Sedgwick's Theory of the Embryonic Phase of Ontogeny as an aid to Phylogenetic Theory.

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In a recent number[1] of this Journal there appeared a paper by Mr. Adam Sedgwick on the significance of the embryonic phase in development, which embodies a principle which, if true, seems to me well fitted to throw light on some obscure problems in morphology.

It is not the object of the present essay to discuss the correctness of Mr. Sedgwick's views, but rather, assuming them to be true, to point out some of their consequences.

These views may be briefly stated as follows. Making a broad survey of the facts of ontogeny, we find that there are two main types or phases of development—the larval and the embryonic. In the former case the immature organism pursues a free life, engaging in the struggle for existence; in the latter case the developing animal is shut off from the influence of external conditions, either inside an egg-membrane or in the uterus of the mother; but in both cases it is relieved from the necessity of having to seek its own living, since nourishment is provided for it either in the shape of food-yolk or fluid nourishment exuded from the uterine walls.

In many cases the whole course of the ontogeny of an animal

[1] "On the Law of Development commonly known as von Baer's Law; and on the Significance of Ancestral Rudiments in Embryonic Development," Quart. Journ. Micr. Sci.,' April, 1894.

is embryonic, but in every case larval development is preceded by a longer or shorter period of embryonic development.

The whole interest of the science of Embryology lies, of course, in the fact that features observed in both types of development seem inexplicable except on the assumption that they are reminiscences of structures possessed by the ancestors of the animals in whose development they appear. Such traces of the history of the race are to be found in the vast majority of larvæ; in embryos they are likewise to be found, though here they are less prominent, as is seen by comparing the development of two allied forms, in one of which the larval type prevails, and in the other the embryonic. Now Mr. Sedgwick's theory of the relation of the two types to one another is that that portion of embryonic development in which ancestral features are observable represents a larval stage passed over inside the uterus or egg-membrane and modified in consequence. Thus the chick during the first four or five days of its existence is to be regarded as an immensely modified larva.

If this view be true it follows that, however modified the record of ancestral history contained in the larval development may be, the embryonic record of the same history can never rise above it in value.

It was until lately customary to assume, explicitly or implicitly, that there was an inherent tendency for the ontogeny of the individual to be a summarised repetition of the phylogeny of the race. In proof of this statement we may adduce Balfour, who in his 'Text-book of Comparative Embryology' (vol. ii, p. 298), says, "Unless secondary changes intervened this record [of ancestral history] would be complete;" and Bateson,[1] in his discussion of the ancestry of the Chordata, commits himself to a similar position. That there can be no such general tendency is, however, shown by the fact that in

[1] "The Ancestry of the Chordata," W. Bateson, 'Quart. Journ. Micr. Sci.,' 1886. "Development within an egg-shell as involving a less complicated struggle with enviromental forces, is less subject to variation than that in the open sea, and consequently is more likely to preserve ancestral features."

bud ontogeny there is no trace of anything which can be interpreted as ancestral structures, and that some most striking and recent changes, such as the loss of limbs in snakes or the reduction of the toes of the ostrich to two, are not recorded in embryology, i. e. the organ concerned shows from its inception the adult arrangement.

How then does the theory we have adopted account for the retention of ancestral characters by larvæ?

So far as we can judge by comparative anatomy, the stimuli to evolution (in the sense of change of structure) have been two, *viz.* (1) change of environment and habits, and (2) increased or decreased demands on the working of certain organs. As we therefore pass along a series of genetically connected animals, we should find, pari passu with the environment and the functional demands of the organism, the structure changing. If these stimuli commenced to act from the beginning of free life, then each individual adult in the chain would show from the beginning the modified structure belonging to it; but if these stimuli were deferred in their operation till the animal had attained a certain size, then what was before a uniform life-history would become differentiated into two periods—a larval during which the ancestral habits were retained and the structures corresponding to them, and an adult in which new habits were assumed and structure correspondingly modified.

