(Dr. Wiegert) regards Unna's "Pockenkörper" only as serving to separate the vesicles from the rete Malpighii, and thus to properly enclose them, "zur Abkapselung dient." In addition, Dr. Wiegert thinks that Dr. Unna's "Pockenkörper" is found only at the periphery of the pustule. I need hardly remind the reader that, according to our description above, I fully agree with Dr. Weigert's interpretation; and I would only mention that Auspitz and Basch (quoted by Dr. Neuman in his 'Textbook of Skin Diseases,' translated by Dr. Pullar, London, 1871, p. 74) knew the condition of human smallpox when "the pustular contents are enclosed, as if by a capsule, by two layers of unnucleated epidermic cells."

NOTES *on the* EMBRYOLOGY *and* CLASSIFICATION *of the* ANIMAL KINGDOM: *comprising a* REVISION *of* SPECULATIONS *relative to the* ORIGIN *and* SIGNIFICANCE *of the* GERM-LAYERS.

By E. RAY LANKESTER, M.A., F.R.S., Professor of Zoology and Comparative Anatomy in University College, London. With Plate XXV.

I.—THE PLANULA THEORY.

Preliminary.—The object of the present essay is to give, in a concise form, the actual phase which those speculations have assumed, which I first put forward in an article entitled, "On the Germinal Layers of the Embryo as the Basis of the Genealogical Classification of Animals," published in the 'Annals and Mag. of Nat. Hist.,' May, 1873. The points of chief importance in that article were the indication of three grades of developmental complexity in the animal kingdom—the homoblastic, limited to the Protozoa; the diploblastic, reaching no higher than the Zoophytes or Cœlentera; and the tripoblastic, embracing all the higher animals which differ from the Zoophytes built up by the modification of two primary cell-layers, in the fact that a third cell-layer appears between these two, and gives rise to muscles, body-cavity, and blood-vascular systems. The precise origin of this third germ-layer, as well as its exact relation to body-cavity and hæmolymph vessels, was pointed to as a matter requiring further observation and consideration. Further, in this article it was shown that both the Diploblastica and Triploblastica, in the course of development from the egg, after passing through a "polyplast" condition, enter upon the Planula phase. The Planula was defined as a sac, the wall of which is composed of two layers of cells, an ectoderm and an endoderm. Such a Planula was presumed to be the common ancestor of all Diploblastica and Tripoblastica, the former of which retained its essential structure with small modifications, whilst the latter proceeded further to add the third layer and the hæmolymph system connected with it. The existence of an aperture leading into the cavity of the two-cell-layered Planula was not an essential feature of the ancestral form thus arrived at, for I was careful to insist, in the essay referred to, that the two-cell-layered Planula took its origin in the actual development of both Diploblastica and Triploblastica in two different ways, which I designated respectively "delamination" and "invagination." When the deeper or endodermal layer of cells arose by delamination from the inner face of a hollow polyplast, whose wall was formed by one primitive layer of cells, a closed two-cell-layered Planula was formed devoid of aperture, and subsequently a mouth was formed by a breaking through of the Planula's wall and an ingrowth of ectodermal cells. This mode of origin appeared to be confined to a few Zoophytes.

The invaginate mode of origin—in which a pushing in of the wall of a single-cell-layered sac gave rise to an internal cell-layer—appeared to be by far the commoner mode of origin of the two-cell-layered Planula, and in this case the cavity formed by the invagination and bounded by the invaginated endodermal cells is (for a time, at least) open to the exterior by the orifice of invagination. I pointed out in the essay, to which these remarks relate, that according to some observers this "orifice of invagination" persists as the mouth of the mature organism, whilst in other cases it closes up, and again in other cases becomes the anus. The difficult questions accordingly arose, Can the disruptive mouth of "delaminate Planulæ" be identical or homogenous[1] with the mouth persisting from the primary orifice of invagination? Is the latter kind of mouth identical or homogenous with the anal aperture of those organisms in which the orifice of invagination persists as anus? Must we regard the orifice of invagination as both mouth and anus, in fact as a "proctostom" or "oranus."

Professor Huxley, who in 1875 published some remarks on this subject ("On the Classification of the Animal

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[1] Homogenous = derived from one and the same ancestral source. See "On the use of the term Homology," 'Annals and Mag. Nat. Hist.,' 1870.

Kingdom," 'Quart. Journ. Mic. Sci.,' January, 1875, and article "Animal Kingdom," 'Encyclopædia Britannica'), adopted the view, to which he still adheres ('Anatomy of Invertebrates,' Churchill, 1877), that we may distinguish among the higher animals the "archæostomatous" from the "deuterostomatous," the first category including those in which the orifice of invagination persists as the mouth, whilst the second category includes those in which the orifice of invagination either disappears or becomes the anus, whilst a secondary mouth is formed by disruption. A further consideration of the subject and new observations led me, about the same time, to the conclusion (see "On the Invaginate Planula of Paludina," 'Quart. Journ. Micr. Sci.,' April, 1875) that we have no ground for assuming that such a substitution of a secondary for a primitive mouth has taken place, since it is very possible (and, indeed, probable) that the orifice of invagination of invaginate Planulæ is in its origin not a mouth at all, but simply the necessary accompaniment of the invagination, destined *normally* to close up, as do other orifices of invagination (optic and auditory vesicles, vertebrate nerve-tube). Accordingly, I proposed to speak of the orifice of invagination, by means of which invaginate Planulæ acquire their endoderm, as simply the "blastopore," leaving thus the question of its relations to mouth and anus open for further inquiry. The view as to the historical relations of delaminate and invaginate Planulæ which I was thus led to adopt amounted to this: that, starting from the condition of a hollow polyplast, a vesicle bounded by a single layer of cells, the second condition, viz. that of a vesicle with a wall formed by two layers of cells, could be attained in two ways—1. More rarely by delamination. 2. More usually by invagination, the blastopore or orifice of invagination *closing up*, and thus rendering the two Planulæ identical in every respect. From this point of reunion the two Planulæ proceed on a common path, mouth and anus, or in Zoophytes mouth only, being formed by new growth and disruption.

This preliminary sketch is sufficient to enable me to make clear the distinction between what I might, for the sake of a name, call my "Planula theory," and Haeckel's "Gastrula" or "Gastræa theory." Haeckel's speculations were first sketched out in his 'Monograph of the Calcareous Sponges,' and were published shortly before the article in the 'Annals and Mag. Nat. Hist.' above mentioned, though the substance of this article had been previously given in my lectures, and was in no way influenced by the closely similar doctrine enunciated by Haeckel. Since the whole of recent theory and inquiry as to the significance of the germ-layers of the embryo in relation to the pedigree of the animal kingdom is, in consequence of the interesting and vigorous writings of Professor Haeckel, commonly spoken of (in this country at least) as "Haeckel's Gastræa theory;" and since the distinctive points of a similar but independent theory are liable in consequence to be overlooked or misunderstood, I shall speak of the latter as the Planula theory, and point out what from the first has been the fundamental difference (coexisting with a fundamental agreement) between Hæckel's Gastræa theory and the Planula theory.

Objections to Haeckel's views.—The developmental and historic form which Haeckel's theory assumes, and to which he gives the name Gastrula or Gastræa, is similar to my diploblastic Planula, with this exception, that it has a mouth. Haeckel definitely regards the orifice of invagination or blastopore as the "Urmund," or primitive mouth, and in his most recent writings has unreservedly committed himself to the proposition that the ancestral Gastræa originated by invagination, that the orifice of invagination is the creature's mouth, and that those recorded cases in which the embryonic two-cell-layered sac is stated to arise by delamination are, like his own statements relative to the delaminate origin of the endoderm in calcareous sponges, cases in which observers have erroneously overlooked the invagination process. In my article of May, 1873, I had in view the possibility of an identity between blastopore and primitive mouth, and, indeed, supposed that the Zoophytes might be distinguished from higher organisms by the fact that they possessed the primitive, as distinguished from a secondary mouth. On the other hand, I have since seen reason to abandon altogether the notion that the blastopore represents a mouth, and differ from Professors Haeckel and Huxley on this point.

I further disagree with them as to the universality of the origin of the diploblastic phase by invagination. I hold that we have at least one *apparently* well-observed case of the formation of an endoderm by delamination ('Fol. Die erste Entwickelung des Geryonideneies Jenaische Zeitschr.,' vol. vii, p. 471), and, further, that even without such evidence (which ought to be re-examined) it is possible to give a more satisfactory explanation of the early phenomena of animal development on the hypothesis that *the endoderm originated primitively by delamination*, which has been superseded by invagination through the operation of readily conceivable mechanical causes, than it is to marshal the same series of facts in accordance with Haeckel's doctrine of the invaginate mouth-bearing Gastræa.

The historic series according to the Planula theory.—Accordingly, I shall briefly pass in review what I conceive to have been the course of historical development, pointing out how these historical phases reappear in more or less modified forms in the embryonic histories of to-day.

1. THE MONOPLAST = OVUM.—The unicellular ancestors of the higher animals are represented by the unicellular ovum. Just as we find existent unicellular animals exhibiting differentiation into ectoplasm and endoplasm, so do we find ectoplasm and endoplasm differentiated in many eggs. The differentiation of anterior and posterior regions, which is more rarely seen in living Protozoa, is the rule in the monoplastic phase of individual development. Just as unicellular animals contain granular matter, which as metaplasm is distinguished from the hyaline protoplasm in which such granules float, so in the egg-cell we find a greater or less amount of granular matter, which it is convenient to speak of as food-material. As in the unicellular organism some of the granular matter present, is the result of chemical activity in the protoplasm—that is to say, is the product of assimilation and subsequent segregation, whilst other (usually coarser) particles are particles of food which have been incepted, but

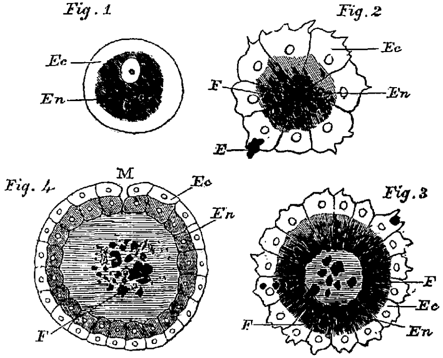

FIG. 1. Monoplast. FIG. 2. Optical section of Morula stage. FIG. 3. Optical section of Diblastula. FIG. 5. Section of Diblastula, with mouth. *Ec*, Ectoderm. *En*, Endoderm. *M*, Mouth. *F*, Food particles.

not yet assimilated—so in the corresponding phase of individual development we find the food material consisting of two kinds of granular matter, one of which has been taken in by the egg-cell from its parent organism, *assimilated* and deposited as the result of a chemical segregation, the other, which is often of enormous relative bulk, consisting of coarse granules or masses which have been *engulphed* by the protoplasm of the egg during its sojourn in the maternal ovary or ducts. Such coarse and bulky food material is prepared for the young egg-cell by neighbouring cells of the maternal organism, and may very fitly be compared, after it has been incepted by the ovum, to the organic masses with which a naked Protozoon gorges itself for purposes of nutrition.[1]

The amount and the disposition of the food material in the ovum varies very greatly in different organisms. Its variation is the direct cause of differences in the arrangement and size of the cells into which the egg-cell divides, and becomes thus the obvious source of discrepancy between the inferred ancestral (phylogenetic) and actual (ontogenetic) developmental phases.

The ancestral monoplast must have been free from any large quantity of granular matter, whether segregated or incepted, but we may assume its mode of taking food to have been similar to that of the Amœba, and that in response to incidental and intrinsic forces its substance was differentiated into an ectoplasm and an endoplasm.

