Some TEACHINGS *of* DEVELOPMENT. By E. A. SCHÄFER, F.R.S., Fullerian Professor of Physiology.[1]

I.

DEVELOPMENT is the term applied to the process of evolution of an organism from its simplest to its most complex phase of existence.

In all but the very lowest animals the development of the individual begins with the ovum or egg, this being the elemental portion or cell of the parent animal which is set aside for the special purpose of reproduction. In most cases the separated cell is incapable by itself of reproducing the parent; it must first blend with a separated part of another parent. This blending with the ovum (female reproductive element) of the antherozoid (male reproductive element) constitutes the process of fertilisation.

The commencement of development follows immediately upon the completion of fertilisation. Once commenced the pr cess is usually continuous, and being accompanied by a general increase in size, the result is the perfect or adult individual. Although these two processes (development, *i. e.* increase of structural and functional complexity, and growth, *i. e.* increase of size) generally go hand in hand, we must be careful to distinguish between them. For mere increase of size may often give the appearance of greater complexity, when in reality the organism has not advanced either in function or in intimate structure. This is the case sometimes when the increase of size takes the form of budded outgrowths which are merely repetitions of the structure of the parent organism. The common freshwater polyp constantly presents us with an illustration of this, for its numerous buds produce an appearance of complexity which disappears when the buds detach themselves as independent organisms. In the compound hydroid polyps, in which the buds remain attached, the appearance of complexity remains throughout the life of the organism, and is accompanied in some by an actual progress in functional and structural complexity.

In the case just alluded to the increase of size accompanying development takes the form of an arborescent repetition of all the chief parts of which the developing individual is composed. But it may instead take the form of a serial repetition such as we see

[1] This article contains the substance of the last two of a series of twelve lectures on Animal Development, delivered at the Royal Institution in Jan., Feb., March, 1879; and has not been modified since that date.

in the Strobila stage of development of the larger Medusæ, and which presents itself in striking contrast to the arborescent repetition of the corresponding stage of development of the Craspedote Medusæ. In the so-called Strobila the developing individual has become partially separated by transverse constrictions into a series of perfectly similar, saucer-shaped segments, each of which comprises within itself in a rudimentary form, a representative of all the parts of the originally simple parent organism. So long as these remain united the Strobila is a compound individual constituted by a serial repetition of similar parts; but they soon prove their individuality by breaking away from the compound body and from one another, and maintaining existence as independent organisms.

This serial repetition is seen in still more characteristic form amongst the Annelids, where almost every one of the many segments which compose the body is complete within itself, and any one might be taken as a representation of the primarily simple embryo which produced them all. And viewing them by the light of the illustrations furnished us by the Cœlenterata, it seems not unreasonable to regard all animals in which such serial repetition is found as compound rather than as simple individuals—to a certain extent comparable to the condition of the united polyps just referred to, but far more closely joined together and interdependent; rendered thereby incapable of maintaining themselves as separate organisms, but, on the other hand, able the better, by their united powers, to carry on the struggle for existence. And the importance of this serial repetition is indicated by the fact that it is found as the main characteristic of the two most highly organised branches of the animal tree—the Arthropoda and the Vertebrata, masked though it often is in them by that tendency to recoalescence which at first sight seems a recurrence to more simple types of existence, but which, when attentively considered, proves to be merely the expression of the closer union and combination of the separate segments, the better to work together for special objects or for their mutual benefit.

I have stated that, once commenced, the process of development of an animal is a continuous one. Nevertheless, it is customary to regard it as advancing by separate steps or stages—to look upon it as a staircase or ladder, the stairs or rungs of which are successively attained, and the number of which depends upon the complexity of organisation of the adult individual. The familiar phrases "scale of development," "scale of organisation" (Latin, *scalæ*, a staircase), are a sufficient indication of the mode in which the subject is generally viewed. And although I think that the continuous nature of the process should on no account be lost sight of, yet it is so manifestly convenient for purposes of description and of comparison to maintain the idea of grades, that I shall here adopt a like simile, choosing a succession of telescopic tubes, instead of a staircase, to represent the succession of developmental phases, because those can be imagined to be more or less drawn out, and shifted upon one another, so as to illustrate the varying relations which the typical successive phases bear to one another in the development of different animals. It will further be necessary to imagine the tubes constituted of some very elastic material, rendering it possible for them to be extended to two, three, or many times their proper length, or, on the other hand, to become shortened so much as to be scarcely perceptible. Each tube of which the telescope is composed may be taken to represent a particular stage of development, and the greater the complexity of the organism the more tubes must be added to the series, and the greater the length of the developmental telescope.