An illustration will make this clear: if young flat-fish when they emerge from the egg were at once to adopt the adult mode of life, then that most interesting larval stage, in which they are bilaterally symmetrical, would be missed out in their development.

Thus we see as a race of animals progressed from point to point in evolution, it would tend to develop a trail of larval stages, each grade of development surmounted being represented by a new larval stage intercalated in the ontogeny. This process, however, could not go on indefinitely; there would soon arise the tendency for the earlier larval stages to be passed over whilst still in the egg-membrane, and so a portion of the development would become embryonic, and so subjected to the various modifying influences which are connected with this type of ontogeny. Therefore it follows, as the first important deduction from Sedgwick's theory, that in seeking to obtain a basis for phylogeny, most importance must be attached to animals which show long larval histories.

Balfour with his usual sagacity has, so to speak, instinctively anticipated this conclusion. Although he points out that "the favourable variations which may occur in the free larva are much less limited than those which can occur in the fœtus," he says that there is "a powerful counterbalancing influence tending toward the preservation of ancestral characters, in that larvæ are compelled at all stages of their growth to retain in a f u n c t i o n a l s t a t e such systems of organs at any rate as are essential for a free and independent existence" ('Comp. Emb.,' vol. ii, p. 299).

The objection, alluded to in Balfour's statement, that larvæ as well as adults have been subjected to the modifying influences of their environment, will readily occur to most minds. Let us consider whether it is possible to approximately estimate the nature and amount of such influences; and, first of all, let us consider what is meant by secondary larvæ.

Balfour imagined that secondary larval forms might be produced by a diminution in the food yolk, and consequent earlier commencement of free existence (loc. cit., p. 300). There is no evidence to suggest that such a change has ever taken place; all the facts point in a contrary direction. We shall see that food yolk produces the most diverse distortions of development; the developmental processes of free larvæ are, on the other hand, remarkably uniform. Secondary larvæ must be regarded as having arisen owing to the young adults having taken to a new mode of life; the best instances of this are perhaps the aquatic larvæ of the may-flies and dragon-flies. We have the strongest reason for believing that the immediate ancestors of insects were terrestrial animals, and the aquatic larvæ mentioned show their secondary character by the fact that their respiratory organs are modified from organs adapted to air breathing. Their "tracheal" gills, instead of like all other gills bringing the blood into close proximity to the water, bring their blood first into contact with air contained in a system of closed tubes, and then this air into contact with the water.

In the case of ordinary larvæ, the probability of modifications due to adaptation to the environment cannot be denied. If, however, Sedgwick's hypothesis is correct that "larval history is constructed out of ancestral stages," or, in other words, that the larva retains ancestral characters *because* it retains the ancestral mode of life, then the environment has remained to a large extent constant (at any rate in the commonest case, that of pelagic larvæ), and the changes they are likely to have undergone, instead of being, as Balfour supposed, unlimited, will be comparatively few in number.

Of these changes reduction in size is the most important. The passage to the adult state is often accompanied by the loss of larval organs, and great changes in those which are retained, necessitating in some cases the complete destruction of their constituent cells, and their reconstruction from rudiments which have retained the embryonic condition (histolysis). It is, therefore, clearly to the advantage of the larva to grow no larger than necessary before it undergoes metamorphosis. Correlated with this loss of size is the frequent disappearance of all traces of segmentation, since this is probably to be regarded as essentially the same phenomenon as vegetative reproduction, only held in check by the individuality of the whole. Metameric series of organs are represented only by those members which are absolutely necessary. Another change which larvæ are prone to undergo, is the acquisition of transparency. What results this carries in its train will be mentioned below. Finally, the occurrence of long spines is a widespread phenomenon, though what their precise use is it would be rash to surmise. Possibly they are of a protective nature.

Let us now apply these principles in a concrete case, for example the larvæ of the Crustacea.