2. THE POLYPLAST = MULBERRY PHASE OR MORULA (Haeckel). —In the course of the historic development of animals, the monoplast gave rise by division to spherical colonies consisting of many adherent cells. These, we assume, continued to nourish themselves by the inception of solid particles at their free surface. The process which development appears to have taken requires us to distinguish two conditions of the Polyplast: *a*, an earlier one (Fig. 2), in which the constitutional cells were closely adherent so as to form a solid sphere, distinguished by Haeckel as the morula; *b*, a later (Fig. 3), in which the accumulation of liquid at the centre of the sphere built up by the cells gradually resulted in the formation of a considerable cavity (the blastocœl, Huxley), so that the polyplast now acquired the form of a vesicle, its wall formed by a single series of equi-formal cells and its cavity filled up by a liquid which had traversed the substance of these cells. This hollow polyplast has been designated by Haeckel the blastula. We must assume that food was still incepted

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[1] See my observations on the ovarian egg of Loligo, in the 'Phil. Trans.,' 1875.

by the naked surface of all the constituent cells. At the same time nothing could be more probable than that the outer and the inner portions of each cell should acquire different structure and properties, such as may, at this day, be seen to be acquired by the cells forming the wall of the blastula-phase of the jelly-fish, Geryonia (Figs. 5, 6). The liquid within the cavity of the blastula was probably enough of a special nature, and together with secreted products from the cells, undigested food particles may have passed through the substance of the cells into this blastocœl, and there have been dissolved, so that an incipient digestive function was acquired by the blastocœl.

3. THE DIPLOBLASTIC PLANULA = DIBLASTULA (Salensky).—The differentiation set up between the inner and the outer portions of the cells forming in a single layer the wall of the blastula now (we infer) advanced so far that each cell divided into two, an inner cell and an outer cell. Possibly, not all the cells composing the wall of the blastula took part in this process. The result was the formation of an endoderm or enteric cell-layer by delamination. The cavity now enclosed by its special layer of cells is conveniently termed the ENTERON or ARCHENTERON (Urdurm); the cell-layer is accordingly the enteric cell-layer; on the other hand, the outer set of cells usually known according to the terminology introduced by Professor Allman in treating of the Hydroid polyps as ectoderm, may also conveniently be termed the DERON or deric cell-layer. The delaminate Planula or Diblastula (a term which I adopt from Professor Salensky) continued to nourish itself by the inception of solid food by the naked protoplasm of its ectodermic cells. We must, however, suppose that as the differentiation of the deric and enteric cell-layers advanced, the inception of nutriment became limited to one spot on the deric surface, and that at this spot solid particles of food were passed through the soft protoplasm into the enteron there, to be digested. The development of cilia on the general surface, and of locomotion, would account for this localisation. A rupture of the sac at this point and the establishment of an open way into the already actively secreting and absorbing digestive cavity, would constitute the mouth.

Whatever view we take as to the original mode of formation of the digestive cavity or enteron, the difficulty has to be encountered of forming a conception of the steps by which the two vastly different modes of digestion which we meet with in the animal series could pass one into the other. The physiology of alimentation in a Protozoon, such as an Amœba or an Infusorian, on the one hand, and of even the simplest of the Enterozoa (the animals with an enteron or gut), differs in the most important manner and to an extent which is hardly sufficiently recognised. Whilst in the Protozoon the raw, unprepared particle of solid food is plunged into the living protoplasm of the cell, and, lying within a temporary cavity partly filled with water, is digested within the protoplasm, no such inception of solid particles by the cells of the enteron takes place, except perhaps in the sponges. In the Enterozoa the food, though, as in all nonparasitic animals, it is seized in the solid state, is yet not introduced into the cell protoplasm in that state. It is dissolved in the enteron by the action of secretions there accumulated, and passes only by diffusion into the protoplasm of the enteric cells. The whole significance of the enteric cavity—the physiological motive of its differentiation—appears to be that of a laboratory retort. The hypothesis of its primitive appearance as a closed cavity into which solid food particles were passed *through* the protoplasm of the cells as into a food-vacuole common to the cell colony, is in harmony with this assumed physiological motive. On the other hand, it does not seem possible to reconcile the physiological significance of the enteron with the hypothesis that it took its rise in a gradually deepening depression of the surface of a spherical blastula—that is to say, by invagination. Such an area of depression is assumed by the invagination-hypothesis to have become the exclusively nutritive area. Its cells must be actively taking in solid particles of food at the surface like so many Amœbæ. What motive is there on such an assumption for the deepening of the depression? In what way can we suppose that the amœboid cells of this area came to cease the habit of seizing and ingesting solid particles, and took to the outpouring of digestive juices and the passive function of absorption? By what influences are we to suppose that the depression was sufficiently deepened and its margin sufficiently narrowed to retain a digestive fluid? The answer to these questions appears to me to involve more difficulty than we encounter in tracing out the hypothesis of the origin of the enteric cell-layer by delamination. This preliminary advantage of the latter hypothesis is, we shall see, independently strengthened and fortified by the facts and arguments with which we meet at later stages.

4. *Formation of the* STOMODÆUM *and* PROCTODÆUM.—The breaking through of the mouth of the Diblastula, in the form of a definite aperture, appears to have assumed neither

an "eruptive" nor a "disruptive" character, but to have been rather "inruptive"—that is to say, the establishment of the mouth as a permanent structure was accompanied by an *ingrowth* of ectodermal cells, no doubt very slight at first, but afterwards attaining great size and importance as the first portion of the alimentary tract. It is this ingrowth which gives rise to what is often called "pharynx" in Mollusca, Arthropoda, and Vermes. I have proposed[1] to designate this ingrowth of the deron, the STOMODÆUM (*στομοδαιον*, like *πυλοδαιον*, the road connected with a gateway), and similarly to call another ingrowth which accompanies the formation of the second orifice (the anus) of the enteron, the PROCTODÆUM. The mouth and stomodæum appear to have existed some time before an anal orifice was developed, and the mouth must have functioned as it does in living Zoophytes, both for the ingress of food to the enteron and the rejection of undigested remnants. The development of an anus and proctodæum may be conceived of as due to the gradual establishment of an, at first, purely mechanical rupture, as a permanent hereditary feature. In the recapitu-

Fig. 5

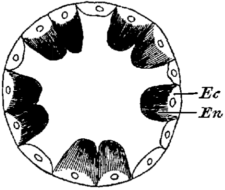


Fig. 6

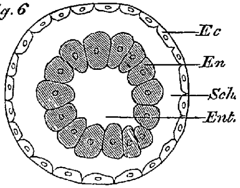
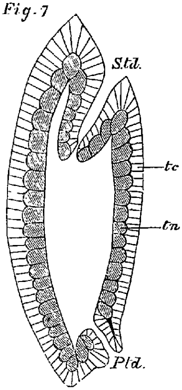


Fig. 7



FIGS. 5 and 6. Delamination of Blastula of a Jelly-fish (after Fol.). *Ec*, Ectoderm. *En*, Entoderm (Enteron). *Sch*, Schizocœl.

FIG. 7. *tc.*, deron; *tn.*, enteron; *Std.*, stomodæum; *Ptd.*, proctodæum.

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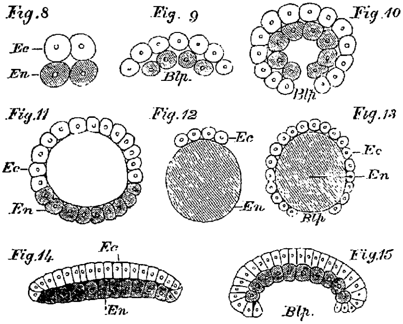
[1] 'Quart. Journ. Mic. Sci.,' April, 1876.

lative ontogeny of a large number of organisms living at this day it forms by rupture.

Leaving now for the moment the task of further detailing the hypothetical changes which the ancestors of the Enterozoa underwent (to which we shall return), let us, having thus pictured to ourselves the steps by which a hollow cell-multiple, derived from a single cell, gave rise to an enteric cell-layer by delamination, and acquired a mouth with stomodæum and an anus with proctodæum—whilst various changes of general form were affected and sundry tentacular and such-like organs probably developed—inquire how the observed facts of the early stages of individual development in animals can be explained by applying to these facts and to our hypothetical sketch the doctrine of heredity, viz. that the development of the individual is a recapitulation of the development of the species, interrupted and modified by processes of adaptation.

Hypothesis of the substitution of Invagination for Delamination.—Whilst according to the above hypothetical sketch of ancestral development from the monoplast to the diblastula—the primitive enteron or digestive cavity is the blastocœl and the enteric cell layer forms by the Delamination of its wall—we find in the actual development of animals that the process of Invagination in one modification or another, is almost universal. Indeed, Professor Haeckel and Professor Huxley are inclined to think that it is universal. We have, how



FIGS. 8, 9, 10. Stages of egg-division and invagination without formation of a pseudoblastula. FIG. 11. Pseudoblastula. FIG. 12, 13. Epibolic invagination. FIGS. 14, 15. Invagination as seen in Earthworm and Nematoda. *Ec.* Deron; *En.* Enteron; *Blp.* Blastopore.

ever, the observations already cited concerning the Geryonidæ and some observations of Kowalewsky on Alcyonium, and on species of Actiniæ, which indicate the development of an enteric cell-layer by Delamination. In the development of the enteron by Invagination, usually a number of cells become depressed in a cup-like manner on the surface of the blastula, sinking more and more deeply into the blastocœl (if such cavity be present), until the once spherical blastula (Fig. 11) has become a hemispherical cup, built up of two cell-layers, one pressed against the other (Fig. 15). The rim of the cup now contracts, and frequently closes; the wider or narrower orifice thus formed I have termed the *blastopore*. The case just described is that of an organism in which the egg-cell contains relatively a small amount of food-material, and when consequently the cells of the morula and of the blastula are of nearly equal size. Haeckel has called this the Archiblastic type. When there is more food-material in the egg, it either collects to the centre of the mass of cells as division proceeds, and segregates in a way which strongly suggests delamination,[1] lying eventually in the central cavity of a vesicle (blastula), formed by a single layer of cells (Periblastic type, Haeckel), *or* the food-material is associated from the first post-seminate phases of the egg-cell with one hemisphere or larger moiety of the egg, namely, that which is destined to form the enteric cell-layer, whilst the part of the egg (often extremely small) which is destined to form the deron or ectoderm is free (or becomes so by segregation) from such food-material. The consequence of this arrangement is that the enteric moiety of the egg-cell is separated in the earlier phases of cleavage from the deric moiety (Fig. 12), and is not only more bulky, but breaks up into new cells more slowly than the latter, so that it becomes overgrown by the deric cells rather than invaginated into them (Fig. 13). Two degrees of this Epibolic mode of Invagination (so called by Selenka, in distinction from the Embolic mode) are distinguished by Haeckel as Amphiblastic and Discoblastic.

It is clear enough that the special modifications of the process of invagination due to the presence in the egg of a large amount of food-material may be dismissed in considering the question as to how the process of Delamination came to be replaced by that of Invagination, since the presence of such an excess of food-material is a secondary and late condition. The facts, however, connected with the behaviour of the food-material, when present, suggest the explanation

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[1] The formation of the enteron in periblastic forms such as the Arthropoda and Anthozoa (Alcyonium) requires much further study.

of the connection between Delamination and Invagination. All differentiation of cells, the development of one kind of cell from another kind, is dependent on internal movements of the physiological molecules of the protoplasm of such cells. When Delamination occurs in the cells of the blastula of Geryonia, or when it occurred in the ancestral blastula, the molecules destined to build up the enteric cell and deric cell, into which one of the primitive cells divides, are already present before they are made visible to the eye by segregation and accumulation on opposite faces of the differentiating cell. Though the substance of a cell may appear homogeneous under the most powerful microscope, excepting for the fine granular matter suspended in it, it is quite possible, indeed certain, that it may contain, *already formed and individualised,* various kinds of physiological molecules. The visible process of segregation is only the sequel of a differentiation already established, and not visible. The descendants of the Diblastula (diploblastic Planula), which had gradually acquired a separate deric and enteric cell-layer in place of one cell-layer with an external deric moiety and an internal enteric moiety to each cell, must have tended in their individual development from the egg-cells of parent Diblastulæ to have established more and more early, in the course of their growth, the important separation of deric and enteric cells, of ectodermic and endodermic elements. In so far as the differentiation of the two kinds of factors or molecules, the deric and the enteric, became dependent on heredity, and less dependent on the direct adaptative causes which first brought about the differentiation, in so far would it be possible for the differentiation, the segregation of deric molecules from enteric molecules, to take place at an earlier point in the embryonic development than that (namely, the blastula stage), at which the direct adaptative causes could come into operation. Thus, since the fertilised egg already contained hereditarily acquired molecules, both deric and enteric, invisible though differentiated, there would be a possibility that these two kinds of molecules should part company, *not* after the egg-cell had broken up into many cells as a morula, but at the very first step in the multiplication of the egg-cell. In fact, some or all of the deric molecules might remain in one of the two first cleavage-cells, and all of the enteric molecules, with or without some of the deric molecules, might remain in the other. We should not be able to recognise these molecules by sight; the two cleavage-cells would present an identical appearance, and yet the segregation of deric and enteric factors had already taken place. This hypothesis may be called that of PRECOCIOUS SEGREGATION: "precocious," since it is the acquirement of a condition in the developing organism, in virtue of heredity, at an earlier period of development than that at which such acquirement was attained by its forefathers through adaptation. The tendency to precocity in this sense, in regard to important structural arrangements, has been insisted on by Haeckel in discussing what he terms "heterochrony in the palingenetic phenomena of ontogeny;" and the existence of such precocity is as well established as any part of the speculative edifice with which we are dealing, both on *à priori* and *à posteriori* grounds.