If we now proceed to compare the development of various animals with one another, we are struck with the resemblance—with the identity I might rather say—of the first stages in all. To begin with all take origin in an ovum; and although at the first glance this appears so different in many (compare the ovum of a mammal with the egg-yolk or ovum of the bird), examination shows it to be in all cases similar in essential composition. For the difference depends solely upon the amount of nutritive material which has been stored up within and in connection with the reproductive protoplasm, and has relation to the greater or less facility with which a supply of food can be obtained from without during the active developmental process. To use a familiar comparison, the difference is precisely the same as that between an army operating in a fertile country where supplies are readily obtainable, and a force which is to operate in a region barren or devastated, and far removed from the base of supplies. In the one case pabulum sufficient merely for immediate use is required, in the other a great store of nutriment must be accumulated and must accompany and proportionately hamper every movement of the army. Moreover, since to a part of the force must be entrusted the duty of guarding the store and distributing it as required, a greater number of men is required to bring the army up to the same proportionate strength as that of the unencumbered force. So in those ova which are provided with a large store of nutritive material, do we find that when the active movements which characterse development commence, those movements are hampered by the presence of the inert food-material, and it is precisely as the store becomes lessened that the apparent difference between such ova as these, and those others which from the first have scarcely any store of nutriment, disappears. The difference is one of degree only and not a difference in the essential nature of the ova; this view is confirmed by the existence of every shade of transition between them, as well as by observing that the difference obtains in the ova of animals which are otherwise closely allied.

Further, in the ovum of all animals there follows immediately on fertilisation the successive division or cleavage of the single cell into first two, then four, and so on until an indefinite number of cells is formed which arrange themselves around a central space —the cleavage-cavity. This, in the majority of cases, is distinct enough, being occupied merely by clear fluid and enclosed by a single layer of cells; but in some instances it is partially or wholly filled up by the excess of food-material and its immediately attendant protoplasm, which may or may not, according to its relative bulk, have participated in the active changes which have been occurring in the rest of the protoplasm, and of which the cleavage is the result. To revert to our military comparison it is as if the two armies had broken up into detachments and arranged themselves so as to enclose circular areas of ground; in the one case the detachments unencumbered and active on all sides, with the enclosed area left clear; in the other case the *matériel*, with the camp followers, packed away in the centre and partly occupying one side of the space, whilst the least encumbered detachments are chiefly accumulated on the side where most activity is required.

Bearing in mind this difference, and regarding it as accidental, we may take the completion of the cleavage process, as far as the arrangement of the resulting cells around a central area in the manner described, as the first stage in the development of all animals. It may be termed the stage of the *unilaminar blastoderm*, or the *blastosphere*. For the name blastoderm has long been applied to the cellular membranes of which the developing ovum is formed at early periods; and the term blastosphere may be used, because at this stage a typical ovum, *i.e.* one with a minimal amount of nutritive material, consists as we have seen of but a single uniform layer of cells forming the wall of a hollow sphere.

We meet with this typical condition of the first stage in Gastrophysema (according to Haeckel), in Phallusia, and in Amphioxus and other animals. But even in those ova which contain only a slight excess of pabulum we find that there are differences observable in the cells which form the wall of the blastosphere, for the food-material becomes chiefly collected at one part of the layer, rendering the cells at this part more granular and larger than the others. This difference may be so slight as to be almost imperceptible, as in the Holothurian blastosphere, or it may be more obvious as in that of the Sponge and Paludina. And every transition is found between these cases and those in which the amount of pabulum is so great in proportion that it can no longer be contained in the typical single layer of cells, but becomes accumulated in the cavity of the sphere as well, either still enclosed in definite cells as in the Amphibian, or for the most part unenclosed in cells as in the Fish, the Bird, and the Crustacean.