The characteristic larva of the Entomostraca is the well-known Nauplius, which shows no signs of segmentation. We have however from comparative anatomy, strong reason for believing that the ancestor of the Crustacea was segmented, and that it was probably related to the Polychæta. How is this apparent contradiction to be explained? We answer that the Nauplius retains the ancestral habits of Crustacea, and with this a certain necessary amount of ancestral structure; but it has diminished in size and external segmentation has disappeared. Since in the ancestor locomotion and prehension of food were effected by one or two pairs of anterior appendages only, we have these alone represented in the Nauplius, though the ancestor doubtless possessed in addition a series of segments bearing undifferentiated parapodia-like appendages. The complete disappearance of these is a mark of the high specialisation of the larva; if we compare the various families of the Entomostraca with one another, we find that in the primitive group of the Branchipoda, the Nauplius shows indications of a postoral segmentation; whereas in the highly specialised Cirripedes and Ostracods we get a specialised Nauplius. In the former case this is brought about by the outgrowth of great spines, in the latter by the precocious appearance of the adult bivalve shell, and in neither instance is there a trace of segmentation.

The larva of the Malacostraca the Zoæa, has been a great puzzle to morphologists. It is quite impossible to regard some of the peculiar features, such as the suppression of the thoracic segments and their appendages, as ancestral, and the question has been raised by Claus,[1] whether it has any phylogenetic significance at all.

Applying Sedgwick's principle, we explain the Zoæa as representing a later ancestral stage than the Nauplius, in which some of the Nauplius appendages had become exclusively masticatory and others exclusively tactile in function; the main locomotor function had been, so to speak, passed on to the two or three pairs of maxillipedes, which are

[1] L. Claus, "Zur Kenntniss d. Malakostrakenlarven," 'Würz. Naturw. Zeitschrift,' 1861.

always large and biramous, whilst at the same time some of the most posterior segments have been modified to form a powerful jointed "tail." The thorax retained its primitive character, and is accordingly suppressed in the larva; though here in comparing the Zoææ of the various groups we meet with a precise parallel to the case of the Nauplii. The Zoæa of the undifferentiated Schizopod possesses only one pair of maxillipedes, and even they are short and somewhat foliaceous, but it shows a distinct segmentation of both thorax and abdomen. Still more instructive are the larvæ of the lower families of the Decapods, the Sergestidæ and Penæidæ. Taking Penæus for example, we find that it escapes from the egg-membrane as a Nauplius: it gradually changes to a Zoæa with two pairs of maxillipedes and the thorax distinctly segmented and with rudimentary appendages; this passes into a form with thorax well developed and all its appendages biramous—the so-called Mysis-stage, closely resembling the adult Schizopod,—and from this it passes to the adult state. On the other hand, in the highly specialised Brachyura we find a highly specialised Zoæa, in which the thoracic segments are totally suppressed and the thorax prolonged into great spines, the Mysis-stage is dropped but a new "Megalopa"-stage is introduced, which strongly recalls the Macrura, and may be taken to indicate a Macrurous ancestor. The existence of the Megalopa and Mysis stages, the significance of which is obvious, affords the strongest reason for maintaining the ancestral significance of the Nauplius and Zoæa stages; in doing so one merely follows the universal rule of science, i. e. reasoning from the known to the unknown.

Turning now to the embryonic type of development, let us examine the causes which are likely to modify a course of development which is primitively larval. First we must discriminate between various kinds of embryonic development. There is, in the first place, the type in which the organism is confined within the egg-membrane and supplied with nutriment by means of yolk stored up in its cells. Secondly, we have cases in which the embryo, still remaining in the egg-membrane, is retained in the body of the mother, the egg being closely applied to the uterine wall, from which nourishment is obtained, and the yolk having consequently in large measure disappeared. Thirdly—a much rarer case,—a number of eggs are enclosed together in a capsule and only one develops; the eggs destined to be eaten being known as yolk cells. As a less extreme case we have the eggs all developing up to a certain stage, but only a few surviving. This condition is seen in Prosobranch Mollusca. Lastly, we may mention those cases in which the uterus or other brood-pouch of the mother is used, so to speak, as a nursery for the larvæ, the embryos escaping from the egg-membrane, and passing the earlier part of their existence as free-swimming organisms inside the brood-pouch.