Having, then, arrived at this point, viz. the separation of deric and enteric elements in the first two cells of the developing organism, as a naturally conceivable sequence to the primary process of the separation of these elements by delamination of the walls of a many-celled blastula, let us pursue the case further.

How, it may be asked, are we to suppose that the enteric and deric cell thus early differentiated should have acquired the faculty of dividing in such a manner that the offspring of the enteric cell form a vesicle which, as it forms, becomes sunk within another vesicle constituted by the deric cells, and that thus the result is a diploblastic Planula or Diblastula identical with that formed by Delamination?

It might be urged that the result of further division on the part of the two primary cells could only be the formation of a vesicular one-cell-layered sac, of the same morphological character as the blastula which precedes the delaminate diblastula, and that we have no suggestion on our present hypothesis of any motive for the invagination of one hemisphere of the blastula so developed within the other. We have, however, first of all to note that the blastula (the one-cell-layered sac) belonging to the invaginate series is never precisely the homologue of the blastula belonging to the delaminate series, inasmuch as, according to our hypothesis (and as a matter of actual observation in all invaginate developments), the cells of the blastula belonging to an invaginate development are not equivalent one to another, as they are in the blastula of a delaminate development. In an invaginate development from the first the offspring of the primary enteric cell are to be distinguished[1] from the offspring of the deric cell, though to the eye there may be no structural distinction (Fig. 8). Accordingly, the blastula of an invaginate development has one hemisphere, or a certain area composed of enteric cells, whilst the rest are deric (Fig. 11).

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[1] By means of the 'directive corpuscles.'

Now, we must remember that, however difficult it may be to form a mechanical conception of the processes by which the cells derived by division from an enbryonic cell take up certain definite positions, so as to form definite organs comparable to those of the parent organisms (thus exhibiting what we call heredity), it is no more difficult to form a mechanical con, ception of this power of self-arrangement and co-ordination-as it exhibits itself after a certain amount of interference with the routine of recapitulative heredity, than as it exhibits itself when that routine is uninterruptedly pursued. In virtue of an hereditarily transmitted molecular structure the cells formed by division of the egg-cell in a delaminate development arrange themselves as a sac, the blastula. In virtue of hereditarily transmitted molecular structure the offspring of the enteric and the offspring of the deric cells, which are differentiated in the first cleavage of the egg of an invaginate development, arrange themselves as two vesicles, the latter within the former, the two groups of cells, each reproducing from the first, the characters of the endoderm and ectoderm of the parental Diblastula, in regard to such points as plane of cleavage, contact of the cells of one layer with one another, and contact with those of the other layer. Accordingly, the immediate apposition of the endodermal to the ectodermal cells (such as often occurs, *e.g.* in mammals, in nematods, and in the earthworm), without the formation of a vesicular blastula, is what we should look for (Figs. 9, 14).

The formation of a vesicular blastula in the course of an invaginate development is a secondary process: such a blastula (Fig. 11) is *not* the representative of the ancestral blastula (Fig. 3) which appears in the course of the delaminate development; it is due to mechanical non-hereditary accumulation of liquid among the primary cells of the embryo, and distorts the recapitulative development. The blastula of the invaginate development may be called a 'pseudoblastula' to distinguish it from the ancestral blastula. Haeckel's archiblastula is a pseudoblastula, and its cavity *does not correspond with the cavity of the delaminate blastula,* which immediately becomes the archenteron. We distinguish the archenteric blastocœl from the pseudoblastocœl.

The space which is formed within or is enclosed by the products of the enteric primary cell is, of course, the homologue of the blastocœl of delaminate development. It is this which becomes the archenteron. As the multiplication of the deric and enteric cells goes on, the cavity enclosed by the enteric cells becomes more distinct. The margin of the incomplete double vesicle tends to bend inward (Fig. 9), and to complete the vesicle by closing up (Fig. 10), and it is necessary to assume that in the early history of invagination it did quite close. In the primary phase of invaginate development the blastopore was obliterated in due course as cell division went on. The persistence of the blastopore and the establishment of a relation sometimes between it and the mouth by means of of the stomodæum, and sometimes between it and the anus by means of the proctodæum were later adaptations.

5. *Coincidence of the blastopore with the mouth and with the anus.*—On examining the actual developmental histories of Enterozoa which have up to the present time been recorded by means of careful observation we find that by far the majority exhibit the formation of a Diblastula by invagination, the invaginated enteron in many cases consisting of but a few large cells, or even at first of only one large cell. The blastopore closes up in many cases; it does so in the molluscs Pisidium and Unio, in many Gastropods and Vermes, in Cephalopods, and in Vertebrata. Subsequently, as has been above described for the hypothetical ancestral form, a mouth and an anus eat their way into the completely closed Diblastula by means, respectively, of a stomodæum and of a proctodæum, or of a stomodæal aud a proctodæal invagination.

On the other hand, there are numerous cases in which the blastopore does not close up, but appears to persist as mouth in one set of cases, as anus in another set of cases. Regarding, as I do, the blastopore as an orifice of a secondary nature existing solely in relation to the invagination process, and originating after mouth and anus had made their appearance in the progress of animal evolution, I seek to explain its occasional relation to the mouth and to the anus as cases of adaptation. A parallel case of the adaptation of an orifice of invagination to functional purposes will be useful for my argument. The primary optic vesicle, like the nerve ganglion-masses, was originally developed by delamination in higher animals, but has in many cases taken to a development by invagination. In the Cephalopods the vesicle presents at an early stage a wide rim or margin, which gradually closes in leaving for a time a small orifice comparable to the blastopore of an invaginate diblastula. This orifice is obliterated in the Dibranchiate Cephalopods, but in Nautilus it is seized upon by adaptation and made use of as the chief optical condition of the whole ophthalmic apparatus. It serves in place of a lens or refractive body, to produce an image on the retinal surface in virtue of its pinhole character. Here we have a secondary accidental accompaniment of the invagination process—namely, the necessary orifice of invagination, rising suddenly to the importance of a substitute for refracting media which were differentiated in the tissues of the eye, before invagination had supplanted delamination in its development. Just as the orifice of invagination in the Cephalopod's eye is made use of in certain Cephalopods, but not in all, so is the blastopore made use of in certain invaginate Diblastulæ, but not in all, and not in all in the same way.

In certain Prosobranchiate Gastropods, most carefully studied by Bobretzky, the stomodæum, the deric (ectodermic) ingrowth belonging to the mouth, occurs either at the spot where the blastopore has just closed, or *before it has closed*, so that the oral ingrowth forms *around the blastopore;* and thus the blastopore does not close, though it is inaccurate to to say that it *becomes* the mouth. The same process takes place, in all probability, according to Kowalewsky's observations, in the earthworm and in some zoophytes; also in nematoid worms, according to Bütschli. These are the cases which have led to the supposition that the blastopore is the primitive mouth of Enterozoa, and these particular forms are those which have been called archæostomatous. But it will be observed that in these cases the normal mode of the formation of the mouth is not departed from; a stomodæum, an ingrowth of ectodermal cells, takes place here as in the ancestral delaminate type, which we have sketched above. The mouth and stomodæum merely avail themselves, as it were, of the blastopore soon about to close, and so a coincidence is effected.

In other cases—the Echinoderms, Paludina, among Prosobranch Gastropods, and probably many other animals—it is the anus, with its proctodæal ingrowth, which adapts itself to the blastopore. In the Pulmonate Limnæus both anal and oral growths develop on the site of the elongated blastopore. By regarding all these cases as late and special adaptations of the blastopore—itself a secondary structure concerned in the mechanism of egg-cleavage, and not developed with a specific function—we are able to explain, in a measure, the very astounding fact that what becomes the mouth of a whelk appears to become the anus of a water-snail. A very slight mechanical variation of conditions may be conceded to be sufficient to cause a small shifting in the position of the unsignificant orifice of invagination, so as to bring it within the predestined area of either stomodæum or proctodæum.

Comparison of the applicability of the hypothesis of a primary *delamination, and of the hypothesis of a primary invagination.* We shall now briefly state the difficulties which are encountered by Haeckel's Gastræa theory in reference to the earlier stages of development, and point out to what extent these difficulties are avoided by the Planula theory.

If we assume with Haeckel that the process of invagination represents the historical mode of the formation of the enteron, and that the blastopore is the primitive mouth, we meet with difficulty as to (1) the transition from the inceptive nutrition of amœboid cells to the absorptive nutrition of the cells lining a more or less completely enclosed digestive chamber; (2) the substitution, by a process of retardation, of delamination in a few rare cases for the supposed more archaic invagination; (3) the disappearance, in some cases, of the supposed primitive mouth, and the formation of a new secondary mouth, whilst in closely allied forms the supposed primitive mouth persists as mouth, or again ceases to be mouth and becomes anus, whilst a new mouth develops; the result being that the mouth of one Gastropod (to take an example) has to be considered as the homologue of the anus of another.

On the other hand, the hypothesis of primary delamination and secondary invagination gives an intelligible scheme of the development of an enteron by the formation of a cavity at the central meeting-point of a colony of amœboid cells, and the subsequent differentiation of two cell-layers already foreshadowed in the differentiation of the outer and inner portion of each cell. The hypothesis of precocious segregation explains the common replacement of the original process of delamination by invagination, and accounts for the blastopore. The blastopore being thus explained, we have no further assumptions to make as to primary and secondary mouths, and we avoid the fatal objection which can be urged against Haeckel's theory—that it admits of a *reductio ad absurdum,* since, in reasoning from it, we are driven to the conclusion that the mouth of a whelk is the homologue of the anus of a water-snail.

II. FORMATION OF THE MESODERM AND BODY-CAVITY (CŒLOM).

So far I have only discussed the origin of the two primitive cell-layers and the primitive dominant organ of the animal economy—the enteron. External changes of shape and prolongations of cells (cilia) or groups of cells (tentacles), as locomotor and prehensile organs, have not been touched upon. These I shall allude to in due course, but first of all must deal with important changes which supervene in regard to the primitive cell-layers in nearly all the Enterozoa, leading eventually to the production of an apparently special layer of cells between deron and enteron, and to the formation of a cavity, also placed between those layers, and known by Haeckel's term "Cœlom."

I shall pursue the method already adopted of giving the results of observation and reasoning, first of all, in the form of a statement of the hypothetical course of differentiation of the ancestral series, taking up the story of the Diblastula with mouth and stomodæum just developed, but destined to acquire anus and proctodæum somewhat later.

1. *Differentiation of a layer of fibres from the deep surface of the deron.*—The ectodermic cells, fulfilling, as Kleinenberg has pointed out, the function of protective, tactile, and contractile organs, now proceeded to differentiate each for itself a contractile tail or appendix, as we actually observe in Hydra.

2. *Delamination of these fibres as fusiform, contractile, and skeletal cells.* Just as at an earlier stage the digestive portion of each primitive cell, separated by delamination from the receptive tegumentary portion, giving rise to ectoderm and endoderm, so now the contractile fibrous appendices of the ectoderm acquired each the characters of a separate cell, and separating by delamination from the ectodermal cells, formed a distinct hypoderic musculo-skeletal layer, in fact, a primitive mesoderm or mesoblast. In this stage, however, the cells do not present that early independence which is what defines the mesoblast. The musculo-skeletal cells of the Zoophytes are deep layers of the ectoderm, and do not take origin as a distinct "mesoblast" at an early period of development. They are not, in fact, sketched out, their progenitors are not marked off as a separate layer, in that phase of development when all the cells of the embryo are undifferentiated in appearance, and when the enteron is beginning to be formed by invagination. This, however, *is* the period at which the musculo-skeletal cells arise in higher forms than the Zoophytes, and hence the name Triploblastica applied to those groups.