The next most important change that occurs in the typical unencumbered ovum is the invagination of one part of the simple wall of the blastosphere, in such a manner as to convert the hollow single-layered vesicle into a cup with double walls. The cleavage-cavity or cavity of the blastosphere is concomitantly reduced in size or even obliterated as it is encroached upon by the invaginated part of the wall, and its place is taken by the cavity of the cup. The orifice of this, at first widely open, becomes gradually closed up by the continued growth of the two layers at the mouth of the cup, until but a narrow aperture remains, which persists for a time, but at length in many cases becomes closed. This aperture is termed by Haeckel the primitive mouth or *protostoma*, by Lankester the *blastopore*.

The result of the completion of this process of invagination is again a hollow vesicle, but its walls are now composed of two layers of cells instead of one. The inner or invaginated layer is termed "entoderm" and the outer or enclosing layer "ectoderm." The cavity which they enclose always becomes the future alimentary cavity, and hence the name "gastrula" has been applied by Haeckel to this stage of development. We may also speak of it as the *cup-stage* or as the stage of the *bilaminar blastoderm*.

In typical ova the original blastosphere is uniform throughout, and it would be impossible to point out the part of the wall which is to be invaginated. But in those ova which have even a small excess of nutritive material and in which therefore, as already mentioned, some of the cells of the blastosphere are characterised by containing this excess, we always find that it is this particular part of the wall of the vesicle which is involuted to form the inner layer of the cup. So that even in the stage of the blastosphere we can predict which cells are to become entoderm and which ectoderm.

Finally, in those ova in which the nutritive material largely preponderates we find that even when the cavity of the blastosphere is not entirely filled up by that material (and of course also when it is so filled up), the mechanical hindrance to any invagination is so great that the process cannot be effected.

Still, even in such cases as these the cup-stage is not absent. The same result is obtained, but in a different way. For the enclosure of the pabulum-containing entoderm by the ectoderm is effected solely by the growth of the latter, without any accompanying invagination of entoderm. In these cases the cavity of the gastrula also is necessarily occupied by the pabulum, and this if greatly in excess may even project beyond the cup-orifice.

We may then take the gastrula or cup-phase as a second stage and note that, like the first, it is met with (modified only by the accidental presence of food material) in all animals above the Protozoa.

There are two apparent exceptions to the general rule of formation of the gastrula stage by invagination. These are met with in the development of the freshwater polyp (Hydra) as described by Kleinenberg, and that of one of the Medusæ (Geryonia) as described by Metschnikoff and by Fol. In these animals the bilaminar blastoderm is said to be formed by the splitting into two portions, inner and outer, of some or all of the cells of the single layer which forms the wall of the blastosphere, the inner parts becoming collectively the entoderm, the outer remaining as ectoderm. Regarding these exceptions the question naturally suggests itself, Are they due to defects of observation ? and further, supposing that there is no flaw in the facts, are they nevertheless explicable as modifications only in the ordinary mode of formation of the gastrula ? Certainly as far as concerns Hydra, the recorded observations of Kleinenberg are too incomplete on this part of the development for his conclusions to be accepted without demur. And it is very generally admitted that the development of Geryonia needs careful reinvestigation with the aid of microscopic sections. It is not improbable that the result of such reinvestigation might prove the existence of some sort of invagination at a much earlier period than that at which the so-called delamination or splitting occurs.

The cavity of the cup at first communicates, as we have seen, with the exterior, by means of the aperture of invagination or protostome, and when this becomes closed, or even before its closure, another aperture appears, and in most cases yet another. These secondary openings into the cavity of the gastrula become respectively the anterior and posterior orifices of the alimentary canal, and their formation is always accompanied by an ingrowth of ectoderm towards the endoderm. One or other of these apertures may be formed in the place which was before occupied by the now obliterated protostome, or in some cases the latter may itself remain persistent as one of the secondary orifices.

We may now pass to the consideration of the third essential forward step in development. This is the separation or segregation of some cells from either one or both primary layers to form an intermediate set, which acquires greater proportional importance the further upwards we trace it in the scale of organisation. Since the cells of this intermediate set in most cases, and certainly in typical ova, are not of independent origin, but are derived indirectly from one or other of the two primary layers, it is clearly a mistake to regard the layer which they form as of equal importance with the other two—an idea which is distinctly implied by the name "mesoderm" usually given to it. The two primary layers—the "foundation membranes" of Huxley; "ectoderm and endoderm" of Allmann—are distinct and well defined. The so-called mesoderm is often very different in these respects, so much so that in some animals parts which are looked upon as mesodermic by some morphologists are regarded as still belonging to the two primary layers by others.

