthys*: the Round-headed Hassar forms its nest of grass; the Flat-headed Hassar of leaves. 'They are monogamous: both male and female remain by the side of the nest till the spawn is hatched, with as much solicitude as a hen guards her eggs, and they courageously attack any assailant. Hence the negroes frequently take them by putting their hands into the water close to the nest; on agitating which, the male Hassar springs furiously at them, and is thus captured.'<sup>6</sup>

§ 117. *Fecundation of Reptiles.*—Salamanders, Newts, Frogs, and Toads are generally apt for breeding

<sup>1</sup> Eckstroem (1831), quoted in xxxix. ii. p. 327.

<sup>2</sup> xx vol. v. p. 67, prep. no. 3229.

<sup>3</sup> Ib. no. 3223.

<sup>4</sup> cccxxxv.

<sup>5</sup> xliii. t. xii. p. 6.

<sup>6</sup> cccxxvi. p. 244.

when they have attained their third year. As the season of impregnation approaches, the expansion of the abdomen, unfettered by costal hoops, becomes enormous, especially in the females. The nuptial tints are assumed, the yellows and pinks being brightest. The males of certain Newts acquire the dorsal crest and a broader tail-fin, aiding in the manœuvres required for the internal impregnation. The male of the large Warty-Newt (*Triton cristatus*) in the spring season seeks the female and pursues her, vibrating his tail with a motion like that of cracking a whip, and, with a rapid evolution the tumid labia of the cloaca in the two sexes are brought into contact, and the spermatozoa get access to the oviduct: the pair sink to the bottom. The *Salamandra japonica* of Houttuyn (*Sal. unguiculata*, Schleg.) at this season has a claw on each digit of the fore limb. The male Frog acquires the dark-coloured swelling of the radial digit or thumb, by which he is better able to retain the female in his grasp during the long protracted business of impregnation. The larynx of the Toads, and especially of the male Pipa, now gains its fullest development and loudest power of croak. Lizards and Serpents exhibit their brightest colours: in the male Constrictors the copulatory anal hooks become conspicuous. The anal scent-glands are in active function in both groups. The male Crocodile, like certain fishes, fights for the female: the musky odour emitted by the submaxillary glands pervades their haunts at this time. Many Chelonia show sexual difference of form. In Land-Tortoises the plastron is concave in the male and flat in the female. In the *Cinosternoidæ* the fore part of the carapace is broader in the female, and the tail is longer and stronger in the male, which has also a patch of rough scales between the thigh and leg, not present in the female. In the *Trionycidæ* the tail extends beyond the rim of the shell in the males only: it is a mere stump in the females: besides this difference, the male of *Trionyx* (*Aspidonectes spinifer*) shows a slightly oval form; and the spines along the front margin, and the tubercles behind them and on the hind part of the carapace, are less prominent. In *Trionyx* (*Platypeltis*) *ferox* the latter character is reversed. In the Emydians the body of the male is usually flatter and longer than in the female. In copulation the male mounts on the back of the female: *Emys picta* performs the act when seven years of age; the female does not begin to oviposit before her eleventh year. Additional ova are developed in the ovary after the first copulation, and a certain number of those already formed begin to acquire a larger size, and 'go on growing for four successive years before they are laid:' thus the species is enabled to lay annually from five to seven eggs after it has reached its eleventh



year.<sup>1</sup> Although the Emydians lay once every year, soon after the period of copulation in the spring, the coitus is repeated a second time every year in the autumn, shortly before the species return to their winter quarters: and Agassiz concludes that in Emydians ‘a repetition of the act twice every year, for four successive years, is necessary to determine the final developement of a new individual.

§ 118. *Oviposition of Reptiles.*—I do not know particulars of this process in the Perennibranchiates. Some Newts (*Triton cristatus*, e. g.) deposit the eggs upon aquatic plants (*Polygonum Persicaria*, e. g.), folding the leaf by means of the hind feet in such a way that its under surface is turned inward, and the fold made to stick by the adhesive coating of the egg which she inserts in the fold. Our smaller Newt (*Lissotriton punctatus*, Bell) frequently glues the egg in the axilla of the leaf.<sup>2</sup>

Oviposition of the Frog takes place during the sexual embrace at the bottom of the water: as each egg is extruded, it is fertilised, and, the chorion absorbing water, the egg acquires a diameter of about three lines, the coloured vitellus appearing as a dot in the middle of the transparent jelly: the ova adhere together in a mass, and this is usually floated to the surface by disengagement of gas in the substance of the glairy envelope.

The ova are excluded under similar circumstances in the Toad; but in a long string of jelly, in which they are arranged alternately in a double series; the string may be a sixth of an inch in diameter and from three to four feet in length. In the obstetric Toad (*Alytes*), the male impregnates in water, assists in the exclusion of the eggs, causes them to adhere to his own hind legs by small pedicles, and then seeks the land: only when embryonic developement is sufficiently advanced does he leave his place of concealment, and betake himself to the water with the young brood with which he has charged himself. The male Pipa is asserted to place the eggs upon the back of the female, which give the stimulus to the formation of the cutaneous cells in which the whole course of metamorphosis is completed, fig. 367. In *Opisthodelphys* and *Nototrema*, the ova are transferred to the common pouch of the dorsal integument, described at p. 588.

The common Ringed Snake (*Natrix torquata*) excludes the eggs, sixteen to twenty in number, connected together by a glutinous coating, usually in some fermenting mass of decaying organic matter, whereby they are often transported and spread abroad in the manuring of fields and gardens. The Viper is not subject to this ovipositing cause of dispersion, and the confinement to a limited locality would seem to be the condition of the viviparity of most

<sup>1</sup> ccc. Part iii. p. 491.

<sup>2</sup> cccxvii.

or all poisonous serpents. It affects, however, the harmless Slow-worm (*Anguis fragilis*) and nimble Lizard (*Zootoca vivipara*), both of which usually produce their young alive. An American *Boa Constrictor* brought forth living young, and also eggs, in the Zoological Gardens of Amsterdam.<sup>1</sup> The old world constricting serpents would seem all to be oviparous; but instead of excluding the eggs where they would have the advantage of extraneous heat, they are arranged by the female in a heap around which she coils herself in a series of progressively decreasing spirals, constituting a pyramid of which the head of the Python forms the apex.

The fact has been observed in respect to species of Python in India: Col. Abbott, in a communication on this subject to the London Zoological Society, states that the incubation lasted more than three months.<sup>2</sup> More exact observations have been made on captive Pythons. In the *Python bivittatus*, in the 'Jardin des Plantes,' at Paris, copulation took place on the 22nd of January, and the act was often repeated until the end of February. On the 5th of May, the female excluded fifteen eggs, between 6 A.M. and 9:30 A.M. The eggs were all separate, of an elongate oval at the moment of exclusion, with a flexible greyish-coloured shell: they soon swelled into an elliptic shape, both ends becoming equal in size, and the shell, as it dried, became hard and of a pure white. The temperature of the female augments several degrees above that of the surrounding atmosphere, and is very sensible to the touch when she has disposed herself in incubating coils about her eggs. Between the 3rd and 7th of July the eggs were hatched. The mother did not eat during the incubating period, but several times drank with avidity water which was offered to her, indicative of a sort of febrile state. The heat of the body gradually fell towards the end of incubation.<sup>3</sup>

A similar phenomenon in the case of a *Python Sebæ* excited the public curiosity at the Zoological Gardens of London in 1861; the temperature of the body rose to 96° Fahr. between the incubating coils.<sup>4</sup>

The *Lacerta agilis* lays her eggs, from twelve to fourteen in number, in hollows which she prepares in the sand, and, having deposited the eggs, covers them with sand, and leaves them to be hatched by solar heat. The Iguana oviposits in the hollows of trees; the eggs, about forty in number, are oblong, about an inch in length.<sup>5</sup> Most of the Lacertilia are oviparous; but the details as to their oviposition are scanty: the shell is slightly calcareous.

All the Chelonians are oviparous, and the shell is calcified

<sup>1</sup> CCCXXXVII, p. 368.