3. *Precocious segregation of mesoderm and enteric origin of the cœlom.*—This early independence of the middle cells of the organism is traceable to *two* distinct causes or antecedents, which it is one of the main objects of the present essay to set forth. These two causes are, firstly, the development of diverticula, or so-called "gastro-vascular" outgrowths of the archenteron, which eventually become pinched off from the enteron, and form a distinct closed cavity, the

cœlom. The second cause is the hereditarily accelerated differentiation of the musculo-skeletal molecules. Just as we saw reason to believe that the departure in the mode of appearance of the enteric cell-layer in living organisms from the mode in which it originated in ancestral forms was due to PRECOCIOUS SEGREGATION, so here, again, we invoke this principle, and find that it is capable of affording an explanation of the most important and, at first sight, anomalous, modifications of the primitive mode of development of the musculo-skeletal cell-layer.

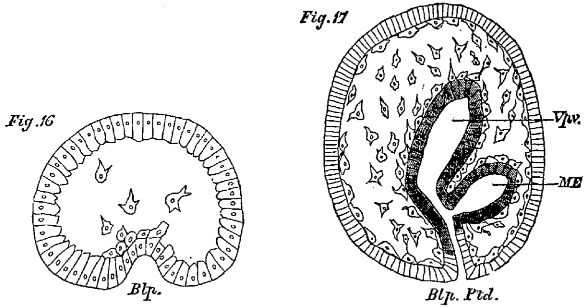
4. *Enteric origin of the cœlom.*—The ancestral form provided with mouth and enteron, ectoderm and endoderm, and a musculo-skeletal cell-layer delaminated from ectoderm proceeded to develop diverticula of the enteron. In the Zoophytes we find such diverticula running into the tentacles or forming a periaxial cavity, (the axis being occupied by the original enteron) or giving rise to periaxial or paraxial canals. The ancestral form proceeded beyond this to develop its enteric diverticula in the form of two large outgrowths, a right and a left, which became shut off from the enteron by the pinching-in of the cells at the root of the outgrowth; and the two diverticula, or "parenteric growths" as we may call them, subsequently united to form one big perienteric (perivisceral, peritoneal) cavity, the cœlom. This was the mode of origin of the cœlom, the genetic source of blood-vascular and lymphatic cavities and canals. We find this mode of development of the cœlom still maintained in many and widely different members of the animal series, for instance, in Echinoderms, in Brachiopods, in Sagitta.

A very little change in this method of development has given rise to the commonest mode of formation of the cœlom in existing animals. The outgrowth of the enteron, or parenteric lobe, instead of being a hollow diverticulum, is *solid*, and only develops its cavity after it has become a considerable mass. Then it opens out or splits to form the cavity or cœlom, which by this retardation is prevented from ever forming a part of the cavity of the original archenteron. This modification of the ancestral mode of formation of the cœlom in the parenteric outgrowths is seen in many Vermes (Kowalewsky, Oligochœta), in Arthropoda, in some Mollusca, and most clearly and strikingly in Vertebrata. I pointed out that this was the probable explanation of the occurrence of the two kinds of cœlom, called by Professor Huxley "an enterocœl" and "a schizocœl" respectively, in this Journal, April 1875, p. 166. Professor Haeckel had maintained, and does, I believe, to this day, that the cœlom originated ancestrally by splitting between the deron with its hypoderic cell-layers, and the enteron with its hypenteric cell-layers, and that it had nothing to do with "gastro-vascular outgrowths." In my paper on the "Invaginate Planula of Paludina," just referred to, I gave the first explanation of the cœlom as uniformly derived from the enteron, and traceable to "gastro-vascular" cavities. This view is entertained by Professor Huxley ('The Anatomy of Invertebrated Animals,' p. 686), though he makes reservations in favour of a schizocœlous condition for Rotifera and Polyzoa. It appears to me to be unnecessary to admit a schizocœlous origin of the cœlom in any case. It is uniformly developed from parenteric growths, and under extreme modifications the essential features of its ancestral relations can be traced in the most exceptional cases. Thus there are not a few developmental histories in which, as a purely embryonic phenomenon, liquid accumulates between the invaginated enteron and the vesicular deron or ectoderm. This cavity is really only a developmental feature, part of the non-historic mechanism of growth, like the blastopore, and is a continuation of the pseudo-blastocœl. Enteric cells grow out in two little parenteric masses from the enteron, and then separate widely from one another, spread out, become amœbiform, crawl all over the inner wall of the ectodermic vesicle and line it throughout (see my "Observations on Pisidium," 'Phil. Trans.,' 1875). They thus spread themselves out and *enclose* a large space; they form ultimately the lining cells of the cœlom, so that even where only a few branched cells appear between deron and enteron, they may carry out the essential features of development of the cœlom from parenteric diverticula.

According to the hypothesis just set forth, we must look, then, in *all* animals with a cœlom, that is to say, in all the higher animals, for parenteric growths, lateral masses of cells of the endoderm, the progeny of which can be traced in further development to *the epithelium* (the lining cell-membrane), *of all and any sanguiferous or lymphatic cavities or canals, and to the corpuscles floating in such cavities.*

The facts observed in the development of higher animals admit very well of this interpretation, only there is this difficulty, that in many cases parenteric growths appear to give rise *to a good deal more* than the cœlom and its epithelium. In fact, in Vertebrata the whole of the muscular and skeletal tissues as well, instead of being delaminated from ectoderm, appear to originate, together with the cœlomic parentera, from masses of cells separating from the primitive enteron. In the Vertebrates it is most clear that only a small axial tract, if any, of the cells which give rise to muscular-skeletal tissues originates from ectoderm. The original mode of formation by delamination has been lost. The parenteric growths, separating early whilst all the cells of the embryo are neutral in appearance, form a large intermediate sheet of cells—the much debated "mesoblast" or "mesoderm"—and from this layer, muscular and skeletal cells, vascular and cœlomic epithelium, all alike develop. Compare with this extreme state of modification the more ancestral mode of development of the corresponding parts of the tissues of Holothurians, as described in the valuable and important memoir of Selenka ('Zeitsch. Wiss. Zool.,' vol. xxvi). In Holothuria, the two elements which in the Vertebrates are confused to the eye, and which are too often mentally confused under the one name of mesoblast, are seen taking their distinct origins, not, I believe, the quite ancestral origin, but presenting a most suggestive departure from that ancestral phase. To agree with the ancestor, as in Zoophytes, the cells of the embryo Holothurian, which are to give rise to muscles and skeletal tissue, should originate from the whole internal surface of the ectoderm or deron by delamination, but instead of doing this, they *either* proceed from the multiplication of a few cells, separated at a very early period at the inner face of the pole of invagination, or they originate a little later from that

Fig.16 *Fig.17*



Development of a Holothurian, after Selenka.
Blp. Blastopore; *Ptd.* Proctodæum; *Vpv.* Vasoperitoneal or cœlomic vesicle, the Parenteron. *M.E.* Digestive Sac or Metenteron.

same point (fig. 16). In any case they maintain a complete independence of the cœlomic "parentera," and only apply themselves at a later period to these outgrowths, in order to form the musculature of the walls of the canals and cavities to which the archenteron gives rise (fig. 17).

The condition of things in reference to the origin of the musculo-skeletal cells seen in the Holothurians may be explained as a derivative of the delamination process seen in the formation of the identical tissues of Zoophytes, by the application of the hypothesis of precocious segregation. Just as the delaminate origin of the endoderm gives place to an invaginate origin, owing to the early segregation of the two elements, so the ectodermic cells at this later stage of evolution cease to develop the musculo-skeletal cells by delamination, and at a time when the embryo is composed of only twelve, eight, or even two cells, the molecules possessing by heredity the power of giving rise to musculo-skeletal tissues are segregated from the cells destined to form ectoderm pure and simple, which now, indeed, having lost its musculo-skeletal elements, should be distinguished from the primitive ectoderm, as epiblast.[1] This segregation taking place before the pseudoblastula is formed (in rare cases of retention of the ancestral delaminate origin of the enteric cells, the musculo-skeletal tissue also originates by delamination) we find that the greater portion of the cells forming the wall of the pseudoblastula are purely epiblastic, and never give rise to musculo-skeletal progeny. But at one part of the pseudoblastula are the cells containing the segregated musculo-skeletal molecules, and others containing the segregated endodermic molecules. In Holothurians the two sets of precociously segregated molecules form distinct cells, and thus at an earlier or a later period we see the musculo-skeletal tissues of these animals originating from cells in the neighbourhood of that area of invagination by which the cavity of the archenteron is formed.

Admitting this hypothesis of the precocious segregation of musculo-skeletal molecules to be true, it is clear enough that

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[1] As Prof. Allen Thomson has recently pointed out, ectoderm and endoderm correspond to epiblast and hypoblast, plus the share which ectoderm and endoderm have in the mesoblast (Brit. Ass., Plymouth, President's Address, 1877). In fact, we arrive now by the light of minute investigations of Invertebrate ontogeny at a striking confirmation of the views of von Baer. The primary cells of the embryo differentiate into two layers, the ectoderm and the endoderm, or deron and enteron. Each of these again divides into two: the ectoderm into epiblast and musculo-skeletal tissue, the endoderm into hypoblast and cœlomic epithelium (parenteric outgrowths).

we *may* have many varieties as to the exact time and mode of such segregation; and thus, I think, we may explain the various modes of origin which careful observers ascribe to the musculo-skeletal tissues in various cases. To return, for example, to the case of the Vertebrates: it appears that the whole, or very nearly the whole, of the musculo-skeletal tissues in those animals are the progeny of the endodermic cells, that is to say, develop from the parenteric outgrowths. Our hypothesis of precocious segregation explains this, for we have only to suppose that, during the first cell-division of the egg-cell, the precociously segregated musculo-skeletal molecules do not form distinct isolated cells, *but accompany the endodermic cells*, and do not segregate from these latter until they have formed the parenteric cell-masses. Thus the parenteric cell-masses of Vertebrata, whilst they represent the gastro-vascular diverticula of the Cœlenterate-phase of animal evolution, contain at the same time the hereditary musculo-skeletal molecules. Hence the mesoblast of Vertebrates represents *in form* the cœlomic diverticula, whilst *in substance* it also is the representative of the musculo-skeletal tissue, primarily differentiated by delamination of an ectoderm. In this way we are able to explain—that is, to form a plausible conception of the mechanism of—two very puzzling embryological phenomena, *by means of one hypothesis*. The phenomena are the formation of an enteron, sometimes by Delamination, sometimes by Invagination with a blastopore, and the formation of the musculo-skeletal tissues, sometimes by delamination from the ectoderm, sometimes by outgrowth of the enteron.

Among the many variations possible in the origin of mesoblast—musculo-skeletal tissue *plus* cœlomic epithelium—we may note that the one factor of that double entity, viz. the cœlomic epithelium, can always be traced to the enteron or to the primitive enteric cell, whilst the other factor may be (1) wholly or (2) partially fused, as we have above explained, with the enteron, or (3) entirely independent of it. Such part of the musculo-skeletal factor as is not appropriated by the enteron *may still continue* to arise by delamination from a fully-formed ectodermic cell-layer, or may appear in the very early stages of development as independent cells, having segregated before the cell-division of the embryo had advanced very far. In Pisidium, Paludina, Limnæus, and other Invertebrates, it appears very probable that, whilst a large part of the musculo-skeletal tissues arise from the parentera with which their elements have become associated through precocious segregation, other parts of the musculature and connective tissues continue to take origin by delamination from ectodermal cells at later stages.

In all the large groups of the animal series, excepting the Cœlentera and Echinoderma, a very great diversity in this matter prevails.