Taking the first case, which is by far the commonest, the disturbances of development which are found in it are due to two main causes—yolk and the egg-membrane. It is owing to the cramping influence of the latter that external differentiation of form is to a large extent lost. The gastrula of Asterina gibbosa, for instance, is almost spherical, contrasting thus with the common form of Echinoderm gastrula, which is more or less elongated. Where the egg is enclosed in a roomy capsule, on the other hand, as in the Pulmonata, this is less frequently the case; for instance, we have the velum of Limnæus and Planorbis. Mere disuse will not suffice to account for the disappearance of external organs, as in this case all traces of ancestral history ought to disappear in internal as well as external organs, and this is not the case.

The presence of food yolk exercises the most distorting influence on development. To Lankester[1] is due the credit of first laying emphasis on this. In treating of the development of Mollusca he points out that the question whether the endoderm is represented by many or few cells, and whether, consequently, these are invaginated to form the gut, or whether the ectoderm grows over them, is entirely determined by the amount of yolk present. Balfour, who had almost at the same time instituted a

1 "On the Invaginate Planula or Diploblastic Phase of Paludina vivipara," E. Ray Lankester, 'Quart. Journ. Micr. Sci.,' vol. xv, 1875.

similar comparison between the segmentation of the eggs[1] of vertebrates, subsequently put forward the thesis,[2] based on a comprehensive survey of the facts of embryology, that the rapidity of segmentation of a given region of the ovum is inversely proportional to the amount of yolk contained in it.

The general effect of the presence of yolk, therefore, when massed specially in the endodermic end of the ovum, is to impede cell division, and render processes of development which depend on folding (e. g. invagination) impossible.

There is, however, another manner in which yolk can be accumulated, and that is in the more central portion of the ovum, instead of at one end. This is characteristic of the Arthropoda. When it is comparatively moderate in quantity, as in the case of Lucifer, segmentation and invagination can proceed normally, though the number of cells composing the blastosphere is small. When it is somewhat greater in quantity, as in Branchipus, segmentation at first proceeds normally, but soon the inner yolky ends of the blastomeres fail to be governed by the rapidly increasing nuclei, and segmentation only affects the outer layer of the egg, the inner ends of the first formed blastomeres fusing together to form a central yolky mass. In most Crustacea the yolk is so large in quantity that only superficial segmentation is possible from the beginning. Invagination of this outer layer to form the gut still occurs in some cases, the yolky mass being pushed before it; but, since the yolk is eventually absorbed by the endodermic cells, even this soon ceases to be possible, and we reach eventually a condition in which the segmentation and first processes of development recall to a certain extent those found in telolecithal eggs when the yolk increases to such an extent as to prevent segmentation at the endodermic pole at all (meroblastic eggs). In the scorpions and insects segmentation in its earlier stages is totally suppressed, and represented merely by the multiplication of nuclei; and in the later stages segmentation only occurs where developing organs require it, and thus a mimetic meroblastic segmentation is produced.

[1] 'Quart. Journ. Micr. Sci.,' 1875. [2] 'Comp. Emb.,' vol. i, p. 121.

The second type of embryonic development, viz. that in which the egg is applied to the uterine wall, is characterised by the reduction of the food yolk, so that the segmentation reverts to the total type. Sharply marked traces, however, of the former presence of yolk remain. The gorging of the endoderm with yolk has rendered the archenteron functionless, and as it still remains functionless when the plan of absorbing nutriment from the uterus through the general surface is introduced it is deferred in development, and in fact the destiny of the first products of segmentation is totally different in Mammalia from what it is, for example, in Echinoderms.