This mistake of regarding the mesoderm as of equal morphological importance with ectoderm and entoderm has originated in the study of the development of the higher animals, in which, in many cases, the relative time of its origin has become shifted, so that it may begin to appear almost simultaneously with the primary layers. And even in some animals, not very high in the scale, the same shifting may be found. Thus, for example, in the Holothurian, the separation of some of the ectoderm cells to form part of the intermediate or mesodermic set has already begun, even before the commencement of invagination, and, therefore, whilst the general development has not advanced beyond the blastophere stage. And the same shifting is carried to a still greater extent in Clepsine, where we find that even when the cleavage of the ovum has advanced but a step or two, certain portions are separated to produce, as the cleavage process continues in them, the whole of the mesoderm. In this case, then, the third stage has begun almost as soon as the first stage itself.

This premature separation or precocious segregation (Lankester) of parts which analogy would lead us to expect later is a very common feature in animal development. It is illustrated in Clepsine in a still more remarkable way, in the premature separation of the portions of the dividing ovum from which the cells of the nervous system are derived. And it is on account of this tendency which the phases of development exhibit to become shifted to periods earlier than usual for their appearance that I have compared them to the tubes of a telescope, for we can so much the better illustrate them in their relations to one another. Thus, in the case of the Holothurian, we should shift the third tube representing the formation of the mesoderm downwards, so as to overlap the second one representing the gastrula, and in the case of Clepsine so as almost to reach the base upon which the telescope rests.

II.

At the end of the previous lecture we had arrived at the consideration of what we, for convenience, regarded as the third stage in the developmental staircase, the third tube in the developmental telescope—the formation, namely, of the mesoderm; and I insisted that the term is a misnomer, because it obviously places itself side by side in the mind with the names which have long been applied to the two primary layers, "ectoderm" and "entoderm," whereas it is secondary to these, being derived from them. The mesoderm consists, in fact, of cells which have been separated or segregated from amongst the cells of the primary layers for the performance of special functions. In the lowest animals in which such a separation occurs it may take place at any part of the primary layers, or even over the whole of their extent. We see this in the sponges and jelly-fish. In these, when intermediate cells are separated, they lie in a jelly-like substance, and the main purpose which the segregation subserves is that of support and connection. Now, it is obvious that this sustentacular function might be almost as well performed by the inert jelly alone—in fact, the soft protoplasm of the cells can be of but little assistance, so that we should naturally look upon the cells in this primitive mesoderm rather as ministering to the nutrition of the jelly than as agents in the performance of its function. This view is strengthened by observing that it is the intermediate jelly-like matrix of this primitive connective tissue which is the first to appear, the cells (when they do occur, for in many cases they are absent throughout life) wandering into it subsequently. In the larger Medusæ (Aurelia) they come, according to the testimony of most observers, from the entoderm; in the Sponge they are derived from the outer of the two layers which are found in the Olynthus stage—the one which is generally regarded as ectoderm.[1]

[1] There seems to be some uncertainty about the interpretation of the two layers of cells which are found in the Olynthus stage of development of the Sponge. According to the descriptions of various observers, and especially that given by F. E. Schulze with regard to *Sycandra raphanus*, the segmentation of the ovum takes place, and a blastosphere becomes formed much in the usual manner. Of the cells of this blastosphere those of one hemisphere are smaller clearer, and provided with long cilia, those of the other and lesser hemisphere being larger, more granular, and without cilia. Presently the latter become invaginated, but the cupping thus produced proves a temporary condition merely; fluid again accumulates in the cavity of the blastosphere and obliterates the cup-

Another proof, if one were needed, that the jelly is the primary and the cells which wander into it the secondary part of the purely sustentacular mesoderm of these lowly organised animals is to be met with in the fact that in some—*e. g.* Hydra and the smaller Jelly-fish—the jelly is the only part of the layer present. The nutrition of the jelly is administered directly by the entoderm cells.