III. CONSIDERATIONS RELATIVE TO THE DEVELOPMENT OF EXTERNAL FORM.

A. *Radial and bilateral symmetry and telostomiate and prostomiate conditions.*—It has been recognised by various writers, but notably by Gegenbaur and Haeckel, that a condition of radiate symmetry must have preceded the condition of dilateral symmetry in animal evolution. The Diblastula may be conceived to have been at first absolutely spherical with spherical symmetry. The establishment of a mouth lead necessarily to the establishment of a structural axis passing through the mouth, around which axis the body was arranged with radial symmetry. This condition is more or less perfectly maintained by many Cœlenterates, and is reassumed by degradation of higher forms (Echinoderms, some Cirrhipedes, some Tunicates). The next step is the differentiation of an upper and a lower surface in relation to the horizontal position, with mouth placed anteriorly, assumed by the organism in locomotion. With the differentiation of superior and inferior surface, a right and a left side, complementary one to the other, are necessarily also differentiated. Thus the organism becomes bilaterally symmetrical. The Cœlentera are not wanting in indications of this bilateral symmetry, but for all other higher groups of animals it is a fundamental character. Probably the development of a region in front of, and dorsal to, the mouth, forming the PROSTOMIUM, was acccomplished *pari passu* with the development of bilateral symmetry. In the radially symmetrical Cœlentera we find very commonly a series of lobes of the body-wall or tentacles produced *equally*—with radial symmetry, that is to say—all round the mouth, the mouth terminating the main axis of the body—that is to say, the organism being "telostomiate." The later fundamental form, common to all animals above the Cœlentera, is attained by shifting what was the main axis of the body, so that it may be described now as the "enteric" axis, whilst the new main axis, that parallel with the plane of progression, passes through the dorsal region of the body, running obliquely in relation to the enteric axis. Only one lobe or outgrowth of those radially disposed in the telostomiate organisms now persists. This lobe lies dorsally to the mouth, and through it runs the new main axis. This lobe is the PROSTOMIUM, and all the organisms which thus develop a new main axis, oblique to the old main axis, may be called prostomiate.

I have introduced these considerations relative to the changed structural axes of prostomiate, as compared with telostomiate organisms, in order to make clear what follows relative to ciliated bands and tentacles.

b. Ciliated bands and tentacles ; identity of these structures in Echinoderms and Vermes with the gill-tentacles of Polyzoa, Brachiopods, and Lamellibranchs ; hypothesis of the Architroch.—To Professor Huxley we owe the first perception of the identity of the ciliated bands of the Pluteus larva with the " wheel apparatus " of the Rotifera. Gegenbaur, in his 'Grundzuge,' further showed most ingeniously how two ciliated bands surrounding the embryo, one in front of and the other behind the mouth, could be derived from one single circlet circumscribing the mouth, and how, further, the hinder of the two circlets might be suppressed, leaving only a præoral circlet, which I have proposed[1] to call uniformly the "velum," whether it appears in Mollusc, Annelid, Rotifer, or Echinoderm.

It does not require very long consideration, in these days of the triumph of the doctrine of "uniformity of type in the structure of animals," to see that it is probable enough that *all the ciliated bands of Invertebrate embryos, and even of adult organisms, can be explained as derivatives of one primitive organ.* By "ciliated bands," I mean, not secondary and unimportant ciliated tracts, but those strongly marked ciliated ridges often drawn out into successive tentacula, which are at one time or other *dominant* organs in the animal possessing them, and which may remain throughout life as chief instruments in the economy. Such ciliated bands are the bands and processes of Echinoderm larvæ, the ciliated girdles of many Annelid embryos, the tentacles of Phoronis, and the tentaculated organ of Actinotrocha, the ciliated trumpet of Gephyræans, the "velum" of Molluscan embryos, the similar apparatus of Rotifera, the crown of tentacles of the Polyzoa, the gills and labial tentacles of the Lamellibranchia, and the spiral arms of the Brachiopods.

All these forms can, it appears to me, be derived from a ciliated girdle, which was developed, in all probability, around the ancestral organism by a specialisation of the ciliated ectoderm, at a time when the organism was telostomiate.

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[1] "Development of the Pond-snail." 'Quart. Journ. Mic. Sci.,' 1874.

The telostomiate planula, I conceive, ceased to develop cilia uniformly over its body-surface and acquired a special circlet of these appendages, not far distant from the mouth (Pl. XXV. fig. 1). The shifting of the main axis and acquirement of the prostomiate condition during later development would bring about the form now exhibited in the early phases of the ontogeny of Echinoderms, with which Gegenbaur starts his consideration of the subject. This form of girdle with the mouth in its centre may be termed the "Architroch" (figs. 2, 3). I cannot call to mind any existing representative of a *telostomiate* architrochophor (the cyclostomous Polyzoa are so only by recurrence), but the early stages of Echinoderms are *prostomiate* or *metaxial* architrochophors. So, too, is Actinotrocha, whilst the tentacles of Phoronis are simply an architroch drawn out into filaments. The gill filaments of the Polyzoa, with hippocrepian, and circular lophophor, alike correspond to a complete architroch drawn out into more numerous processes than we find in the Pluteus-larvæ or in Bipinnariæ, and must not be mistaken in consequence of their filamentary modification (figs. 17, 19). This development of tentacle-like filaments along the line of the ciliated band is a quite common, indeed, characteristic feature of the architroch and the circlets into which it divides. Thus in Rotifers (Stephanoceras), and in Gastropod embryos (Macgillivrayia, Ethella), the 'velum' is drawn out into filamentous ciliated tentacles (fig. 15).

The gill-filaments of the Lamellibranchs, *together with* the labial tentacles, form an incomplete architroch (fig. 16). To be complete the line of origin of the double set of gill-filaments which form the gill-plates,[1] should be continued on each side behind the foot (between the foot and anus). At this part the Lamellibranch's architroch is broken, but this will not appear surprising when the case of Rhabdopleura (see this Journal for 1874) is considered, in which alone, amongst Polyzoa, the architroch is incomplete and reduced to a pair of plume-like appendages; still less is it to be wondered at that the architroch should be broken through at this point, when we consider the enormous development of the muscular lobe within the architrochal area, the foot, truly a hypertrophied chin.

An important consequence of the view now advanced as to the nature of the gill-filaments of acephalous Mollusca is the serial homology of the labial-tentacles of Lamellibranchs with the gill-plates of the same animals. Continually all sorts of special homologies have been proposed for these organs. In reality, they are only specially modified parts of the architrochal band, not giving rise to filaments, but by a late modification of an original series of filaments giving rise to spongiose erectile lobes. They complete, anteriorly or præorally, the architroch of the Lamellibranch.

The reduction of the filiferous architroch in the Polyzoan Rhabdopleura to a plume is of the greatest importance, because *it allows us to assume, in other cases, that branchial plumes have possibly been developed by reduction of an architroch.*

Whilst the larvæ of certain Echinoderms (the Pluteus and Auricularia of Echinids and Holothurians) are architrochic, the Bipinnaria and Brachiolaria of Asterids present us with an important modification of the primitive condition, as does also the Auricularia of Holothurians, when it passes into the polytrochous condition. The ring surrounding the mouth becomes drawn out in such a way that it extends round the larva on each side (fig. 4), and its two extremities meeting and joining we have, as Gegenbaur has shown, two rings developed, whose plane is at right angles to that of the original single peristomial ring from which they develop. The anterior circle embraces the prostomium, the posterior, which is usually larger and oblique in direction, is metastomial. We find in the Echinoderms very near approaches made to this breaking of the architroch by a dorsal nipping-in, without the actual fusion being accomplished. I propose to call that condition of the cillary tract in which the fusion *is* accomplished "zygotrochic." The Asterid larvæ (fig. 12) are zygotrochic, so it appears is Tornaria (fig. 8), the larva of Balanoglossus. The two secondary circlets into which the architroch divides may be conveniently distinguished as the "cephalotroch" and the "branchiotroch." The "cephalotroch" is also known as the "velum." It is this portion only of the differentiated architroch which makes its appearance in the larvæ of the Gasteropodous Mollusca; it is this part only which appears in the case of many Annelid larvæ and in the Rotifera. The "branchiotroch" is so named on account of the fact that it is this portion of the differentiated architroch which most constantly gives rise to ciliated branchial filaments. Such are the filaments of Actinotrocha (fig. 13); such are the gill-filaments of the Lamellibranchs. I am inclined to think that gill-filaments in the adult, which cannot be directly traced to a larval branchiotroch, in fact, in cases where the larva possesses only a "velum," or cephalotroch, may yet be regarded justly as modifications of the branchiotroch in consequence of their position and structure alone. The two portions of the zygotroch, once differentiated from the architroch, may have acquired a considerable independence of one another in their development in some races, whilst in the archaic group of Echinoderms they retain a consentaneous growth.

In many Chætopoda, Platyelmia, and Eucephalous Mollusca, the embryo, when still almost spherical in form and diblastulous in structure, acquires the cephalotroch, which takes at this early period the position of an equatorial girdle (Pl. XXV, fig. 6). Such a larval form I have called the "trochosphere." It is clearly not a primitive form, but is derived, by the steps I have just indicated, by a series of adaptations from the telostomiate architrochopor. It is an *adaptational* larval form common to many marine organisms, and indicates that its ancestors must at one time or another, in larval or adult life, have exhibited the following conditions—(1) telostomiate architrochal, (2) metaxial architrochal, (3) zygotrochal, (4) cephalotrochal—that is, suppression of the branchiotroch.

Professor Semper has recently made the attempt to set up this much modified larval form, with its premature cephalic circlet, as an important ancestral form, and has announced a "Trochosphæra theory."

If the views which I have here expressed are well founded, Semper's theory of the trochosphere is not more valuable than his theory of Amphioxus.

Many ciliated larvæ have been called "telotrochic" (figs. 8, 13), in consequence of their possessing a perianal circlet of cilia. Gegenbaur is inclined, though not decisively, to refer this "telotroch" to the architroch, regarding it as the equivalent of the branchiotrochal moiety. This I cannot consider to be justified. The telotroch appears to be a *metameric* repetition of the architroch, or of its branchiotrochal moiety. That such is the case is suggested by the condition of the Tornaria-larva of Balanoglossus. It is possible that the ciliated circlets which are posterior to the area of the architroch or its derivatives, are to be regarded as altogether secondary structures, and indeed they are so upon any view of the case, in so far as metamerism is a secondary condition. Such secondary circlets as the telotroch and the other more or less numerous circlets of polytrochic larvæ, I propose to call "epitrochs," and, accordingly, a ciliated larva, whilst either architrochic or zygotrochic, may be "anepitrochic," or "monepitrochic," or "polyepitrochic."

The most remarkable polyepitrochic larvæ are those to which the Auricularian architrochic larvæ of the Holothurians give rise. The architroch of these larvæ becomes a zygotroch, a distinct cephalotroch or velum, belonging to the prostomial region, being pinched off from the branchial circlet; but this latter, instead of remaining as a single girdle, again breaks up into four circlets by development of cross-pieces in correspondence with a metamerism, often indicated also by the deeply-marked lobulation of the body. It is interesting to note that in this transient metameric segmentation of the Holothurian, the metameres agree with the more fully developed metameres of lineally segmented worms in the fact that, *whilst the first metamere consists of prostomium and metastomium, each succeeding metamere corresponds only to the metastomial portion of the first metamere.* This is clear in the case of the polyepitrochic Holothurian larva, since the metastomial circlets are developed by direct conversion of the metastomial portion (branchiotroch) of the zygotroch. In other polyepitrochic larvæ, as well as in monepitrochic larvæ, the epitrochs develop quite independently of the architroch or its parts. Terebratula and other Brachiopods present us with a polyepitrochic larva having an architroch anteriorly. Actinotrocha has one epitroch and an architroch. The larva of Dentalium possesses a cephalotroch, followed by many epitrochs independently developed. The same is true of some Pteropod larvæ. Many Chætopod larvæ are also in this condition.

It seems to be quite possible that the branchial filaments of Chætopod worms, as well as the branchiæ of the Eucephalous Mollusca, may, like the branchial filaments and plumes of the Acephalous Mollusca and the tentacular crowns of Phoronis and the Gephyræa, be ultimately traceable to the branchiotrochal moiety of the architroch.

Enumeration of the modifications of the Architroch.

A.—Architrochic forms:

1. Anepitrochic—

Pluteus of Echinids and Ophiurids; Auricularia of Holothurian; larval and adult Polyzoa; Lamellibranchs and Brachiopods; adult Phoronis; and also Bonellia, Thalassema, Sipunculus.

2. Monepitrochic—

Actinotrocha.

3. Polyepitrochic—

Larval Brachiopods (Kowalewsky).