In the third type of embryonic development, in which the ovum is enclosed in a capsule with a number of yolk cells, the most weird changes are produced in development. We read of a complete separation and subsequent reunion of the blastomeres for instance; this type is almost confined to the Platyhelminths, and is alluded to here only for the sake of completeness, and to show how few traces of ancestral history the development of these animals affords. One family only, the Dendrocœla, lay their eggs singly, and in this case we have a large amount of food yolk present; yet Platyhelminths have bulked largely in many phylogenetic speculations.

Lastly, we have those few cases in which the developing animal escapes from the egg-membrane, but remains in the uterus or brood-pouch. In these cases we have comparatively little interference with the normal course of development. The early stages occur in a perfectly regular manner, and we have, in fact, free-swimming larvæ within the brood-pouch; it is only in the later stages that they commence to absorb fluid from its walls. It is necessary to emphasise this type of development, though it is comparatively rare (Brachiopods, Paludina, and Amphiura squamata) because if it is confounded with the foregoing types, its totally different characteristics would seem quite inexplicable.

I ought perhaps to mention that the earlier stages of Amphiura squamata are described as being abnormal by

Russo,[1] but neither the figures nor the methods of this author are calculated to inspire much confidence. These earlier stages are very difficult to obtain, but I have strong reason to suspect from those which I have seen, that the earlier development follows the ordinary Echinoderm type.

Having thus rapidly reviewed the principal disturbing factors in embryonic development, we can employ our knowledge in attacking one of the most vexed questions in morphology, viz., the significance of the mesoderm and its contained cavity the cœlom.

Is the former to be regarded as a differentiated portion of the gut-wall, and the latter as a portion of the enteric cavity, or is the cœlom to be regarded as a mere enlargement of the cavity of the gonad as Hatschek[2] has suggested?

In all Annelids and all Mollusca (Paludina and Cephalopods excepted) the mesoderm first appears as two symmetrically situated large cells—the primary mesoblasts. In Paludina, Echinodermata, Sagitta, Brachipoda, and Amphioxus, it arises as one or more pouches of the gut. Now, leaving out of account Anthropods, Vertebrates and Cephalopods, where the development has been complicated by the enormous amount of yolk present, we find that of the other groups the Echinoderms have by far the most prolonged larval development. They are unique amongst the Cœlomata in the fact that the blastosphere is a free-swimming larva, and that consequently the development of both endoderm and mesoderm takes place during their free-swimming life. Here, then, we may on our hypothesis expect to find ancestral structure preserved, and here we find that the cœlom is developmentally a part of the archenteric cavity.

No Annelid or Molluscan larvæ commence free life so early; most of them may be ruled out at once for the purposes of this comparison, since the disturbing presence of yolk shows itself plainly in the fact that the endoderm is represented by a few large spheres, and the production of a pouch has become

[1] Achille Rosso, "Embryologia d' Amphiura squamata," 'Rendiconti della Società Reale di Napoli,' tome vii (2nd series).

[2] 'Lehrbuch der Zoologie,' 1891, B. Hatschek.

an impossibility. A few Annelid eggs have, however, very little yolk, and the larvæ commences a free life in the gastrula stage.[1] Even here, however, if the blastosphere be compared with that of an Echinoderm, one is struck at once by the comparatively small number of cells it has, and one understands why the mesodermal rudiment should be represented by a single cell. The small number of cells is doubtless due to the comparatively large quantity of yolk, even if it be fairly uniformly distributed. This is probably, however, not the only reason why the cœlomic gut pouch is not found in the Annelid larva. If we compare Echinoderm larvæ with one another, we find that the blastocœle or segmentation cavity and the cœlom vary inversely with regard to one another. Thus in the creeping larva of Asterina the cœlom is very spacious, and the blastocœle reduced to a mere slit; in the pelagic larva of Asterias, on the other hand, the blastocœle is exceedingly large, and the cœlom has the form of two narrow tubes the lumen of which is in parts occluded. A similar comparison can be made between the ordinary Tornaria larva of Balanoglossus and Bateson's larva. The reason of this difference is not far to seek. It is to the over-development of the blastocœle with its contained jelly that pelagic larvæ owe that transparency which is so invaluable to them; hence the great development of the blastocœle in pelagic larvæ and consequent feeble development of the cœlom.