<sup>2</sup> Ib. p. 188.

<sup>3</sup> CCCXXIV.

<sup>4</sup> CCCXXXVII. p. 367.

<sup>5</sup> CCCXXXIX.

almost as completely as in the bird, though in most retaining some flexibility. In the Painted Terrapin (*Emys picta*) the ovarian eggs do not show much difference in size until the seventh year, and oviposition does not begin before the eleventh year. Agassiz is of opinion that all American Emydians begin to lay eggs from the eleventh to the fourteenth year, when individual growth is checked and proceeds more slowly. Each species makes a single nest, and lays the eggs of that season at one time.<sup>1</sup> *Emys picta* digs with the hind legs a perpendicular hole near the stream she frequents, and may repeat the operation several times before selecting one as fit for oviposition: in this she deposits from five to seven eggs. The Snapper (*Chelydra serpentina*) excavates at first directly downward and then laterally, making the widest part of the hole where the eggs are deposited on one side of the external opening. When the eggs are laid, the female tramples down and smooths over the earth, so that, when dry, the place is hardly noticeable. She lays from twenty to forty, about the size of a walnut. *Cinosternon* lays only from three to five eggs. *Nanemys guttata* is usually limited to two or three eggs. Land Tortoises rarely lay more than four or five eggs at a season, and make the nidamental burrow in dry ground. The Gopher (*Testudo carolina*, L.) has a dwelling burrow, but forms a separate cavity near its mouth for oviposition: in this the female lays five eggs, then fills the nest up with earth, and flattens it down smoothly by her own weight.

The *Trionycidæ* lay from twelve to twenty eggs, or more, of the shape and size of a musket-ball, in a hole in the sand near the water's edge. The shell is thick and brittle.

The Sea Turtles (*Chelone*, *Sphargis*) are the most prolific of the order. They oviposit in May or the beginning of June, in dry sand, on the shore above high-water mark. The female selects a still moonlight night, when her senses of hearing and seeing may best avail her to detect an enemy. If satisfied, she proceeds to scoop out the sand with her hind fins, using them alternately, and when the sand has accumulated behind her, she scatters it abroad by violent jerks of the paddles; a hole being made between one and two feet in depth, the eggs are dropped in one by one, and disposed in regular layers to the number of from 150 to 200. The period of the entire operation may be half an hour. When concluded, the Turtle scrapes the loose sand back over the eggs, and makes the surface level and smooth. She then retreats to the water, and leaves the hatching of the eggs to the heat of the sand.<sup>2</sup>

<sup>1</sup> ccc. Part iii. p. 500.    <sup>2</sup> Audubon, quoted in cccxvii. p. 4, and ccc. Part ii. p. 328.

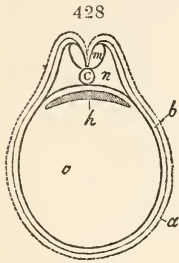
The Crocodilians, like the Chelonians, are all oviparous, and the process of oviposition is very similar. The eggs, of an elliptical form and with a firm calcareous shell, are buried on the shore, and left to hatch by extraneous heat.

§ 119. *Development of Batrachia.* — After impregnation of the batrachian ovum the dark or germinal part of the yolk is always uppermost, and its central point may be defined as the germinal pole. Here begins, usually about three hours after impregnation in the Frog, fig. 452, *a*, the process of segmentation,<sup>1</sup> by a fissure which passes in a determinate direction through the canal of the yolk, dividing it into two ellipsoid masses, *ib. b*. About the fifth hour a second cleft appears, near the point where the first commenced, crossing the first at right angles. If an ovum in this state be frozen, it splits into four segments of a sphere. Fissures next appear, which, in relation to the two foregoing, might be termed 'equatorial,' but with varieties exemplified in *e, f, g*, fig. 452. New 'meridional' furrows follow, *ib. h*, crossed again by other 'equatorial' ones, until the surface of the yolk presents the form of a blackberry. Further subdivision proceeds to such an extent as to render the surface again apparently smooth. This series of phenomena, resulting in the formation of the germ-mass, occupies about twenty-four hours, or less, according to the temperature. The fissures at their first appearance show minute lines at right angles, indicative of the molecular movements causing them. After the surface of the yolk has resumed its smoothness on the completion of the germ-mass, peripheral cells become filled with dark pigment, and constitute a general 'cambium' or outer investment, fig. 428, *a*. At the point where the formation of this investment, as well as of the germ-mass, began, an eminence appears by the developement of new cells beneath the investment, which loses its colour at this part, indicating the first rudiment of the embryo as an oval clear spot, divided at its hinder end by a crescentic fissure from the contiguous yolk, and with its anterior end sunk therein. The embryonal cells, as they accumulate, assume a polyhedral figure, and their different strata are seen by transverse sections. The first superficial appearance of the embryo is an oblong rising,

<sup>1</sup> The phenomenon of the division and subdivision of the yolk in animals was first observed by Prevost and Dumas in the ovum of the Frog (*Annales des Sciences Nat.* t. ii., May 1824, p. 112). Franz Bauer, in the same year, delineated partially the same important phenomenon, in the beautiful drawings which he prepared for Sir Ev. Home (cccxvi. pls. v. and vi.); but his employer had no appreciation or comprehension of what was thus shown him. Bergmann detected, in 1841, the hyaline nucleus in the centre of each subdivision of the yolk; and the combination of the spermatized cell progeny of the germinal vesicle with other elements of the yolk-substance appears to be a necessary prelude to segmentation.



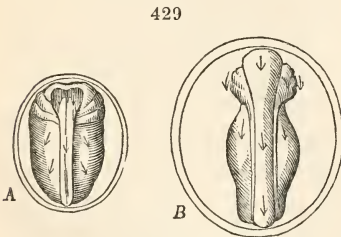
largest at one end, and impressed by a slight longitudinal fissure. The rudiments of the neural axis are first recognisable in the two parallel longitudinal elevations ('primitive trace' or 'laminae dorsales,' *ib. m, n*) bordering the fissure. Beneath these is at the same time forming the notochordal rudiment of the vertebral column, *ib. c*. The albuminous principle is concentrated in *m*, the gelatinous one in *c*: this chemical differentiation does not affect *n*. The polyhedral cells extend the vertebral layer on each side of the 'primitive trace,' which also increases in length: the neural columns, at first flat and horizontal, rise at their outer margins, approximate, and ultimately unite above, where they are covered by the peripheral cell-layer, *a*: they are also defended by the nascent neurapophyses, *ib. n*. Meanwhile the 'animal' layer is extending laterally, *ib. b*, beneath



Section of yolk and embryo, Frog, magn. LXXIV.

the investing membrane, *a*; and the cephalic end of the embryo enlarges and raises itself from the yolk-bed. A section of the ovum just prior to the coalescence of the 'laminae dorsales' to form the neural axis, as in fig. 428, shows, *a*, the dark investing membrane, or 'cambium:' *b*, the musculo-tegumentary layer, inclosing the whole yolk, *v*; *m*, the myelonal columns; *c*, the notochord; *n*, the blastema, in which cartilaginous rudiments of the neurapophyses begin; *h*, the cavity, beneath the germ due to solution of the yolk-substance.

On the ventral aspect of the embryo layers of cells have been forming two parallel ridges projecting into the yolk; and the intermediate space is converted by liquefaction of cells into a primitive alimentary groove. But all the systems and organs for the support of the embryo begin to be developed after the main basis of the neural and vertebral parts has been established.



Embryo of the Frog. CCXXXVIII.