B.—Zygotrochic, with separated cephalotroch and branchiotroch:

1. Anepitrochic—

Brachiolaria and Bipinnaria (of Asterids), some Gastropods (?)

2. Monepitrochic—

Tornaria.

3. Polyepitrochic—

Vermiform larva of Holothurians and Comatula.

c.—Cephalotrochic (with suppression of the branchiotroch):

1. Anepitrochic—

Adult Rotifera, the trochosphere larva of Worms and Molluscs, the veliger of Gastropods and Pteropods.

2. Monepitrochic—

The common two-girdled larva of Chætopods.

3. Polyepitrochic—

The polytrochic larvæ of Chætopods, and other worms, as also of Dentalium (Mollusc) and some Pteropods.

IV. THE NEPHRIDIA OR SEGMENTAL ORGANS OF THE ENTEROZOA.

In all classes of the Enterozoa there are other openings, usually small, into the cavity originally belonging to the archenteron, besides the mouth and the anus. In those Cœlentera which foreshadow the cœlom by developing a periaxial extension of the enteron or a perienteron, we find such apertures especially associated with the rudimentary cœlom. In the Actinozoa such apertures exist in the tentacles or at the aboral pole. In some Ctenophora two canals open from the as yet unspecialised cœlom to the exterior by two apertures placed at the aboral pole.

When once the cœlom is accomplished as a cavity definitely shut off from the "metenteron"—the name we now give to what remains of the archenteron—its communications with the exterior acquire a more important character. Whether it be that the respiratory trees or that the orifices of the ambulacral system in Echinoderma represent the communications established between the cœlom and the exterior in the Cœlonata, this appears certain, that in Rotifera, Flatworms, Gephyræa (*not* the genital ducts), Mollusca, in the metameres of Chætopoda, in the Vertebrata, and even in some Arthropoda, we have evidence of the existence of a single pair of canals more or less highly modified by glandular developments, which usually open by ciliated funnel-like mouths into the cœlom at one end and directly to the exterior in the neighbourhood of the anus, or into a cloacal chamber, at their other end, thus placing the cœlom in communication with the exterior.

This pair of ciliated funnels appears to be the same organ in all cases.[1] Primarily it develops like the stomodæum and proctodœum by an ingrowth of the ectoderm or deron. At present no name is in use for this important pair of organs; they are spoken of as "segmental organs" in some groups, as "primitive excretory organs" in others. Since very usually these canals acquire an excretory function and give rise to kidneys, though they may also serve as genital ducts, I propose to call them by the diminutive of the Greek word for a kidney—namely, "nephridium." The nephridia in Rotifers, and Turbellarians and Trematods, are the ciliated canals, though in the flat-worms it is impossible to say where in the canal system "nephridium" ends and "cœlom" begins. In Chætopoda the nephridia are the segmental organs, in Gephyræa the pair of organs opening into the cloaca, in Lamellibranchs they are the organs of Bojanus, in Brachiopoda they are the oviducts (so-called hearts), in Gasteropods they appear, at any rate, in the embryo, in many cases (Urnieren). In tracheate Arthropods the Malpighian filaments possibly are the nephridia, whilst the Vertebrate kidney and genital ducts have recently been traced by Balfour and Semper to a series of nephridia.

The terminology of the new doctrine as to the Vertebrate genito-urinary canals appears to me to need some clearing up, and I therefore submit the following:

The metameric segmentation of the primitive Vertebrate gives us a series of nephridia, derived from one single pair of nephridia in the still earlier unsegmented Vertebrate. The nephridia are not, however, in the metameric Vertebrate separate from one another, each with its own external aperture, as in Chætopod worms, but all (on one side) are developed on a common stem or duct, so that they form one organ on each side of the animal. This compound organ is a kidney; it may be called the "archinephron," its duct the "archinephric duct." By longitudinal fission parallel with its axis, the archinephric duct splits into two—one, the "pronephric duct," in connection with the more anterior nephridia which form the "pronephron;" the other, "the mesonephric duct," in connection with the posterior nephridia, forming the "mesonephron." The pronephron (Kopfnieren) aborts, the pronephric duct becomes the oviduct; it is frequently called Müller's duct. The mesonephron is the Wolffian body, its duct the Wolffian duct. Its anterior

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[1] Gegenbaur recognises two kinds of primitive excretory organs which, if really distinct, might be called 'anterior' and 'posterior nephridia' respectively.

nephridia form the ducts for the testis. Finally, a metanephron, with metanephric duct distinct from the Wolffian or mesonephric duct, may develop by a later increase of nephridia posteriorly. This metanephron with metanephric duct exists in sharks; in abranchiate Vertebrates it becomes the permanent kidney, and its duct the ureter.

V. LATER DEVELOPMENT OF THE DERON AND ENTERON.

In what has preceeded we have given the outline of the cellular foundations of the superficial and deep tissues of the body-wall—of the lining membrane and corpuscles of the lymphatic hæmal spaces and vessels, and of the internal and external tissues of the alimentary tract.

Origin of Nerve-tissues.—It only remains to point out briefly, in order to complete this sketch, that the ectoderm having broken up (as we saw above) into epiblast and the musculo-skeletal portion of the mesoblast—or, as we may put it, into neurodermal and myoskeletal moieties—now proceeds further in differentiation. For the neurodermal tissue, which in position is the true representative of the original ectoderm, now separates into neural and dermal groups of cells. This does not, however, occur by a general splitting of the neuroderm or epiblast, but by *localised* differentiation. In all classes of organisms possessing nerve-centres or masses of nerve ganglion-cells these structures have been traced in development to the neuroderm or epiblast. It is probable that primitively the whole nervous apparatus is to be traced to epiblast, and that where (as appears very frequently to be the case) masses of nerve-cells and fibres arise deeply by differentiation of cells lying in the mesoblast, such nervous structures are not to be supposed to have taken their origin by a gradual metamorphosis of musculo-skeletal or of vascular elements, but their present ontogenetic development at points devoid of direct connection with epiblast is to be explained as we have explained other shiftings from ancestral connections—namely, by a very early passing over of hereditary nervous molecules from cells destined to form epiblast into cells destined to form mesoblast.

In all Prostomiata, or, what is same thing, in all Bilateria or cœlomate Enterozoa, the main tracks occupied by the differentiated nervous tissue have the same position. They appear primarily as paired laterally placed centres within the prostomium. From them radiate fibrous tracts. Their further development consists in elongation, so that they become lateral cords, and the fibrous and spherical cell-elements which make up nerve tissue may be evenly distributed along these tracts, or the spherical elements may be concentrated at important points in obedience to the proportions assumed by other parts of the body, *e. g.* metameric segmentation of muscles, or development of a mesopod (molluscan foot), or of a special sense organ. The lateral tracts once established show the strongest tendency to unite into a single tract by gradually taking up a median position. This junction of the lateral tracts may occur either dorsally or ventrally, and the result is the production of a dorsal or of a ventral nerve mass. In most of the higher Enterozoa the junction is effected dorsally in the region of the prostomium and ventrally in the metastomial region. Cases of very partial or altogether ineffective fusion of the metastomial portions of the nerve tracts are common.

Archenteron, Parentera, Metenteron, Mesenteron, and *Hepatic Cæca*—The successive differentiations or subdivisions of the original digestive cavity (archenteron), lined by the endoderm or enteric cell layer, may be rapidly summarised as follows:—The archenteron (Urdarm) breaks up into the two (subsequently fused) *parentera* and the axially-placed *metenteron.* The parentera become cœlom, the metenteron retains digestive functions. The parentera form cœlomic and vascular epithelium, blood-corpuscles and female reproductive tissue (ova). According to Ed. Van Beneden the male reproductive tissue is formed from ectodermal (deric) cells. The metenteron is joined by stomodæum and proctodæum, and now gives rise in a large number of cases to two cæcal outgrowths (the hepatic cæca), often of great size, which resemble in some cases the cœlomic parentera. According to the view here taken, however, they have nothing to do with the cœlomic parentera, but are of much later origin. They become widely separated in character from the rest of the metenteron, which must now be distinguished as *mesenteron,* and continue to open into it by a narrow passage, through which their secretion passes. Thus, then, as archenteron divides into parentera and metenteron, so metenteron divides into *hepatentera* or hepatic cæca and *mesenteron.*

Other diverticula to which the mesenteron gives rise do not require notice here. The salivary diverticula, it may be well to note, are parts of the stomodæum, whilst the glandular cæca, ducts, and tooth-like hardenings, which belong to the sexual organs very generally, are developed from the proctodæum just as similar parts belonging to the mouth develop from stomodæum.

VI. The more general Causes and Modes of Development.

In the preceding sections of this essay we have discussed the probable succession of forms and the particular phases of increasing complexity which animal organisms have presented in the course of their historical development, and an attempt has been made to show that the phenomena of individual development from the egg may be considered as more or less slurred and interrupted recapitulations or epitomes of the historic development.

Now, let us take a more general point of view, and endeavour to state *what* are the more general causes or antecedents of organic development, and what the more general effects of those causes, that is to say, the *modes* of their operation; so we shall come nearer to the ultimate goal of biology which is the accounting for the phenomena of living matter or protoplasm by reference to the laws of chemistry and physics.

In order to look at development from the physiological point of view it is necessary to take a glance at the structure of organisms in relation to their activities.

The following propositions contain the essential doctrine of the interdependence of structure and function.

1. Every organism is either a single corpuscle of protoplasm or an aggregate of such corpuscles, variously modified.

2. A corpuscle of protoplasm or "unit of organic structure" is called a plastid. A plastid which possesses a differentiated kernel or nucleus is called a cell; one devoid of nucleus is called a cytod.

3. The living substance of all organisms, whether consisting of many or of one single plastid, exhibits the following activities, which are explained by its chemical and physical constitution:—1. Contractility. 2. Irritability. 3. Reception and assimilation of foreign matter. 4. Chemical change and secretion. 5. Respiration, *i. e.* combination with oxygen and excretion of carbonic acid. 6. Reproduction, either resulting in growth or, when accompanied by self-division, in multiplication of individuals.

4. In the lowest organisms, which consist of one single plastid, these various activities are carried on by one and the same corpuscle of protoplasm. In the higher organisms, consisting of many plastids, they are exhibited more or less clearly by each and all, but are intensified variously in particular plastids. According to their position and the particular

activity which they pre-eminently exhibit, the plastids of such an organism vary in form, and the nature and amount of chemical change to which the protoplasm composing them has been subject varies also. They may be spherical, columnar, prismatic, scale-like, star-shaped, spindle-shaped (fusiform), branched, or united to form fibres. The substance between the plastids may be absent (when the plastids are continuous), very small in amount or large in amount. It may be solid and dense, or gelatinous and viscous, or fibrous or liquid.

5. When a number of plastids exhibiting pre-eminently one kind of activity (see sec. 3), and having one particular form and one particular kind of intermediate substance (if any) are found forming a layer or separable tract in an organism they are said to constitute a TISSUE.

6. In a higher organism the activities enumerated in sec. 3 (each of which is exhibited more or less by each of its constituent plastids) are carried on through the agency of a number of specially adapted parts, which are known as ORGANS. Every organ has its FUNCTION in relation to one or other of these activities. Many tissues may enter into the composition of an organ. A series of connected organs forms a SYSTEM.

7. The development of organisms (of which in the earlier part of this essay we have traced the concrete expression, so far as relates to animals) is primarily caused by the advantage gained for an organism in the struggle for existence by the distribution of the activities specified in sec. 3—amongst special parts, that is to say, by the advantages gained by the possession of elaborate tissues and organs.

8. The possibility of development is solely due to the physico-chemical constitution of protoplasm, in virtue of which constitution it is subject to (A) *unlimited Variation* by the action of incidental forces, and to (B) the *permanence of impressions* or *Memory*. In virtue of the memory of protoplasm, *fortunate* variations, acquired in the life-and-death conflict with the environment, become *permanent* adaptations in such organisms as survive (survive as individuals or as new generations). Those with unfortunate variations die off in consequence of the want of fitness of their variations (both newly acquired and constitutional) to the conditions presented by the struggle for existence. Thus the selection of new variations, and the constant accumulation of old-acquired improvements by the operation of the protoplasm's memory in the survivors of the struggle for existence goes on. The elaborate distribution of functions amongst specialised

parts of the organism has been in this way slowly built up. The final advantage of highly complicated structure has been gained by certain representatives of the animal and the vegetable pedigree through Adaptation, due to the property of unlimited variation, and through Heredity, which is only another name for Memory or permanence of impression, as manifested by the detached reproductive bits of an organism.