Now whatever may be the functions of the cœlom in Echinoderms, in Annelids its main functions are excretion, and the production of the sexual cells. Of these the first is performed in the Trochophore (the characteristic Annelid larva) by the so-called protonephridium, and the second has, of course, no place in larval economy. Hence, if we regard the Trochophore as bearing somewhat the same relation to the Echinoderm larva as the Zoæa of the crab does to that of Penæus, we see why the cœlom should have been entirely suppressed and the mesoderm represented only by a few large cells.

[1] Compare figures given in Korschelt and Heider's 'Lehrbuch der Vergleichende Embryologie.'

Thus the cœlom appears to be, phylogenetically, simply a differentiated portion of the archenteron; when the lumen of the latter is small, and its walls are composed of only a few large cells, the mesodermic walls of the cœlom are represented by a single large cell on each side.

A little consideration will throw light on the reason why what we see to be probably the primitive mode of development should appear in Paludina Brachiopods and Amphioxus. In all these cases the yolk is exceedingly small in quantity and uniformly distributed; in the first two cases we have a pseudo-embryonic development—the fourth type mentioned above,—and of course in this case there are no pelagic conditions to require a suppression of the cœlom. Amphioxus has a long larval history. Sagitta, on the other hand, pursues a true embryonic development within the egg-membrane; but the yolk appears to be quite uniformly distributed, and hence its primitive character.

A second vexed question which naturally follows directly on that of the origin of the mesoderm, is the origin of the endoderm, and consequently of the gastrula itself. Echinoderm development suggests the idea that the ancestral form of metazoon was a sphere of ciliated cells, and that the archenteron arose through the specialisation of a portion of the surface of the sphere to fulfil digestive functions and its invagination into the anterior. This is the view adopted by Korschelt and Heider;[1] and it is, of course, the famous gastræa hypothesis of Haeckel.[2] On the other hand, contrary opinions have been put forward by Metschnikoff,[3] Lankester,[4] and Sedgwick.[5]

[1] 'Lehrbuch der Vergleichende Embryologie,' vol. i, p. 81. Heider showed experimentally that carmine granules were swept by the cilia to the posterior end.

[2] Haeckel, 'Studien der Gastraea Theory,' Jena, 1877.

[3] El. Metschnikoff, "Spongiologische Studien," 'Zeit. für wiss. Zool.,' Bd. xxxii, 1879.

[4] E. Ray Lankester, "Notes on Embryology and Classification," 'Quart. Journ. Micr. Sci.,' vol. xvii, 1877.

[5] A. Sedgwick, "The Development of the Cape Species of Peripatus, pt. iii," 'Quart. Journ. Micr. Sci.,' vol. xxvii, 1887.

Metschnikoff starts, like Haeckel, from the blastosphere or blastula as an ancestral form; he supposed it, however, to have become filled up by cells wandering in from the periphery. In the midst of these a digestive cavity was later developed, and finally the mouth was formed by the specialisation of the area through which food was taken in. Lankester, starting from the same form, supposes the inner ends of the cells of the blastula to have become differentiated so as to be specially digestive in function, and later that they became separated off as a special layer. The cavity of the blastosphere was thus the digestive cavity, and food at first taken in over the whole surface, was later taken in only at one point, and thus a mouth was formed.