We see then that in the lower forms the only function which is delegated to the intermediate layer is the mechanical one of support. But in all the higher animals the segregated mesoderm cells are deputed to perform other and more important functions as well, for, besides the connective and supporting structures of the body, the actively contractile tissues which are concerned in effecting the movements of the body are derived from them. In the Medusæ or jelly-fishes this function is still performed by a tissue which is undoubtedly part of the ectoderm, although at first sight it seems to constitute a distinct layer of cross-striped fibres beneath the ectodermal epithelium. For if these fibres are carefully investigated, it will be found that they are many of them placed in the interior of large cells which project to the

form. After a certain interval a more decided cupping again takes place, but this time it is the clear ciliated cells that are invaginated. This condition remains permanent. The cup-like sponge settles down and the orifice of the cup becomes closed; a jelly-like substance accumulates between the two layers of which the cup is formed, and cells pass into it from the outer layer; one or more canals become bored through the jelly so as to effect a communication between the cavity of the sponge and the external medium; and the sponge may be regarded as formed. Now it is generally assumed that the first cupping being temporary is a mere accident, and that the second represents the gastrula stage of other animals. If this is really the case there is of course no fault to find with the generally received interpretation which sets down the large cells of the ciliated chambers of a sponge as entoderm and all the rest of the sponge (viz. the flattened cells which cover the external surface and line the water-canals, and the general thickness of its jelly with its included branched cells), as ectoderm (and mesoderm). But it is difficult to avoid the thought that by ignoring the first cupping and setting it down as accidental or at least as unimportant on account of its transciency, an error may have been made and a divergent if not a retrograde process of development regarded as a normal and progressive one. It is admitted that the microscopic appearance of the ciliated hemisphere of the sponge-blastosphere is in favour of its being looked upon as ectoderm rather than entoderm, and conversely with regard to the non-ciliated hemisphere. The origin of the branched cells in the jelly from the non-ciliated cells is a fact pointing in the same direction. And although our knowledge of the physiology of the sponge is too imperfect to be of much service in deciding the question, nevertheless the vegetative mode of life which sponges exhibit would lead one to expect a proportionately increased entodermal and diminished ectodermal development.

If the conjecture thus sketched out is a sound one it follows that sponges, as compared with other animals, are turned inside out.

surface between the cells of the general layer of ectoderm, which covers the under surface of the umbrella, and they evidently belong to that layer. In other words, the deeper parts of some of the ectoderm cells are modified to form the muscular structures. In Hydra, according to the descriptions of Kleinenberg and Korotneff, this is still more clearly the case—in fact, almost all the large superficial cells of the ectoderm are thus modified in their deeper part, although the muscular development is less characteristic. Now, supposing these muscular cells of the jelly-fish, in place of remaining amongst the rest of the ectodermal cells, to sink deeper into the surface of the jelly, or even to become imbedded in its substance, they would then appear altogether distinct; and although originally derived from the ectoderm, would be reckoned as part of the mesoderm. This is, indeed, the condition which is actually found in many other Cœlenterates.

We have seen that in the lower forms of the Metazoa the cells of the intermediate layer are derivable from almost any part of the primary layers. But in all the higher forms the mesoderm is developed from one part only of those layers, and this part is very frequently close to the contracted orifice of the gastrula, at the place where ectoderm and entoderm pass round into one another.[1] And from this place of origin the mesodermic cells—consisting of those which are to minister to support, and those which are to minister to movement intermixed—spread out between the two primary layers. We see a typical instance of this in Paludina and also in Unio. Now, if we suppose that the segregation appeared first at one particular point at the margin of the protostome, and afterwards spread in all directions from that point, we can comprehend how bilateralism might have appeared as the result of the separation of mesoderm cells (accidentally ?) at one part only of the margin of the protostome. But whatever might have been the original conditions, the mesoderm as we now actually see its development, appears from the first in two halves, and bilateralism makes its appearance simultaneously with these.

Our third stage, then, such as we see it in all animals above the Cœlenterates,—the segregation, namely, of an intermediate

[1] If we agree with Haeckel in surmising that in the earliest stage of animal evolution in which the cup-form or gastrula appeared, the orifice functioned as a mouth, we can readily understand how it is that a general mesodermic cell-segregation should have tended to localise itself in the neighbourhood of that aperture. For this would probably, earlier than other parts, become the seat of special active functions; *e.g.* the opening and closing of the orifice or even the sucking in of aliment, such as we see occurring in the early embryo of the earth-worm.

set of cells from the entoderm and ectoderm, destined to subserve the functions of support and motion, and termed "mesoderm"—has in reality in all probability been produced by the coincident occurrence of at least two distinct segregations. Perhaps one of these, the muscular, is precocious, and has blended with the other, the sustentacular, which should have preceded it. If this is the case each of the two segregations should be regarded as constituting a distinct stage in development. But they are so completely blended in their origin in the higher animals that it is impossible to differentiate them.