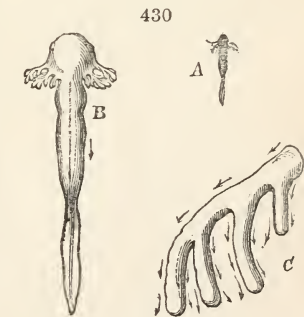
Figure 429, A, gives a view of the embryo of the Frog from the dorsal aspect, showing the myelonal columns at the period of their meeting above the myelonal canal and the commencing encephalic expansion, the extension of the neuro-vertebral tracts outward, and the indication of hæmal arches of the cephalic

segments. In B, the cervical constriction begins to define the head from the trunk: the complete coalescence of the myelonal tracts obliterates the linear trace of the median furrow, and the neurapophysial rudiments border the myelon. The embryo and its supporting yolk-mass are separated from the chorion by a clear fluid; and in the above-figured stages of development the ciliated epithelium begins to act upon the fluid in the direction indicated by the arrows, proceeding backward and downward along the sides: the currents are strongest on the hæmal arches, from which the branchiæ are about to be developed. In the mass of embryonal cells between the cephalic enlargement of the embryo and the yolk, the heart, fig. 431, *r*, is formed, which becomes hollow, and pulsates before the red blood appears; when the communication with the system of vessels is established, the heart propels blood, at first pale and with spherical corpuscles, in channels formed by liquefaction of cells in the blastema of the second hæmal arch; and these primary vascular arches establish the communication with the longitudinal aortic trunk similarly formed along the under part of the notochord. The blood returns by venous channels along the yolk, now progressively becoming inclosed by the lateral intestinal plates, and the simple circulation is complete.

From the substance around the vascular arches are formed as many branchial arches, as subordinate developements from the second primary hæmal or visceral arch; and from the branchial arches are budded the succession of vascular loops and coextended ciliated integument, constituting the outer gills on each side of the batrachian larva, fig. 430.

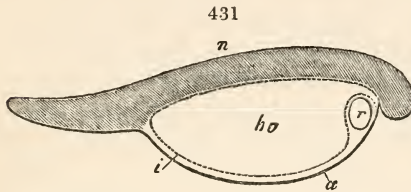
In the magnified portion of the gill, *c*, the arrows indicate the direction of the ciliary currents. Soon after the appearance of the heart, and of the arches which encompass the primitive bucco-branchial cavity, a pericardium, lined with epithelial cells, is formed around the heart. Between the cephalic hæmal arches interspaces are opened, communicating with the bucco-branchial cavity, and from one of these the budding gills begin to protrude.

The growth of the neurovertebral axis is chiefly lengthwise, and, as it proceeds, its two extremities lift themselves above the level of the rest of the germinal basis; the shorter and more



Larva of Frog; A, nat. size. CCXXXVIII.

obtuse as the head, the more acute and longer free part as the tail. In this growth the amphibian passes from a state in which a longitudinal section would show it supported by a spherical yolk, to that represented in fig. 431, in which the vitelline, or



Longitudinal section, Embryo of Frog. LXXIV.

'hæmal,' portion presents a semioval section, *hv*: it is inclosed, as in fig. 428, by the hæmal prolongations of the organic layer forming the abdominal parietes, *a*, and lined by the 'mucous' layer, *i*: this be-

comes differentiated as the tunics of the alimentary canal, inclosing the vitellus as the primary contents of such canal in all *Batrachia*. The canal now communicates with the bucco-branchial cavity; and this opens externally on the lower part of the head by a vertical fissure, on each side of which a small protuberance buds out, forming a special organ of adhesion—a pair of temporary cephalic limbs. A pair of branchiæ budding out from the gill-aperture, the whole yolk being now closed in by both the intestinal and cutaneous layers, and the tail having gained its muscular segments and cutaneous border-fin, the little tadpole, by increasing vigour of its movements, bursts the egg-membranes and comes forth. The external stimulus which most influences this stage is warmth. In Italy, Rusconi observed the eggs of the Frog to be hatched in four days; Bauer figures one extricating itself, in a warm spring, at Kew, after the fifth day:<sup>1</sup> in a cold spring, it may be prolonged through four weeks. In *Alytes obstetricans*, the developement of the 'mucous' layer proceeds to form a convoluted intestinal canal before 'extrication.' In *Rana esculenta*, and probably other Frogs, the vegetative organs are later in developement, and the cavity, fig. 431, *hv*, has not assumed the intestinal form when the embryo quits the egg: but in all *Batrachia* the whole yolk is wanted for the formation of their long spirally wound larval gut. Herein is a differential character between the *Batrachian* and the *Fish*. In the latter, the supply for the mid-period of developement is received, primarily, from the vascular rather than from the digestive system, and a part only of the yolk is required for the formation of the straight and simple intestinal canal. Accordingly, the mucous layer, as in the diagram, fig. 432, *i*, in

<sup>1</sup> cccxvi. pl. vi., fig. 1 A.

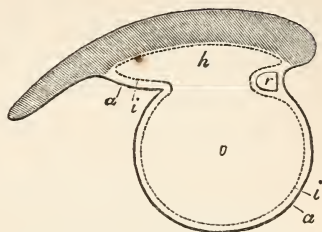
forming the intestinal canal, *h*, excludes a portion of the yolk, *v*: the tegumentary or 'serous' layer, *a*, accompanies the 'mucous' layer, *i*, in the process of severing the vitelline from the intestinal cavities, and an outer yolk, or 'vitellicle,' results.

The embryo of the Frog is extricated at a less advanced stage of development than that of any other vertebrate animal: the neural laminae have united along the trunk, and two of the hæmal arches have become complete below the head, but, in other parts, the neural and hæmal canals are closed only by the corresponding laminae in a state of membrane, the original investing membrane of the yolk being retained over all.

After extrication, the tadpole rapidly grows, and the chief change of form is witnessed in the gills: each of the two lateral gills puts forth four plates, which have vascular and richly ciliated surfaces, fig. 430, C: a short additional leaflet is sometimes developed from the base of the hinder gill. 'The current of the blood poured in regular pulsations at each contraction of the heart passes up each stem or main branch of the branchiæ, and a distinct stream is given off to each leaf; it is propelled to the extremity, and then returns down the opposite sides in the most regular manner, and the parts are so transparent that every globule of blood is distinctly and beautifully visible.'<sup>1</sup>

The first cutaneous mouth is defined by epidermal jaws, in the form of a very short transversely extended beak, fig. 433, 22, surrounded by a lip armed with minute rasp-like denticles, and aided by the pair of cephalic suckers projecting behind the mouth. The wide pharynx, communicating also with the outer world by the lateral branchial slits, is extended posteriorly by a short œsophagus to a simple gastric enlargement, beyond which an equally simple intestinal sac, laden with the remnant of the vitellus, gives issue to a short and straight rectum, which is continued to the long tegumentary and transitory cloacal canal at the fore-part of the subcaudal fin. The contained yolk, fig. 431, *hv*, is not, as in Fishes, fig. 432, *v*, a mere 'food-yolk:': it is part of the germ-mass, and consists of the embryonal cells, with their nutritious oil-globules. Whilst, therefore, it serves to nourish the growing embryo, it also

432



Longitudinal section, Embryo of Fish. LXXIV.

<sup>1</sup> cccxvii. p. 101.



continues to be the seat of progressing development, and coil after coil of intestine is formed between the duodenum before, and the rectum behind the primitive simple vitelline sac, the coils being disposed in a close double spiral, fig. 433, *l*. Thus, the fully developed larva is provided with an alimentary canal,

433

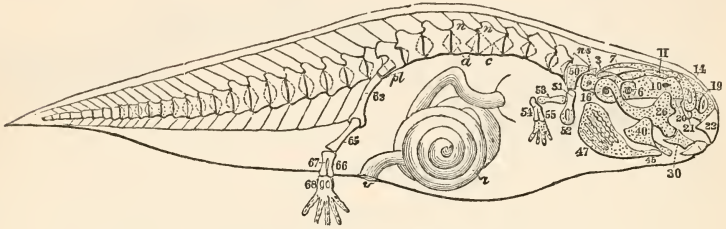
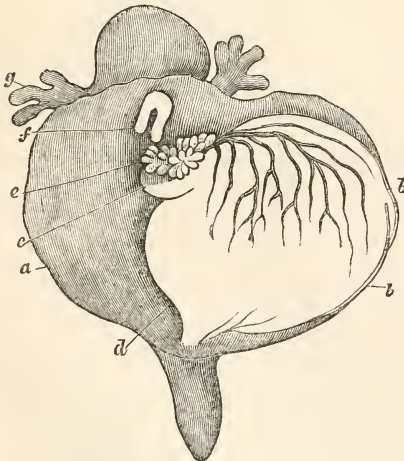