9. The process of the development of new tissues or new organs in a race of organisms where such tissue or organ has no previous existence, must follow certain definite methods. From the nature of the causes at work (secs. 7 and 8), the new development must be excessively gradual. It may be taken as a law of development that no *really new* part *ever* does make its appearance, every apparently new tissue or organ which may strike the morphologist as novel, being necessarily only a modification of a pre-existing tissue or organ. The absolute continuity of forms is a deduction from the law of evolution, and the hypothesis of unity of organization.

The processes of differentiation by which organisms acquire modifications in structure, may be grouped under the following general heads: (1) Polar Repetition of units of structure. (2) Segregation of chemically and physically differing materials. (3) Hypertrophy and Atrophy of parts relatively to one another. (4) Concrescence (of polar units or of appendages and tissues).

Polar Repetition stands first in this list, since it is dependent on one of the most important and distinctive features of protoplasm, with which only crystalline polarity can be compared. The existence of multicellular organisms instead of large unicellular organisms is due to the peculiar conditions of molecular cohesion in protoplasm; in fact, the polar repetition of the simplest organic unit is at the bottom of all the higher organic differentiation. Further, we find that the groups formed by the primary units or plastids, and which Herbert Spencer calls "aggregates of the second order," may, like the primary units, cease to grow indefinitely as secondary units, and, with or without fission, the growing secondary unit arranges itself as a *number* of such secondary units (in line as in worms, or irregularly as in polyp-trees, or radially as in compound Tunicates), and itself becomes "an aggregate of the third order."

Thus the polarity of protoplasm is a very important element in the differentiation of organic forms.

Segregation may slowly bring about a difference in the lish the sharpest demarcation between such portions; all separation of constitutional and structural elements at one time united comes under this head.

Hypertrophy and *Atrophy* are the most obviously efficient methods of differentiation when once a beginning has been made, either by polar repetition or mere segregation. Hypertrophy enlarges one unit or set of units, whilst the rest remain stationary, or the one half of a cell already differentiated by segregation is atrophied, whilst the other is hypertrophied.

By Atrophy cilia disappear from the surface of the body, and become confined to a single band; by Hypertrophy this band becomes drawn out into filamentous tentacles.

The majority of developmental differentiations, which the careful study of ontogeny and the cautious use of the "recapitulation hypothesis" enable us to infer as having historically occurred in the course of animal evolution, can be reduced to terms of Hypertrophy and Atrophy.

Concrescence finally, though a less striking, is by no means a less important form of structural modification than those which we have already noticed. Concrescence undoes the work of Polar Repetition and Segregation. By it multicellular tissues become syncytia, segmented animals lose all trace of their segments, or their segmentation becomes obscured and obliterated over large tracts.

This is the process exhibited in the fusion of nerve-ganglia, in the adhesion and combination of gill-filaments and in the substitution of one continuous unit for a number. In the last case it is not to be confused with hypertrophy and concurrent atrophy.

VII. Classification.

Classifications of many kinds are possible and convenient for various purposes in reference to the series of animal forms. A classification may be said to be "subjective" or to derive its importance from subjective relations which sets up some particular characters chosen for reasons best known to the person who chooses them, as the test-points in reference to which animals shall be classified. It has only lately been recognised as possible (namely since the fact has been admitted, that all living and extinct organisms are members of one great family tree) to investigate the claims of a system of classification to acceptance by reference to an objective standard. Whilst many classifications may be and are termed "objective" (because they are logically correct), which, in consequence of their being purely mental abstractions, *arbitrarily* chosen from among many possible abstractions, would be more justly termed "subjective;" yet there is one objective classification possible, which is no mental abstraction, but as corresponding with the actual order in which the objects of classification were brought into existence may claim to be *the* objective and natural classification *par excellence*. This classification would be exhibited in a complete statement of the pedigree of the animal kingdom.

It is certain that we shall never be able to set forth with anything like completeness this real or objective genealogical classification. Accordingly, all our attempts at it may be called, as they have been, subjective classifications, since they depart from the objective reality in proportion as our imagination has to supply the gaps in our knowledge—in proportion as in them inference is given a particular form where our acquaintance with fact only justifies a general form. But it is clear enough that in its broad outlines we are likely enough as knowledge increases to make our genealogical classification correspond with the reality if we consistently aim at that object.

What there is of objective in such classifications is at any moment capable of being tested and discussed, whereas classifications which ignore genealogical speculations, thougb they may claim indisputable objectivity as their justification, yet fail to commend themselves equally to their authors and to contemporary naturalists. Such classifications may be as numerous as they are true, but, after all, their utility is measured by the approximation which they make to the formulation of what they profess to ignore, namely, the pedigree. The logical fact set forth in this kind of classification, however indisputable, is one of small or even over-estimated consequence.

In fact, if we agree with Mill that the higher kind of classification is that which seeks " to arrange objects in such groups, and those groups in such an order as will best conduce to the ascertainment and remembrance of their laws," we cannot doubt that a classification of animals which keeps the law of evolution steadily in view is more likely to be that which will best conduce to the ascertainment and remembrance of its operations than one which expressly ignores that law.

Homogeny and homoplasy—Progression and degeneration.—In the attempt to draw up a true pedigree of the animal kingdom it is clear enough that we are seeking to trace the lines of heredity, and that we must proceed primarily on the assumptions (1) that organisms of like structure—that is, with like adaptations—are related to one another by blood with a degree of closeness which is in direct proportion to the closeness of the likeness; (2) that the general effect of evolution in relation to organisms has been to effect a progress from simpler structural conditions to more complicated, whence it is inferred that the more simple organisms which to-day exist are surviving representatives of the earlier phases of organic evolution, the race to which they belong never having attained a higher level than it does to-day, and that all existing organisms may be arranged according to the degrees of complication of their structure in several ascending series, the degrees in which represent so many stages attained to and passed through by the ancestors of the most highly complicated member of the series.

Having started with these two assumptions, as all those who have attempted phylogenetic classification have done, it is very soon found to be necessary to qualify and relax the general application of both the principles assumed. It is very soon recognised (and, indeed, is universally admitted) that there are many cases of a pair of organisms which are, on the whole or as to some striking detail, alike in structure—that is to say similarly adapted—and yet (as we learn from their developmental history or from some one indisputable structural feature) do *not* owe that similarity to heredity, but to an independent identity in adaptation occurring in the two cases in consequence of a recurrence of the same adaptational conditions. Such similarity is said to be due to homoplasy,[1] whilst hereditary likeness is due to homogeny. In phylogenetic classification, then, we have to be especially on our guard against mistaking homoplastic for homogenetic agreements.

An "objective" method of classification which should ignore the doctrine of evolution could not fail to confuse organisms related by homogeny with others related to them only by homoplasy; and, indeed, this was notoriously the case with the classifications of the first half of this century.

Again, as to the second assumption of "a continuous progression" in all the myriad branches and twigs of the organic family tree—the assumption of a continuous flow *onwards* (slower or faster, but always forward) in all the multifarious streamlets into which the original stream of life has subdivided, this, too, has been universally qualified. It has been admitted in certain very obvious cases, *e. g.* many

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[1] This term was first proposed in my article "On the Use of the term Homology in Modern Zoology," 'Annals and Mag. Nat. Hist.,' 1870.

parasitic and sub-parasitic animals, that there has been a *reversal* of the stream of development, and that *these forms are the result, not of progressive adaptation, but of retrogressive adaptation or degeneration.*

In regard to both assumptions, the qualification has been admitted grudgingly and insufficiently up to the present time. It is not, as a rule, sufficiently conceded that homoplasy is as much a *vera causa* of structural likeness as homogeny, and that, whilst we pursue the logical method of assuming (to begin with) a uniform cause—namely, homogeny—in order to account for structural likeness, yet we should be on the alert whenever difficulty arises in the consequences deduced in a particular case from the employment of homogeny, to test at once the applicability of homoplasy.

Thus Mr. Jhering, appropriating to himself the doctrine and the term "homoplasy," has suggested that, in the group of the Mollusca (as usually recognised by naturalists), are included two homoplastic groups of totally different origin. There is nothing improbable in this application of the doctrine of homoplasy, and indeed I am inclined to think that some such application of it to the group of the Arthropoda is the only escape from the difficulties which the hypothesis of homogeny presents in regard to that group. With regard, however, to the Mollusca, Mr. Jhering appears to have been singularly unfortunate in the skill which he has displayed in using borrowed tools. The two homoplastic groups which Mr. Jhering fancies he has detected under the common type Mollusca have each of them, according to him, *independently developed that very remarkable apparatus, the lingual ribbon, with its cushions and muscles.* Such an assumption is entirely devoid of justification. We see in Mr. Jhering's case an interesting exhibition of the necessity for ascertaining and respecting the limits within which homoplasy may reasonably be assumed as a possible cause of structural identity in a comparison of organisms. We know of no case in which there is any ground for inferring that homoplasy—that is, independent adaptation—has produced two structures so complex and varied in detail and yet so absolutely the same in all respects as are the lingual apparatus of Chiton, on the one hand, and of the normal Gastropoda, on the other. The assumption, without any collateral evidence in its favour, of such potency for homoplasy, is a violation of common sense, sufficiently reckless, even without the employment of folio paper, to give to its perpetrator a temporary notoriety.

We have every reason to hold homoplasy responsible for the agreement (such as it is) between the beak of the turtle and the beak of the bird, between the gill-plate of Lamellibranchs and the pharynx of low Vertebrates, between the segmentation of some Platyelmia and the segmentation of Appendiculata, possibly for the change of legs into jaws in Crustacea on the one hand and in Tracheata on the other, or possibly for the development of tracheal tubes once in Peripatus, and also a second time in Insects; but in none of these cases are we led to ascribe anything to homoplasy beyond the production of *very general* or *very simple* agreements, and until we have reasons for supposing that it can act continuously and cumulatively so as to produce *elaborate* correspondences, we are clearly not justified in assigning this power to it in a particular case.

It is chiefly through the valuable pamphlet of Anton Dohrn[1] that attention has been directed to the logical necessity of admitting the possibility of very widely prevalent degeneration. At present naturalists are so very generally persuaded (by habit, not by reason) of the universality of progression—that no one has attempted to face the counter theory of universal degeneration which Dohrn put forward.

Whilst this theory is passed over with silent contempt it appears to me to have as strong a logical position as the theory of universal progression. The evidence of degeneration is admitted as conclusive in the case of the parasitic Crustacea and Cirrhipedes. It is equally incontestable in that very large and varied group of non-parasitic organisms, the Tunicata (Urochordate Vertebrata).[2] The destruction of a very few forms from among the Tunicates would leave us without the evidence of their degeneration. We should then, on the assumption of the prevalence of progression, regard the Tunicates as representing the highest pitch of structural complexity to which their race had attained, and assign them an erroneous position. Obviously, we must be liable to make this mistake with regard to every isolated group, but especially liable to do so in the case of very small groups or isolated genera of simple structure. So strong is the case in favour of degeneration, that at present all that can be said against it and in favour of progression, with regard to any

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[1] 'Ursprung der Wirbelthieren.'

[2] The whole argument as to the Tunicates of course rests on the view supported by many arguments, that the larval urochord, which many of them possess, is *not* a larval organ acquired by larval adaptation, but is hereditary and transmitted from adult ancestors.

particular case, is this—that the general doctrine of evolution justifies us in assuming, at some period or other, a progression from the simplest to the most complicated grades of structure; that we are warranted in assuming at least one progressive series leading from the monoplast to man; and that *until we have special reason* to take a different view of any particular case we are bound to make the smallest amount of assumption by assigning to the various groups of organisms the places which they will fit into, on the supposition that they do represent in reality the original progressive series. Nevertheless, any naturalist would find it very difficult to prove, or render highly probable, that many of the Protozoa are *not* descended from Enterozoa by degeneration; that Dicyema is *not* a degenerate flat worm; that the whole race of corals and polyps are *not* degenerate descendants of far more highly developed, worm-like, free-swimming ancestors.

When, therefore, the hypothesis of degeneration presents itself as a solution of any special morphological difficulty, we need have no scruples or prejudices in favour of the doctrine of universal progression, which should prevent us from accepting it.