There is no reason to suppose that the two layers into which the mesoderm subsequently splits, in animals in which a body-cavity, or cœlom becomes formed, have anything to do with this supposed primary double segregation of the layer. For the segregated cells are entirely intermixed as the mesoderm spreads; although they may afterwards become again partially separated in groups (for the constitution of muscles, cartilages, &c.), according to the function for which they are destined. The formation of the cœlom is a distinct forward stage in development, and is the first step in the direction of the formation of a circulatory system. The cells which bound both the cœlom and its offsets are in most animals segregated from the general mesoderm, and belong to the set of sustentacular cells, but in the Holothurian, according to the description given by Selenka (and also in Sagitta and Amphioxus as shown by Kowalewsky), they are derived directly from the entoderm of the alimentary cavity, and already before their severance from this, enclose a commencing cœlom. There is not sufficient ground for regarding these lining cells of the cœlom and vascular system as constituting a special segregation. In vertebrates they are certainly of the same nature as those of the sustentacular part of the mesoderm (the connective tissue), and the same is probably the case in the other animals where they are found.

Another well-defined forward stage in development is the occurrence of a special segregation of ectodermic cells for the performance of the nervous function. These differ from those which are destined for the muscular function in that they are never blended in their origin with the mesoderm, and indeed do not in any animal lose their primitive connection with the ectoderm until development is comparatively advanced, if even they do so then.

As in the case of the muscular segregation the first indication of a separation of some of the ectodermic cells for the performance of nervous and special sensory functions is met with in the Cœlenterata. This takes the form of a prolongation of the attached ends of some of the ectoderm cells into branched fibres, which interlace with those of neighbouring cells, and probably serve to convey any impressions received by the cells of which they form a part, to deeper lying muscular cells which have lost their place in the superficial ectodermal layer and their connection with the external medium.

The "nerve-epithelium cells" thus formed may themselves tend to sink below the general surface of ectoderm. If this happens they lose the characteristic shape of epithelium cells, and become rounded, with extensions in the direction of the nerve-prolongations. In fact, like the muscular tissue, they assume a minute structure which is similar to that of the nerve-cells and nerves of the higher animals. Nevertheless these nerve-cells in the jelly-fishes in no case separate themselves from the ectodermal layer. They lie, in fact, between it and the muscular layer in those parts in which the latter occurs.

And the sense-organs in this branch of the animal kingdom also show that their essential place of origin is from the ectoderm. For visual organs first make their appearance as patches of ectoderm-cells filled with coloured pigment, and some of them with nerve-fibre processes connecting them with adjacent nerve-epithelium cells; auditory organs as ectoderm-cells, containing crystals in their interior, and similarly connected; and olfactory organs as little pits lined by ciliated ectoderm-cells, and connected likewise to a nerve-epithelium.[1]

Amongst other animals we observe that in Sagitta also the segregation of ectoderm to form a nervous layer is in the first instance general and not localised. Eventually this segregation becomes accumulated mainly in two situations to form the cephalic and abdominal ganglia. In Amphibia, too, the separation of ectodermic-cells to form a nervo-sensory layer is at first general. But in most animals, *e. g.* the Earthworm, Euaxes, Ascidia, Amphioxus, the segregation in question begins at one part only of the edge of the protostome, as is the case with the mesodermic segregation—this situation having been possibly determined by the high functional importance of this orifice (assuming as before with Haeckel that it originally served as a mouth). Extending from this situation, the nervous separation would no doubt be chiefly guided by the arrangement of the pre-formed muscular segregation, and would hence tend to assume a bilateral condition such as we see it to possess.

[1] It is the opinion of Professor Claus that the depression which is seated above the base of each lithocyst in Aurelia and allied forms of Medusæ represents an olfactory organ. And the comparative researches of Drs. O. and R. Hertwig have rendered it more than probable that the otoliths of the jelly fish even when they appear, as in Aurelia, to be connected with entoderm alone, are originally derived from the ectoderm.