Diagram of the anatomy of the Tadpole.

adapted, by its length and complexity, for the assimilation of the decaying vegetable matters which chiefly constitute its food. In the conversion of this digestive apparatus into that of the purely carnivorous Frog, the horny cutaneous beak is changed into a wide mouth formed by well-ossified jaws, the lower one armed with sharp teeth. The branchial pharynx is contracted and closed at the sides, except where it communicates

with the ears. The œsophagus and stomach are elongated; the intestine is marvelously shortened; the rectum contracts, and is found to open, after the absorption of the tail and cutaneous anal fold, just in front of the symphysis pubis, now completed by the development of the hind limbs. Whilst the heart, as a bent tube, fig. 434, *f*, sends off the branchial arteries from its fore part, it is connected behind with vessels ramifying on the vitellicle, *ib.*, *b*: a portion of this is soon seen to be marked off from the rest, as the

434



Tadpole of Toad, magn. CXXII.

basis of the future liver and pancreas.

The embryonal cells that lay the foundation of these glands, fig. 434, *e*, are situated in the angle between the intestinal yolk-mass, *ib. b*, and the stomach, *ib. c*; not behind it, as in Fishes, fig. 435. They form a hollow gland or cæcum with a wall of compacted cells; and, after a communication has been established with the gut, other cavities or cæca pullulate in the cell-blastema, and the liver becomes conspicuous. 'Nowhere,' says Reichert, 'is the new generation of cells within parent-cells so obvious as in the blastema of the liver and pancreas.'<sup>1</sup> The primordial kidneys, or de-azotising organs, have now begun to be developed between the aorta and the intestinal plates, and the ducts of these, together with the anal prolongation of the intestinal tube, open upon the temporary tegumentary vent. In the Tadpole, as in a Fish, the mouth is destitute of tongue, but at the entrance of the mouth over the lips we find among the cartilaginous teeth at that region numerous conical-shaped bodies. These labial papillæ consist of an external border of prismatic epithelial cells provided with cilia. The tongue makes its appearance when the fore limbs, fig. 433, 54, 55, are evolved. The habits now alter: the Tadpole no longer feeds on decomposing substances, and cannot live long immersed in water. As the tail of the Tadpole atrophies, the fungiform papillæ appear upon the nascent tongue, increase in size, and acquire the permanent complex form.

Soon after the external gills have reached their full development, they begin to shrink, and finally disappear; but the branchial circulation is maintained some time longer upon the internal gills (p. 516, fig. 345); these consist of numerous short tuft-like processes from the membrane covering the cartilaginous branchial arches, fig. 433, 47: they are protected by the growth of a membranous gill-cover, which, as the external branchiæ are absorbed, leaves only one small external orifice, by which the branchial streams admitted by the mouth continue to be expelled. This orifice may be very plainly seen like a crescentic cicatrix, a little behind and below the left eye, in the larva of the *Rana paradoxa*.<sup>2</sup>

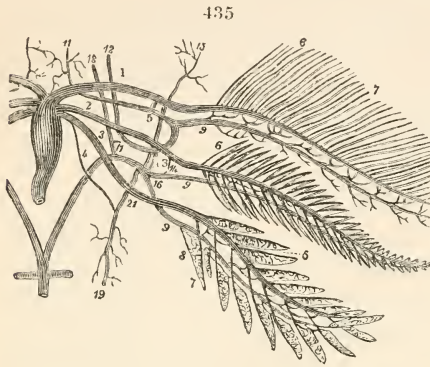
The chief distinction between the fully developed branchial circulation in the Batrachian larva and that of the Fish consists in the presence of small anastomosing channels, between the branchial artery and vein of each gill, proximad of the gill itself.

The part which these anastomoses play will be understood by the following description and figures of the vascular transformation as observed in the Newt. When the gills are in full development

<sup>1</sup> CCCXXVIII.<sup>2</sup> XX. vol. v. p. 77, preps. nos. 3286-3287, E.

and activity, the principal circulating vessels present the arrangement shown in fig. 435.

The vessel, ib. 4, originally distinct and large before the development of the gills, is now very small, and so close to the origin of 3 as to appear to be its first branch: it anastomoses with the branch 21 from the aortal root of its own side, and proceeds to the nascent lung 19. The artery 3 supplies the hind-



Branchial circulation; larval Newt (*Triton*). CCLXXXII.

most gill, and distributes its branches to the several branchial leaflets, 5, where they are resolved into the capillary network, fig. 343, p. 514; the blood is returned by the branchial veins, fig. 435, 7, 8, to the trunk 9, which at 16 joins the corresponding vein of the middle gill to form the aortal root or arch of that side: this receives

the anastomosing vessel 13, from the branchial vein of the first gill, and then sends off the accessory origin, 21, of the pulmonary artery, 19. The third primary vascular arch, 2, is the branchial artery of the middle gill: it effects a small anastomotic communication, 14, with the vein of the gill before proceeding to expend itself upon the branchial lamellæ, 6; the returning trunk, 9, after receiving the anastomotic twig, 14, joins the vein, 16, of the third gill to form the aortic arch. The foremost primary vascular arch, 1, before going to the first gill, anastomoses by a small channel, 5, with the vein, 9, of that gill; which vein, after the above anastomosis, sends off the vessel 11 to the head: before the anastomosis it passes back and divides into the vessel 13, joining the beginning of the aortal arch, and the recurrent branch 12, which also conveys arterialised blood to the head.

As absorption of the branchiæ proceeds in the progressing metamorphosis, the following changes are observed in the above described vessels, fig. 436: the anastomosing channel, 5, between the roots of the artery and vein of the first gill, dilates as the circulation through that gill is checked, and sends more blood into the artery 11, into the anastomotic channel 13, and into the artery 12. In like manner the blood of the second gill begins to be diverted by the anastomotic channel as its base leading to 16, which assumes

a size that gives it the character of the aortic arch. The pulmonary vessel, 4, now equals in size the trunk, 3, of which it was a branch; and it exceeds the tributary 21.

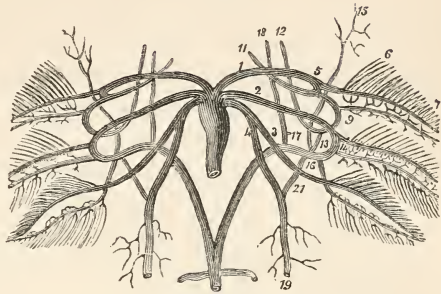
With the total disappearance of the gills the blood of the foremost vascular arch is carried into the two chief arteries of the head, fig. 437, 12, 18; either directly, or by the transformation of the anastomotic channel into a recurrent origin of one of these: it is thus converted into the carotid arteries. In higher Reptiles the origins of 1, 1, are blended or produced into a common trunk of the carotids.

The next vascular arch, 2, 2, is now transformed into the right and left arch of the aorta, by the enlargement of the anastomotic channel 14, fig. 435; with changes in length and position by which it gives off the cutaneous artery of the neck, 15. The tributary, 21, to the pulmonary artery, 4-19, is now shortened, and transverse in position: in higher Reptiles it is still more shortened, and finally obliterated as the 'ductus arteriosus' on each side. The orbital artery, 18, fig. 436, and 11, fig. 437, continues to be sent off from the aortic arch.

The first or hindmost of the primitive vascular arches is now converted into the pulmonary artery, and the blood which was transmitted by 3, figs. 435 and 436, is now diverted from the largest of the gills to the lungs.