Sedgwick, on the other hand, is inclined to start from a protozoon in which cell territories were non-existent, though many nuclei were present. He supposes that the gut originated as a digestive vacuole, and that the nuclei acquired a definite arrangement with regard to this vacuole and other organs, and thus tissues were constituted. Cell territories, in so far as they exist in the adult, he regards as due to secondary rearrangement of the protoplasm.

We have already pointed out that Echinoderm development tells strongly in favour of the view supported by Haeckel and Korschelt and Heider, and that Echinoderm development, from its almost exclusively larval character, is of the very greatest importance in deciding such a question. Its evidence is by no means solitary; the statement may be made that, in all Cœlomata without exception, when the yolk is feebly developed and evenly distributed we find the embryo pass through a blastula stage which is converted into a gastrula by invagination (cf. Leucifer among Crustacea, Polygordius and Serpula and many others in Annelids, Paludina and Chiton in Mollusca, Amphioxus and Cyclostomes in Vertebrata, &c.). The groups which constitute the chief support of Metschnikoff's theory are Sponges and Cœlenterata. We may leave the first entirely out of account, as it is quite possible that they constitute a distinct phylum to the rest of the Metazoa. In many Cœlenterates we start from a blastosphere, which is in some cases a free-swimming larva. This blastospere, however, becomes filled up by cells which wander in from the external layer; in most cases this seems to take place from one end of the somewhat elongated blastosphere, and in Aurelia this process is replaced by invagination. Now the important point to notice in these larvæ is that during their free-swimming life the gut is functionless; and this accounts for the fact that it is represented by a solid rudiment. A precise parallel to the difference between the endoderm of the Cœlenterate and Echinoderm larvæ may be found amongst the larvæ of the Ectoproct Polyzoa. In the pelagic larva of Membranipora (Cyphonautes), which has a long free-swimming life, we find a perfectly well-developed gut with mouth and anus; on the other hand, in the larva of Alcyonidium we have a stomach of yolky cells, an almost occluded œsophagus, and no intestine, whilst in that of Bugula the whole mesoderm and endoderm is represented by a solid mass of cells. These larvæ are developed from yolky eggs and take in no nutriment during their free life. I hold, therefore, that Heider[1] is perfectly justified in his statement that the ancestor of the Cœlenterata was "a ciliated, oval, free-swimming form, in which by invagination at the posterior end an archenteron was formed."

Lankester's view finds its chief support in the development of Geryonia. In fact, this form is the only known one in which such a process as he supposes to have taken place in the blastula ancestor appears in the ontogeny. Are there any reasons for regarding the development of Geryonia as specially primitive? I think we may fairly say none; but that on the contrary it shows manifest signs of its secondary character; the egg is yolky, and the development proceeds directly to the medusa form, the hydra form being suppressed. The most conclusive argument, however, against Lankester's hypothesis is that on his assumption the cavity of the blastosphere is identical with the cavity of the future gut. Now all recent investigations have gone to show that the blastocœle is the rudiment of the

[1] 'Lehrbuch der Ver. Emb.,' vol. i, p. 81.

blood system, and has no connection with the gut whatever. In many Cœlenterates the stage of the hollow blastosphere is missed out, and segmentation results in a "morula" of which the external layer is the ectoderm and the rest endoderm. I think we must imagine that in the development of Geryonia the shortening process has gone one step further, and that as a result of segmentation we reach at once the stage of the hollowed-out planula.

Sedgwick's hypothesis was suggested from a study of the embryos of Peripatus capensis. Their developmental history is, however, the very last place where one ought to seek for indications of the ancestral meaning of the earlier stages —at any rate if Sedgwick's own hypothesis as to the significance of the embryonic phase be correct. All species of Peripatus so far as is at present known are oviparous; in Peripatus Novæ-Zelaniæ, however, the eggs are large and yolky, and the development conforms to the ordinary centrolecithal type so characteristic of Arthropods—the peculiarities of which we have described above. In Peripatus capensis nutriment is supplied by the wall of the oviduct, and the yolk has in large measure disappeared, at any rate its more solid portions; but the development still bears the impress of centrolecithal segmentation, i.e., in the imperfect definition of the blastomeres. It is obvious one might with equal justice expect to find information as to the character of the ancestor of Metazoa in the eggs of mammals.