We also find that cells which are set aside for the sole performance of special functions invariably become modified in the arrangement of their living substance, and in some cases also in its chemical nature. The structural changes which thus accompany and indicate the assumption of any special function by cells, constitutes the science of histology. It would be carrying us too far from our immediate subject to enter into a detailed account of the nature of these structural changes here, so I will only point out two facts with regard to them. One is that the special modifications of structure which the cells assume, that have been set aside for the sole performance of special functions, are similar throughout the animal kingdom in all essential features. The second is that in the lowest types where they occur the structural characters appear before the segregation of the cells is complete, whilst on the other hand in the development of an individual belonging to the higher types such segregation may have been long effected before either the functions or the accompanying structural changes in the cells begin to be manifest; another instance of premature segregation.

We have thus far been speaking of the separation of special sets of the cells of which a simple organism is composed for the performance of special duties. But in the united or compound organisms, before considered, it very frequently happens that one or more of the units of which the compound body is composed becomes altogether specially modified for the performance of one duty to the exclusion of others. Thus we see that some of the individual buds, of which the compound organism of a hydroid polyp consists are adapted for purposes of prehension and alimentation, whilst others are adapted solely for reproduction. This localisation of function in the different buds of a compound organism is carried to an extreme degree in the Siphonophora—animals which on the whole resemble the hydroid polyps, but instead of being fixed to a rock at the bottom of the sea, float near the surface of the water, looking like strings of beautifully iridescent hyaline beads. In them we find the specialisation of individuals to have proceeded so far that whilst one of the innumerable individuals which have been produced by budding from the original single one, is set aside to perform the purely mechanical purpose of suspending the united colony near the surface of the sea, and is changed into a minute balloon enclosing a bubble of air; others are deputed to propel the organism through the water and become wholly transformed into so many pulsating bells; others again have merely to receive tactile impressions from objects in the external medium, and are chiefly metamorphosed into long feelers; others are occupied solely with the seizure and ingestion of victims for the food of the whole compound organism, and mainly consist of a stomach with a long stinging trailer appended; others have confided to them the reproduction of the organism; whilst all the more delicate of the thus modified individuals can shrink for shelter under certain other of the members of the colony which have degenerated into firm protecting scales. And in that higher type of compound organism which is characterised by serial instead of budding repetition, whole individual segments are often as distinctly set apart for the performance of a special function, although from their close union one with another it is generally difficult to trace such complete specialisation. The extensively found adaptation for prehensile and masticatory purposes of one or more of the anterior segments in so many of these organisms readily comes to mind as an illustration of this.

But let us revert to the consideration of the sets of cells which become segregated for special purposes from the primary blastodermic layers. Once formed they are found to proceed through stages of their own, varying in number with the extent of development of the organs which they compose in different animals. In one group of animals it will often be found that one or more such segregations have progressed in their functional, and correspondingly in their structural development much further than others. In illustration of this we may notice that in the Vertebrata it is the nervous segregation, in the Arthropoda the muscular segregation, which above all others has attained the greatest development. What mammal, for instance, is capable of the tenth part of the activity in proportion to its size, which is evinced by the sustained flight of the dragon-fly or the prodigious leap of the flea!

As an illustration of the progression in development of a special segregation, it will for our present purpose be most instructive if we trace out the early stages of formation of the nervous system in one of the highest types, and if we compare those stages with what we find in animals lower in the scale.

In the Toad, which we may select as a typical Vertebrate, there is at first a uniform layer of cells which is separated at an early period from the ectoderm; then a thickening of this layer occurs on either side of the axis of the embryo, extending forwards from the protostome, the two thickenings forming the boundaries of a groove which lies between them; we next find the groove becoming roofed over by upward extensions of ectoderm, both from behind the protostome and on either side, and thus converted into a canal which is at first open in front and communicates behind through the protostome with the alimentary cavity; next (or even before the roofing in is completed) we observe that the anterior part of the nerve-tube becomes enlarged and subdivided to form the primary parts of the brain, and finally, the wall of the tube becomes differentiated to form nerve-cells and nerve-fibres.

If now we compare these stages of development of the nervous system of the Toad with temporary or permanent conditions of the same system in certain animals lower in the scale, we are struck at once by the fact that the various stages described are more or less represented by those conditions.

Without again referring in detail to the mode of formation of the nervous system as a general segregation from the ectoderm, which is met with in the Medusæ and in Sagitta—for it might perhaps be accounted too bold to attempt a comparison between these and the earliest stage, that of general segregation, in the Toad—we find that in the Earth-worm the nervous system commences exactly as in the Toad, in the form of two thickenings of the ectoderm which extend forwards from the cup-orifice and form the boundaries of a shallow groove. But the development does not proceed further in the same way as in the Vertebrate, for the groove is never converted into a canal.