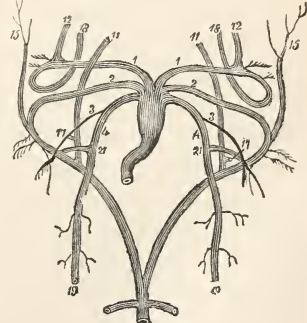
The blastema, which lays the foundation of the lungs, is situated behind and at the sides of the fore part of the alimentary canal, where it enters the bucco-branchial cavity. The lungs begin to be formed as soon as the intestine behind has taken on its first sigmoid curvature. They are not developed from the alimentary canal, but communicate with it soon after the establishment

436



Branchial circulation during absorption of gills; larval Newt (*Triton*). CCLXXXII.

437



Changes in branchial vessels after absorption of gills; Newt. CCLXXXII.



of the respiratory cavity in their primitive and independent blastema: their communicating duct advances with the elongation of the œsophagus, and at the point of its communication therewith the larynx is ultimately developed. The lungs themselves extend, as simple elongated sacs slightly reticulated on the inner surface, backward into the abdominal cavity. These receptacles are no sooner formed than the larva rises to the surface and swallows air, which passes into and expands the prepared cavity. When the pulmonary respiration has regularly begun, the fore-limbs are liberated from the branchial chamber, which now begins rapidly to contract its dimensions, and to be completely partitioned off from the abdominal cavity with which it had previously communicated.

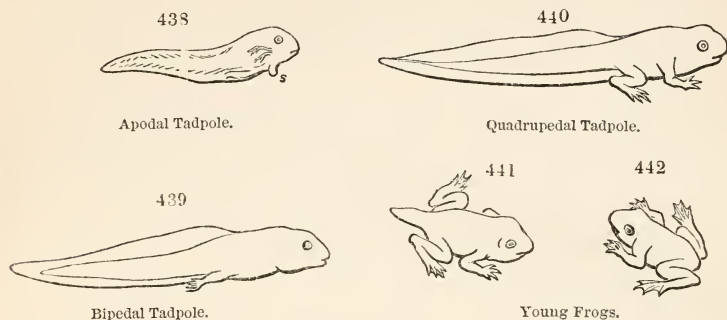
The changes in the hyo-branchial apparatus, accompanying those of the breathing organs, are defined at p. 90, and illustrated in figs. 69-71 and 74. The developement of the vertebræ is attended with the conversion of biconcave into cup-and-ball joints, by ossification of the substance of the cavities, *a*, fig. 433, and its coalescence either with the fore (*Pipa*) or back (*Rana*) part of the centrum, *c*. The chief facts in the formation of the skull are stated at p. 86, figs. 68-71.

About the middle period of aquatic life, the true or permanent kidneys begin to be formed from and upon the primordial ones; and the basis of the ovaria, or testes, may now be discerned. The oviduct is soon distinct from the ureter; but the testes retain the same excretory duct as the kidneys: their vasa deferentia communicate with retained cæca of the primordial kidneys before penetrating the later glands: the upper or anterior ends of the first remain for some time behind the heart.

In the often-quoted experiments of Edwards,<sup>1</sup> it is not clearly shown that the Tadpoles of the Frogs were constantly supplied with proper temperature and food, and therefore it is not satisfactorily proved that the arrest of the metamorphosis was due solely to the absence of light. Mere absence or diminution of this stimulus does not in all cases check the progress of the tadpole to the Frog-state. Ova of a Frog, deposited on March 11, were placed in a vessel covered with six or eight folds of black glazed calico in a dark part of a room, but in a temperature of from 55° to 65° Fahrenheit, and supplied with proper food.<sup>2</sup> The larvæ were hatched on March 20; attained the length of an inch on May 1, fig. 438; had pushed out their hind-legs, fig. 439, on May 10, and their fore-legs, fig. 440, on May 16: the tail began to be absorbed

<sup>1</sup> CCXCVII.<sup>2</sup> CCCXVIII.

at that date, was reduced to a stump, fig. 441, on the 18th, and was removed by May 20; the metamorphosis being fully completed, as in fig. 442, in all the tadpoles by May 22.



*Rana temporaria.*

The figures 438 to 441 illustrate the chief outward changes which accompany the batrachian metamorphosis, as exemplified in *Rana*.

In *Bufo* the tadpole is smaller and blacker in all the stages of growth and metamorphosis. In both genera of Anourans the growth is greatest at the phase figured in 439; with the subsequent phases the bulk of the body is diminished: and this is remarkably the case in the *Rana paradoxa*.

In the Newts (*Triton*) the gills are in three pairs, larger and more complex than in the Frog: the fore-limbs are the first to emerge, and the gills persist long after the hind-limbs are developed. If late hatched and in a cold season, the gills may be retained through the ensuing winter: they are absorbed before the next breeding season comes on.

Much ingenious conjecture has been expended on the influence of external circumstances and internal volitions and efforts during the struggles for existence in the origin of species by progressive transmutation; and their succession on this planet has been speculatively assigned to such causes. In the metamorphoses of the Batrachia we seem to have such process carried on before our eyes to its extremest extent. Not merely is one specific form changed to another of the same genus; not merely is one generic modification of an order substituted for another; the transmutation is not even limited by passing from one order (*Urodela*) to another (*Anoura*): it affects a transition from class to class. The Fish becomes the Frog; the aquatic animal changes to the terrestrial one; the water-breather becomes the air-breather; an insect diet is substituted for a vegetable one. And these changes, moreover, proceed gradually, continuously, and without any interruption

of active life. The larva having started into independent existence as a fish, does not relapse into the passive torpor of the ovum, to leave the organising energies to complete their work untroubled by the play of the parts they are to transmute, but step by step each organ is modified, and the behaviour of the animal and its life-sphere are the consequence, not the cause, of the changes.

The external gills are not dried and shrivelled by exposure to the air, nor does the larva gain its lungs by efforts to change its element and inhale a new respiratory medium. The beak is shed, the jaws and tongue are developed, and the gut shortened, before the young Frog is in a condition to catch a single fly. The embryo acquires the breathing and locomotive organs—gills and compressed tail—while imprisoned in the ovum; and the tadpole obtains its lungs and land-limbs while a denizen of the pool: action and reaction between the germ and the gelatinous atmosphere of the yolk, or between the larva and its aqueous atmosphere, have no part in these transmutations. The Batrachian is compelled to a new sphere of life by antecedent obliterations, absorptions, and developements, in which external influences and internal efforts have no share.

The phenomena of batrachian metamorphosis, that each spring are observable wherever there is a pool of water in a green field of England, are amongst the most suggestive and instructive which the animal economy affords.

§ 120. *Development of Scaled Reptiles.*—From the difference in the structure of the ovum in the scaled and naked Reptiles, the proportion of the food-yolk to the germ-yolk is much greater in the former, and the formation of a germ-mass by the diffusive process of successive fissions is restricted to a smaller proportion of the ovum than in Fishes. The formation of the embryonic trace closely resembles that in the Fish and Frog; but, instead of rising above the yolk-ball, the embryo sinks into it; first by the head, which, as it plunges in, gets covered by a fold or hood of the ‘serous’ or outer embryonal cell-layer, drawn progressively over the body until it is sheathed to beyond the heart; then the tail, bending down, acquires a caudal sheath; and the rest of the trunk sinking, the margins of the serous bed are produced over it continuously with the bodies of the cephalic and caudal sheaths, contracting concentrically until the whole embryo is inclosed in a ‘serous’ bag, reflected, as it seems, from the umbilicus, and thus the ‘amnios,’ fig. 445, *a*, is constituted. The embryo being imprisoned in the serum of this bag, branchiæ could not act, and are not developed;

but a temporary air-breathing organ is substituted to remove the carbon as the organic machine becomes more complex, and its actions more vigorous and various. From the fore-part of the cloaca a vesicle is protruded which elongates, escapes by the umbilicus, and, carrying along with it blood-vessels, applies their ramifications to the inner side of the shell: this is the 'allantois,' figs. 445 and 450, *b*.