Let us now briefly rehearse the conclusions to which the foregoing discussions seem to point. The earliest well-marked larval stage which we have discovered is the blastula—a sphere of uniformly ciliated cells. This "animal Volvox," as Huxley[1] calls it, may be regarded as a protozoon colony, not in the sense of consisting of independent units any more than does Volvox, but rather in the sense of being built up by the repetition of a unit as a result of what Lankester[2] calls "eumerogenesis," just as is the colony of a Hydromedusan. At first all

[1] 'Anatomy of Invertebrates,' p. 678.
[2] Art. "Hydrozoa," 'Encycl. Brit.'

elements in the blastophere were alike in structure and function. Later, however, coincidently with its acquiring the capacity for moving in a definite direction, a change would take place: the form first became elongated, and it is interesting to observe that the free-swimming blastulas of both Echinocyamus and Eudendrium have this form; then the cells at the posterior end, being least favorably situated with regard to promoting the locomotion of the colony, and best situated for seizing food particles, since they are in a kind of backwater from the eddies produced by the ciliary motion of the rest, would become specially digestive; increase in their number could only take place coincidently with invagination if the form of the colony were to be preserved and at the same time the digestive cells were to remain in contact with the surrounding medium—and thus we have the archenteron formed. The cells at the anterior end, on the contrary, are in the best position for receiving stimuli from the outer world; and here we should expect the first sense-organ to appear, and it is just at this spot that we find the larval sense-organ of Comatula with its associated nervous tissue, and the still more primitive sense-organ of the Echinocyamus larva, this latter consisting of a thickened patch of ectoderm bearing stiff cilia, which take no part in locomotion. In the same place the apical plate or larval brain of the Trochophore is found, also bearing cilia or more probably sense hairs.

Metschnikoff's[1] great objection to regarding invagination as the primitive method of forming the endoderm was that the blastopore sometimes became the mouth and sometimes the anus. Sedgwick's suggestion, however, that mouth and anus were differentiated from a slit-like blastopore, seems to answer this difficulty. That a slit-like opening can be represented by two independent perforations is shown by Echinoderm development. Thus in Holothurians the larval mouth by a shift of position becomes the adult; in Asterids and Echinids, on the other hand, it is represented by a totally new perfora-

[1] "Vergleichend Embryologische Studien. (3) Über die Gastrula Einiger Metazoen," 'Zeit. für wiss. Zool.,' Bd. xxxvii.

tion. No one can suppose that the ancestral form gave up its old mouth and developed a new one; the change was one of size and relative position only. We must assume that the original mouth was a wide one, and that part is utilised by the larva and aborted in the adult.

The cœlom, as we have seen, arose as a specialised portion of the gut.

It is to be observed that the history we have just sketched is in accordance with that rule which seems to hold in all cases where we can by means of comparative anatomy show with reasonable probability that evolution has occurred, viz. that new organs never arise de novo, but by the differentiation of older organs. This rule seems, however, to me to be violated by supposing that either archenteron or cœlom arose as a split in a solid mass of cells. The history affords also an explanation of that rigorous separation of primary and secondary body cavities, the blastocœle or hæmocœle, and the cœlom, which all recent research has tended to emphasise. The first is, in fact, morphologically inside and the second outside the primitive blastosphere.

Lastly, the conception of the primitive metazoon as a colony of Protozoa is in accordance with that repetition of similar parts on which Bateson[1] has laid so much stress as one of the most marked characteristics of living things. We should recall also the high individuality acquired by colonies of Siphonophora, Polyzoa, and Ascidians.

[1] 'Materials for the Study of Variation,' W. Bateson, Cambridge, 1890.