In the Ascidian we observe as the first stage in the development of the nervous system the formation of a neural groove, with its boundaries of thickened ectoderm—so far, as in the Earth-worm; but the development proceeds a stage further. The groove becomes gradually roofed in from behind forwards, forming a tube which long remains open in front and is traceable behind, through the protostome, into continuity with the alimentary cavity. But although the anterior extremity becomes enlarged, nevertheless the development of the nervous system in Phallusia turns aside from the Vertebrate road, and passes through a series of transformations which are special to the Tunicate type. Indeed these are of such a nature that the tubular character of the nervous system soon becomes no longer recognisable.

In Amphioxus exactly the same early stages are passed through; there is first the groove, then the enclosure of this to form the neural canal, open at first in front, and communicating with the alimentary cavity behind. But these apertures before long become closed, and the neural canal shut off as a distinct simple tube. In this condition it remains permanently, only that the walls of the tube become much thickened, so that the cavity is almost obliterated. Although there is no very apparent departure from the path which we have seen that the nervous system of the Toad takes in its development, nevertheless there is no further progression; the anterior enlargement to form the brain never appearing.

This brief sketch is sufficient to show that the various stages in the development of the nervous system of a Vertebrate are represented by transitory or even by permanent conditions of the nervous system of a series of animals lower in the scale of organisation. If we were to analyse in the same way the development of any other specialised segregation of one of the higher animals, we should find that exactly similar results would be arrived at. Did time and space allow, it would be easy to trace the correspondences of development in the case of the heart, of the central axis or notochord, of the branchial slits, of the renal organs, and so on. And if this correspondence of permanent conditions in lower animals, with stages of development in higher animals, is thus found to obtain to minute detail in the separate and specialised parts, it stands to reason that it must be found also in the aggregate which those parts compose. And indeed, in many cases, even in the mere matter of external form, the correspondence is often such as to strike the most ordinary observer. Compare, for example, the polyp stage of development of the jelly-fish with the permanent conditions of some of the Hydroid polyps; compare the Scyphistoma stage of Aurelia with the permanent condition of Lucernaria; compare the tailed larva of Phallusia with the permanent condition of Appendicularia; compare the several stages of transformation of one of the higher Crustacea with permanent conditions of the lower Crustacea; compare the various stages of the developing Amphibian with either transitory or permanent conditions of Worms, of Tunicates, of Amphioxus, and of lower Vertebrates!

In conclusion I will attempt to formulate as briefly as possible, some of the general results at which we are able to arrive from a consideration of the facts we have had before us:

I. If we compare the processes of development of any two animals, from Sponges upwards, we find complete correspondence up to a certain point; from which point they may diverge from one another. This point is sometimes placed near the bottom of the development-scale, sometimes near the top; or, it may be, in any intermediate position.

II. Development is essentially localisation of function and concomitant or consequent modification of structure; such modification being accompanied by segregation of the cells concerned with the function localised.

III. The path of development of all the more important of these segregated parts is the same up to a certain point in the development of each segregation. From this point it may, in any animals or group of animals, diverge from the rest; or may remain stationary, whilst in the others, specialisation and modification progress further.

IV. The various stages or phases of development of an animal, as well as of its specialised parts, are often found to correspond with either permanent or transient conditions of animals lower in the scale.

V. Since the phases of development of individual animals are often seen to be representations of the permanent conditions which are met with in a series of animals belonging to lower grades of organisation, it is impossible not to infer that these successive phases in the development of the individual represent similar phases in the process of formation or development of the race to which the individual belongs. To revert to a former simile, we may safely say that the developmental telescope of the individual is the same as that of the race, but with the tubes shortened or shifted one upon another so that in many cases their original order is no longer recognisable. The history of the development then of any individual animal from the egg it an abridgment of the history of formation in time of the race; or, to state the matter in as few words as possible, "developmens represents descent."

We conclude, therefore, that the ancestors of every animal have successively exhibited structural conditions which are represented in a more or less modified form by the successive stages of development of the individual. This is the only logical conclusion to which the study of animal development leads. Modifying slightly the words of Darwin I would say, "to take any other view is to admit that the structure of animals, and the history of their development, form a mere snare laid to entrap our judgment."