On the part of the yolk supporting the embryo blood-channels appear which form a circular canal called 'vena terminalis;' it bends towards the embryo at the part near the head, and passes through the opening of the cephalic hood to a transverse canal, 'vena afferens,' behind the heart: this is now an obliquely bent tube, which pulsates and sends the circulating fluid to a dorsal vessel, which soon distributes vessels, right and left, in the abdominal region to the 'vena terminalis,' towards which numerous channels pass from the included space, fig. 450, *c*, the whole now forming the 'area vasculosa' upon the yolk. The fluid first circulated in this system of channels is pale plasma with granules.<sup>1</sup> The first circulation in an amniotic embryo may be described as passing from the heart-tube by vascular arches to the 'dorsal artery,' which supplies the parts of the embryo, and sends 'omphalo-mesenteric' branches to the 'area vasculosa,' from the 'vena terminalis' of which area the blood returns by the 'vena afferens' to the heart. The dorsal artery bifurcates posteriorly, and returns along the abdomen as the 'venæ cardinales:' the arteries to the head also return as 'precaval veins,' and all these terminate in the 'vena afferens.' Dilatations of the heart-tube indicate a ventricle, fig. 443, *a*, and a 'bulbus arteriosus, ib. *b*:' the latter is more prominent at first. An auricular dilatation behind the ventricle next appears. A protuberance in advance of the caudal curvature is formed by what soon is recognisable as a hollow sac, ib. *d*; which, as it expands, carries with it branches from the dorsal artery: these are the 'umbilical' or 'allantoic' arteries, fig. 450, *i*, which convey, as the bag protrudes and expands, part of the circulation to receive the influence of the air through the pores of the shell; and, the blood returning by the 'umbilical' or 'allantoic veins,' a subsidiary circulation to the vitelline, ib. *e*, is established, analogous to the branchial one of Batrachians and Fishes. The blood has now become red, and of shades indicating its arterial and venous conditions. The blood-corpuscles, at first globular, become slightly flattened, but the discs are circular before acquiring their elliptical form.<sup>2</sup> The omphalo-mesenteric

<sup>1</sup> Hunter, CCLXXX. (1794) p. 45, and XX. vol. v. p. xxiv.

<sup>2</sup> When the heart begins to lose its tubular shape the blood-particles are minute



arteries diverge from a common trunk, and the venous channels become more concentrated towards the heart. A venous sinus is formed behind the auricle, and this is divided by a valvular structure from the ventricle, which now is larger than the bulbus.

The changes of the primitive vascular arches into the arterial trunks arising from the adult heart are effected more speedily and directly in allantoic Reptiles than in Batrachia, pp. 519, 520, because no branchial organs and vessels are developed: such special respiratory apparatus for a temporary aquatic existence is interposed in the anallantoic species, and interrupts, so to speak, the course of the transformation which is now to be described.

The primitive distribution of blood from the 'bulbus' of the embryonal heart in 'Vertebrates' is by a series of symmetrical arches on each side the alimentary canal, dorsad of which those loops or arches unite to form or join the aortic trunk: they relate to the primitive segmental character of the embryo, co-existing with maxillary, mandibular, hyoidean, and scapular segments, all of which at this period are unclosed arches on the sternal aspect of the fore-part of the body.

The four or five primitive vascular arches have no essential relation to gills, any more than the clefts or depressions between the budding piers of the maxillary, fig. 444, *a*, mandibular, *ib. b*, and hyoidean, *ib. c*, arches are necessarily the precursors of the branchial openings. Both primary structures exist in the embryo of those vertebrate classes that never possess the true branchial organs: these are superadded developements upon the common segmental type of pleurapophysial and pleurararterial parts, which developements are peculiar to Fishes and Batrachians, persisting in the first, and vanishing in most of the latter Vertebrates. Of the three vascular arches on each side by which the blood passed from the bulbus to the dorsal vessel, the hindmost are progressively converted, with the growth of the lungs, into the 'pulmonary arteries,' each retaining a connection with the second pair of vascular arches; the third, or anterior pair, with the developement of the head and fore-limbs, in like manner become diverted to their exclusive service, but for a time retain a con-

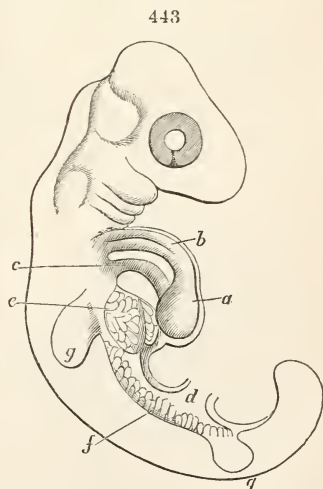
transparent globular cells, with a large granulated nucleus (mesoblast, Ag.), attached to the wall. 'By the application of water the nucleus bursts and the whole granular contents come out, but still retain their globular state and appear to have a membrane about them. From this it would appear that the apparently granular contents of the mesoblast constitute, in reality, an entoblast (nucleolus), which fills the mesoblast.' The flat elliptic form is not attained until very late. The mesoblast is faint and homogeneous to within a short time before extrication of the turtle: in the adult it contains a darker entoblast. ccc. p. 617.

nection with the mid-pair, as shown in fig. 332, p. 504, at A. The returning blood from the expanding lungs leads to the development of a distinct chamber in the auricle, which finally becomes the left auricle. Partitions in the bulbus arteriosus effect a distinct communication of the pulmonary arteries with the ventricle, and a division of what now becomes 'aorta' into two trunks. Of these one is appropriated to the left of the primitive pair of middle arches; the other becomes the trunk of the right arch of that pair, and also of the anterior pair in course of change into brachial and carotid arteries. The 'ductus arteriosi,' between the anterior and middle arches (fig. 332, A), are usually absorbed (as at D, fig. 334): those between the posterior and middle arches (D, fig. 335) are longer retained through the same course of change. The trunk, which gives off the carotids either exclusively or in common with the brachials, is posterior in Reptiles to the trunk of the left aorta, and to that of the pulmonary artery. With the development of septa in the bulbus, there proceeds a like change in the ventricle itself, but it does not reach the condition of a complete 'septum ventriculorum' until the crocodilian type of *Hæmatocrya* is attained (figs. 339, 340).

The substitution of kidneys for Wolffian bodies is preceded by an enlargement of the latter, fig. 443, *f*, at their middle part, with attenuation of their ends: the true kidneys begin to be formed at the upper medial part, and their uriniferous tubes are larger and more convoluted. The genital organs appear as a narrow white band upon the ventral side of the Wolffian body.

The development of the brain closely resembles that in the Fish (pp. 604, 607), but it soon bends down at a stronger angle with the myelon. The cerebellar fold is first distinguishable; afterwards the deflected anterior part of the encephalon becomes divided into mesencephalon, cerebrum, and olfactory lobes, and the cerebrum speedily attains the superiority of size which

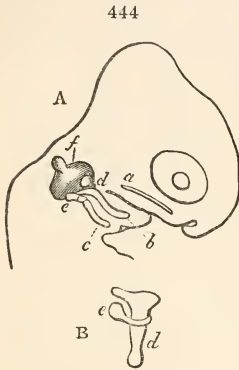
distinguishes the brain of the Reptile from that of the Fish. The pineal gland shows a large proportional size in the embryo Turtle, as does also the 'thalamus' or lower lobe of the mesencephalon,



Embryo of *Lacerta viridis*.

in which the optic nerves chiefly originate: the ventricles are large in each mass. The eye-ball is formed, as in Fishes, by the bending of a sausage-like bag about the lens, and the coalescence of the ends brought into contact. The cicatrix, shown in fig. 443, soon disappears. The capsule is next differentiated from the lens proper. The eye-ball is, at first, unprotected, as in Fishes; but the contiguous skin-border begins to encroach upon its fore part, with modified growth, to form the eyelids.

After the development of the labyrinth from the primitive ear-capsule, a tympanic cavity is formed, in which the 'stapes' appears as a short thick cartilaginous cylinder in the *Chelonia*, in which the 'meatus auditorius' broadens outwards to a trumpet shape, which it retains. In the *Ophidia* the 'stapes,' fig. 444, B, *e*, is similarly developed, independently of the tympanic and mandibular (or so-called Meckel's) cartilage, *ib. d*, as shown by Rathké, in *Natrix torquata*. The nostrils appear as deep depressions at the fore end of the head, the margins of which become incurved, and the bottom of the sac is produced into a canal communicating with the mouth.



Hemal arches of cranium; embryo  
Snake. CCCXXX.

In and from the membrane of the notochord, continued along the basis cranii, is developed the cartilage of the basi-presphenoid, blending laterally with the ear-capsules: the basal cartilage bifurcates anteriorly, and reunites surrounding the hypophysial fissure: it is then continued singly forward, and expands anteriorly in connection with cartilaginous plates from which, in *Chelonia* and *Ophidia*, the profronto-nasal bones are developed. In *Lacertilia* the large 'lacrymal' bones grow from the same embryonal cartilage. Behind these foremost representatives of neurapophyses are three pairs, more clearly showing the neurapophysial characters: the pair resting on the bifurcated presphenoidal part of the basal cartilage, in relation to the optic nerves, become 'orbitosphenoids';<sup>1</sup> the next pair, in relation to the trigeminal nerves, situated anterior to the 'ear-capsules,' become the 'alisphenoids';<sup>2</sup> the pair behind the ear-capsules, resting on the basioccipital, become the ex- and par-occipitals.<sup>3</sup> Thus the

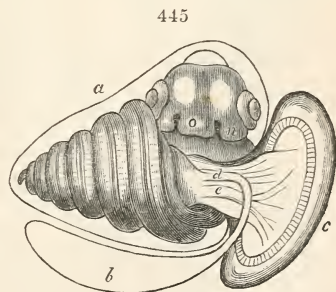
<sup>1</sup> CCCXXX. taf. vii. fig. 17, *f*, 'vorderer Keilbeinflügel.' <sup>2</sup> *Ib. e*, 'hinterer Keilbeinflügel.'

<sup>3</sup> *Ib. b*, 'Seitentheil des Hinterhauptbeines.'

neural arches of four vertebral segments are plainly indicated in the development of the reptilian cranium. The hæmal arches make their first appearance as pairs of slender rib-like bones: the foremost, fig. 444, *a*, becomes the palato-maxillary arch;<sup>1</sup> the next early shows more clearly its division into the pleur- and hæm-apophysial parts of the tympano-mandibular arch, *ib. b*; the third, *ib. c*, is the hyoid arch: the fourth has no longer the cephalic relation which it shows in Fishes; and the four neuropophyses are matched below by only three hæmapophyses in the reptilian cranium.

In the oviparous Snakes, *Natrix torquata*, e. g., a certain progress in the development of the embryo is found to have been made when the egg is laid, and the rest is completed and the young extricated in the course of about two months, sooner or later, according to the surrounding temperature.

When development has advanced to the formation of the amnios about the embryo, the head is distinct, and shows the eyeball and ear-sac; also the maxillary and mandibular processes and the beginning of the hyoid, with the intervening depressions, mis-called 'branchial clefts:' the heart, as a sigmoidally bent tube, fills the concavity between the frontal process and the chest: the allantois has protruded, as a globular vesicle, about the size of the head; and beyond its emergence the tail forms a single spiral coil: the vascular area on which the vitelline vessels ramify covers half the food-yolk. The long trunk of the Serpent grows in a series of decreasing spirals, and when five or six are formed, the rudiment of the liver and the primordial kidneys are discernible. Fig. 444 shows the embryo at this period magnified four times: *a* is the amnios, *b* the allantois, *d* its tubular stem, produced from the cloaca, or 'urachus:' the front view of the head shows the 'frontal process,' *o*, and the bases, *n*, of the palato-maxillary hæmal arch. The primordial kidneys are remarkable for their length: *c* indicates a portion of the vitellicle. With the dilatation of the fore-part of the alimentary canal indicating the stomach, a small appendage, the pancreas, appears, marking the beginning of the intestine. The lungs are next seen as a



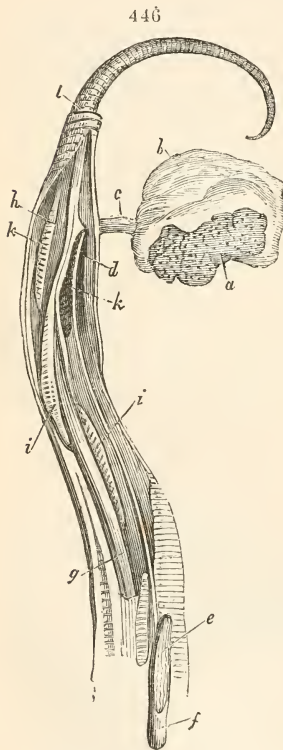
Embryo Snake (*Natrix*). cccxxx.

<sup>1</sup> cccxxx. taf. vii, fig. 11, e, 'Oberkiefer.'



symmetrical pair of longish simple sacs, extending from the pharynx on each side of the œsophagus to the beginning of the liver: the left division soon begins to exceed the right in length, and then seems to monopolise the power of growth. The common stem or neck of the pulmonary sacs elongates, contracts, and begins to show traces of the transverse cartilages; and at about the latter third of the developmental period the right lung appears as a mere appendage to the beginning of the left. The appearance of malpighian bodies, as minute red points on part of the surface of the primordial kidneys, is the first indication of the development therefrom of the kidneys: these grow between the primordial kidneys and the vertebræ at the hindmost end of the abdominal cavity. The testis, or ovary, is differentiated from the ventral surface of the fore-part of the primordial glands: at

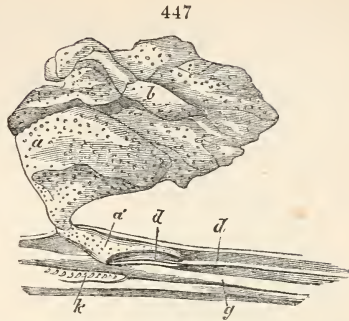
one period of development the primordial ducts coexist with the sperm-duct and ureters. Four or five ducts emerge from the liver and unite into a common one before communicating with the intestine; a similar duct, proceeding from the common one, expands at its opposite end into the gall-bladder. This remains near the pylorus: the hepatic ducts elongate as the intestine recedes on the growth of the snake. The spleen first appears as an appendage to the narrow end of the pancreas. In the male embryo, the two bifurcate penes project from the cloaca before the period of extrication.



Fœtus of Viper. XLIII.

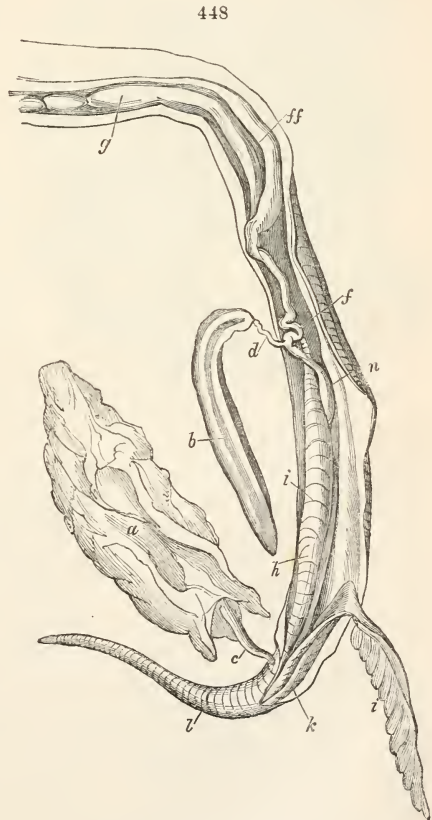
Figure 446 shows the posterior half of the embryo of the Viper at a late period of development. The yolk bag, *a*, is much reduced in size, but is not yet taken into the abdominal cavity; *b* is the portion of the annios adherent to the vitellicle; *c* is the short pedicle, including part of *d*, the ductus vitello-intestinalis, which ascends to terminate at *e*, between the longitudinal folds of the mucous membrane of the small intestine, *f*. The continuation of the intestine to the cloaca, *l*, is shown at *g*, *h*; the ovaria at *i*, *i*; the kidneys at *k*, *k*.

In figure 447, the vitellicle of a Viper, at a more advanced period, shows part of the food-yolk entering the abdominal cavity, at *a*: the ductus vitello-intestinalis, *d*, is reduced to a thread: *g* is the intestine, and *k* the kidney.



Vitellicle of a Viper at a more advanced period, showing the yolk partially taken into the abdominal cavity. XLIII.

Figure 448 shows the body of a Viper just before the period of extrication from the egg-coverings; the parietes of the abdomen are partly removed to show the vitellicle, *b*, which has now become inclosed in that cavity, with almost complete obliteration of the umbilical cicatrix: *a*, the remains of amnios and allantois: *d*, the much shortened ductus vitello-intestinalis: *g*, the liver: *ff*, the stomach: *f*, the duodenum: *n*, the small intestine: the other letters indicate the same parts as in the preceding figures.



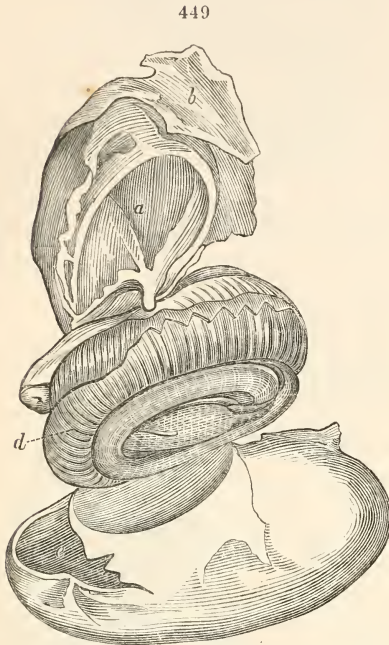
Body of a Viper just before it is hatched. XLIII.

The gravid Viper is more than usually sluggish, and loves to bask in the hot sunshine, turning her belly as if to court the aid of the extraneous warmth in accelerating the internal incubation of her eggs.

Figure 449 shows the egg and embryo of the Monitor Lizard near the period of extrication: *a* is the remnant of the food-yolk: *b* the amnion laid open to show the embryo, *d*; its long trunk and tail are packed in spiral folds as

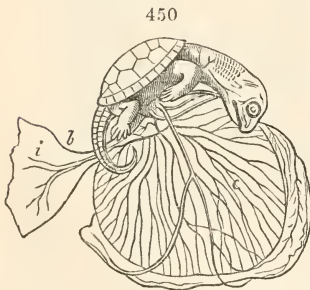
in the embryo Serpent: *e* is the leathery and partially calcified egg-shell. An embryo Lizard, at an earlier period of development, is shown in fig. 443.

Hunter left the following preparations illustrative of the development of the Crocodile. No. 3364 shows the calcareous outer crust of the inner 'membrana putaminis' of the egg: No. 3365 shows the attachment of the vascular allantois to that shell membrane in an embryo in which part of the yolk has been received within the abdomen. In No. 3366 the hinder half of the Crocodile is dissected to show the condition of the vitelline and allantoic sacs at the close of fetal development: the vitellicle presents an irregular lobated form, and its short and narrow duct communicates with the small intestine a little below the duodenum: the allantois communicates with the lower and fore part of the cloaca



Egg and embryo of the Monitor Lizard. XLIII.

by means of a long and slender duct homologous with the urachus: but no part is dilated, as in certain Lizards, to form the urinary bladder. In No. 3370 is shown the vitellicle, after inclusion within the abdominal walls; it is much reduced in size, and its contents are hard and stringy.



Embryo Tortoise, *Chelydra serpentina*. ccc.

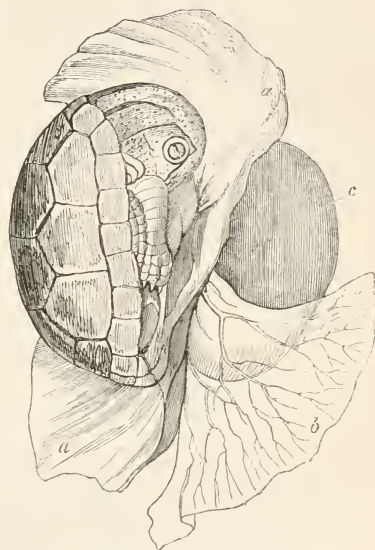
The period of external incubation by the action of the sun's rays upon the sand-nest of the eggs of the Turtle (*Chelone Midas*) has been ascertained to be seven weeks.

Figure 450 shows the embryo of a Snapping Turtle (*Chelydra serpentina*) from an egg laid June 21st and opened September 21st of the same year. The amnios is cut away: *c* shows the 'area vascu-

losa,' with the omphalo-mesenteric vessels; *b* is part of the allantois with the allantoic or 'umbilical' vessels, *i*. The outline of the carapace is just marked on the back of the embryo, and the proportion of the vertebral column not so modified appears to be greater, as is its resemblance to the type-form of Reptile, than in the adult.

The condition of the carapace and the outward form of a Fresh-Water Tortoise (*Emys*) is shown in figure 451. The amnios, *a*, is

turned back to show the position of the limbs and head in the egg: *b* is the part of the allantois; *c* the remnant of the yolk. The central opening of the plastron, which is permanent in the marine *Chelonia*, is seen at this period in all the order, but is quickly filled up in the land and fresh-water species. The chief speciality in the development of the scaled Reptiles, compared with each other, relates to that of the carapace and plastron of the *Chelonia*: and this has been explained at pp. 557-9, and illustrated in figs. 369-72.



Embryo of an *Emys*.

When the Turtle is hatched, the bones of the head show different degrees of ossification. The premaxillary and premandibular are most advanced for the purposes of feeding; the maxillary, the back part of the mandible, the prefronto-nasal, frontal, and parietal come next in hardness. The superoccipital shows an outer layer of bone, the rest being gristle; the basioccipital and basisphenoid begin to be ossified from the centre; the alisphenoids and exoccipitals are still cartilaginous.

The limbs begin to show the digital divisions soon after the carapace is outlined, and the cartilages of the metacarpals and metatarsals are first discernible; the phalanges are composed of compacted polygonal cells at near the term of incubation, which then become 'cartilage cells,' widely divided by blastema. The long bones of the limbs show a thin outer crust of bone inclosing cartilage, which is progressively ossified, solidifying the shaft, without subsequent excavation of any medullary cavity.



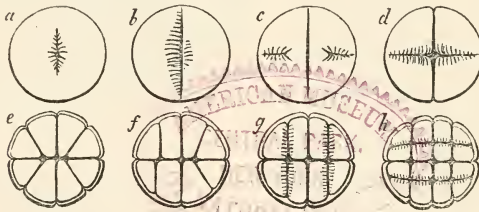
In the cold-blooded reptiles, hatched by external heat, independently of incubation, the course of development may be interrupted for longer periods, without hurt to the embryo, than in the warm-blooded Ovipara. Agassiz states that in *Testudinata* the common period of hatching may be 'postponed for months.'

In Snakes and Lizards a sharp tooth is developed in the premaxillary of the embryo, towards the close of incubation, where-with they cut through the tough egg-shell.<sup>1</sup> The operation of this transitory and purposive weapon has been observed by Weinland:<sup>2</sup> it totally disappears in the adult of most Ophidia. For breaking through the more brittle shell in *Chelonia* the embryo is provided with a sort of horn or hard excrescence above the end of the upper jaw: this afterwards disappears. In the Crocodilia the snout of the nearly hatched young is sufficiently hard to break the egg-shell; but there is no distinct tubercle, nor any precociously developed premaxillary tooth.<sup>3</sup>

<sup>1</sup> CCCXXXVI.

<sup>2</sup> CCCXXXVI.

<sup>3</sup> ccc. p. 288.



Initial steps of Vertebrate Development. Germ-yolk of *Rana temporaria*. CCCXXXVI.

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49