In the following tables of classification I have made use of the term "phylum," proposed by Haeckel, instead of "sub-kingdom," "embranchement," or "typus." The phyla are so many great diverging branches of the family tree of animals. Classes are the branches borne by phyla, orders are the branches borne by classes. I have introduced the term "branch" as an equivalent for subphylum, or subclass, as the case required.

The most important explanation which is necessary here is with regard to the terms "grade" and "appendix," which I have frequently introduced. Whilst all the other terms indicate branches of the pedigree diverging from a very nearly common point (thus all the classes in a phylum are supposed to diverge from one common point unless it is otherwise indicated), the various "grades" are introduced to separate the starting-points of the branches; a certain advance in differentiation of structure separates the branches of a higher grade from those of a lower. An 'appendix' is an assemblage of 'degraded' examples of the group to which it belongs.

Tabular View of the Phyla of the Animal Kingdom.

ANIMALIA.

Organisms incapable of assimilating either N or C from their simpler water-soluble compounds, and therefore provided (excepting parasites) with the means of ingesting and acting upon the solid substance of other organisms.

Grade I.—PLASTIDOZOA.

Animals consisting of single plastids, or of groups of plastids not differentiated into cell-layers.

PROTOZOA.

Grade II.—ENTEROZOA.

Animals consisting of many plastids primarily arranged in two layers surrounding a food-receiving cavity—the enteron (the lumen of which is obliterated in some parasites).

Grade 1 (of the Enterozoa) CŒLENTERA (Diploblastica).

Enterozoa in which the enteron remains as a continuous cavity, either simple or much ramified, coextensive with the body wall. Persons telostomiate, generally with radial symmetry.

Phylum 1.—PORIFERA.
,, 2.—NEMATOPHORA.

Grade 2 (of the Enterozoa) CŒLOMATA (Triploblastica).

Enterozoa in which a second cavity containing hæmolymph—viz. the cœlom—entirely shut off from, though in its origin a part of, the enteron, is developed between the body wall and the enteric wall. Persons primarily prostomiate, bilaterally symmetrical, with paired nephridia and nerve tracts.

Phylum 1.—ECHINODERMA.
Branch *a*. Ambulacrata.
,, *b*. Tentaculata.

Phyl.	*Phyl.*	*Phyl.*
2.—PLATYELMIA. Br. *a*. Ciliata. ,, *b*. Suctoria.	4.—GEPHYRÆA.	6.—ENTEROPNEUSTA.
3.—APPENDICULATA (PARAPODA). Br. *a*. Chætopoda. ,, *b*. Rotifera. ,, *c*. Gnathopoda.	5.—MOLLUSCA (MESOPODA). Br. *a*. Eucephala. ,, *b*. Lipocephala.	7.—VERTEBRATA. Br. *a*. Urochorda. ,, *b*. Cephalochorda. ,, *c*. Craniata.

Phyl. 8.—NEMATOIDEA. *Phyl.* 9.—CHÆTOGNATHA.

N.B.—On account of their very dubious affinities and probable degeneration, no attempt is made in the above synopsis to include the following forms: the Gastrotricha (Chætonotus, &c.), Desmoscolex, Echinoderes and the parasites Dicyemida and Echinorhynchus.

CLASSES AND ORDERS OF THE PROTOZOA.

Grade A. Gymnomyxa.

Class.	*Order.*	*Examples.*
I. GYMNOMYXA	1. Homogenea	*Protomyxa.* *Protamœba.*
	2. Reticularia	*Pleurophrys* *Miliola.* *Nummulites.*
	3. Amœboidea	*Arcella.* *Pelomyxa,* *Amœba.*
	4. Flagellata	*Monas.* *Anthophysa.*
	5. Catallacta	*Magosphæra.*
	6. Labyrinthulida	*Labyrinthula.* *Chlamydomyxa.*
	7. Radiolaria	*Sphærozoon.* *Acanthometra.* *Actinospherium.*

Grade B. Corticata.

I. CORTICATA	Gregarinidæ	*Monocystis.* *Gregarina.*

Grade C. Stomatodea.

I. SUCTORIA	Suctoria	*Acineta.* *Ophryodendron.*
II. CILIATA.	1. Holotricha	*Opalina.* *Trachelius.*
	2. Heterotricha	*Stentor.* *Paramœcium.*
	3. Hypotricha	*Euplotes.* *Schizopus.*
	4. Peritricha	*Vorticella.* *Peridinium.* *Codonella.*
	5. Calycata	*Torquatella.*
III. PROBOSCIDEA	Noctilucida	*Noctiluca.*

CLASSES OF THE PORIFERA.

I. CALCISPONGIÆ	*Ascon.* *Leucon.* *Sycon.*
II. FIBROSPONGIÆ	*Euspongia.* *Spongilla.* *Thethya.* *Euplectella.*
III. MYXOSPONGIÆ	*Halisarca.*

Classes and Orders of the NEMATOPHORA.

Class.	*Order.*	*Examples.*
I. Hydromedusæ .	1. Hydriformes .	*Hydra, Tubularia.* *Sertularia.*
	2. Siphonophora	*Physophora.* *Velella.*
	3. Monopsea .	*Geryonia.* *Æginopsis.*
II. Podactinaria	Podactinaria .	*Lucernaria.*
III. Discomedusæ	Discomedusæ .	*Rhizostoma.* *Aurelia.*
IV. Hydrocorallinæ .	1. Petrosa . .	*Stylaster.* *Millepora.*
	2. Graptolitidæ .	*Graptolites.*
V. Anthozoa .	1. Hexactiniæ .	*Actinia, Oculina.* *Antipathes.*
	2. Tetractiniæ .	*Cerianthus.*
	3. Octactiniæ .	*Alcyonium.* *Tubipora.*
VI. Ctenophora.	1. Eurystoma .	*Beroë.*
	2. Saccata . .	*Pleurobrachia.* *Callianira.*
	3. Tæniata. .	*Cestum.*
	4. Lobata . .	*Bolina.*

Classes and Orders of the ECHINODERMA.

Branch A. **AMBULACRATA.**

I. Holothuridea	1. Pneumonophora	*Holothuria.* *Molpadia.*
	2. Apneumona .	*Oncinolabes.* *Synapta.*
II. Echinoidea .	Grade A.	*PALÆECHINI.*
	1. Melonitidæ .	*Melonites.*
	2. Eocidaridæ .	*Eocidaris.*
	Grade B.	*AUTECHINI.*
	Branch 1.	Desmosticha.
	1. Regularia .	*Echinus.* *Cidaris.*
	2. Exocyclica .	*Galerites.* *Echinoneus.* *Dysaster.*
	Branch 2.	Petalosticha.
	1. Clypeastridæ .	*Clypleaster.* *Echinocyamus.*
	2. Spatangidæ .	*Ananchytes.* *Pourtalesia.*

Class.	*Order.*	*Examples.*
III. ASTEROIDEA	Grade A.	*ASTERIÆ.*
	1. Colastra	*Uraster.* *Solaster.* *Astropecten.*
	2. Brisingastra	*Brisinga.*
	Grade B.	*OPHIURÆ.*
	1. Ophiastra	*Ophiura.* *Ophiothrix.*
	2. Phytastra	*Euryale.* *Saccocoma.*

Branch B. **TENTACULATA.**

I. CRINOIDEA	1. Tessellata	*Cyathocrinus.* *Marsupites.*
	2. Articulata	*Comatula.* *Rhizocrinus.*
II. BLASTOIDEA	1. Elœacrina	*Elœacrinus.* *Pentatrematites.*
	2. Eleutherocrina	*Eleutherocrinus.*
III. CYSTIDEA	1. Agelacrina	*Hedriaster.* *Hemicystites.*
	2. Echinencrina	*Sphæronites.* *Stephanocrinus.*

CLASSES AND ORDERS OF PLATYELMIA.

Branch A. **CILIATA.**

I. PLANARIÆ	1. Rhabdocœla	*Mesostomum.* *Microstomum.*
	2. Dendrocœla	*Polycelis.* *Bipalium.*
II. NEMERTINA	1. Anopla	*Lineus.* *Nemertes.*
	2. Enopla	*Borlasia.* *Prorhynchus.*

Branch B. **SUCTORIA.**

I. TREMATOIDEA	1. Monogenea	*Aspidogaster.* *Polystoma.*
	2. Digenea	*Distoma.* *Monostoma.*
II. CESTOIDEA	1. Caryophyllidea	*Caryophyllæus.*
	2. Tetraphyllidea.	*Tetrarhynchus.* *Phyllobothrium.*
	3. Diphyllidea	*Echinobothrium.*
	4. Pseudophyllidea	*Ligula.* *Bothriocephalus.*
	5. Cyclophyllidea	*Tænia.*

Class.	*Order.*	*Examples.*
III. Hirudinea	1. Pericœla	*Astacobdella.*
	2. Bdellidea	*Pontobdella.* *Nephelis.* *Hirudo.*

Classes and Orders of the APPENDICULATA.

Branch A. **CHÆTOPODA.**

I. Oligochæta	1. Naidina	*Nais.* *Chætogaster.*
	2. Sœnurina	*Tubifex.* *Enchytræus.*
	3. Lumbricina	*Lumbricus.* *Acanthodrilus.*
II. Polychœta	1. Vagantia	*Nereis.* *Polynoe.*
	2. Sedentaria	*Arenicola.* *Sabella.*
	3. Haliscolecina	*Capitella.*
Appendix a	Myzostoma	*Myzostoma.*
Appendix b	Archisyllidea	*Saccocirrus.* *Polygordius.*

Branch B. **ROTIFERA.**

Rotifera	1. Arthroptera	*Pedalion.*
	2. Chœtoptera	*Triarthra.* *Polyarthra.*
	3. Loricata	*Brachionus.* *Noteus.*
	4. Tubicola	*Stephanoceras.* *Melicerta.*
	5. Bdelligrada	*Hydatina.* *Rotifer.*
Appendix	Mutica	*Balatro.* *Asplachna.*

Branch C. **GNATHOPODA.** (Syn. Arthropoda).

Grade A. Malacopoda.

I. Peripatidea . . . . . . *Peripatus.*

Grade B. Condylopoda.

Class.	*Order.*	*Examples.*
I. Crustacea .	*Grade* A.	*ENTOMOSTRACA.*
	1. Cirrhipedia .	*Lepas.* *Peltogaster.*
	2. Copepoda .	*Cyclops.* *Lernæa.*
	3. Ostracoda .	*Cypris.* *Cypridina.*
	4. Branchiopoda .	*Daphnia.* *Apus.*
	Grade B.	*MALACOSTRACA.*
	Branch A.	Thoracostraca.
	1. Schizopoda .	*Mysis.* *Thysanopus.*
	2. Stomapoda .	*Squilla.*
	3. Decapoda .	*Astacus.* *Pagurus.*
	4. Cumacea .	*Diastylis.*
	Branch B.	Arthrostraca.
	1. Isopoda .	*Oniscus.* *Anilocra.* *Tanais.* *Praniza.*
	2. Amphipoda .	*Gammarus.* *Hyperia.* *Cyamus.*
Insecta II, Hexapoda .	Grade A.	*MASTICANTIA.*
	1. Tocoptera .	*Campodea.* *Libellula.* *Phryganea.* *Termes.* *Blatta.*
	2. Coleoptera .	*Dystiscus.* *Stylops.*
	3. Hymenoptera .	*Vespa.* *Formica,*

Class.	*Order.*	*Examples.*
	Grade B.	*SUGENTIA.*
	1. Rhyncota .	*Aphis.* *Cicada.* *Nepa.* *Cimex.*
	2. Diptera .	*Musca.* *Tipula.*
	3. Lepidoptera .	*Papilio.* *Sphinx.*
INSECTA III. MYRIAPODA .	1. Chilognatha .	*Julus.* *Polyzonium.*
	2. Chilopoda .	*Scolopendra.* *Scutigera.*
IV. ARACHNIDA .	*Branch* A.	TRACHEOPULMONATA.
	1. Scorpionidea .	*Scorpio.* *Chelifer.*
	2. Pedipalpa .	*Phryne.* *Thelyphonus.*
	3. Galeodea .	*Galeodes.*
	4. Araneida .	*Mygale.* *Lycosa.*
	5. Phalangida .	*Opilio.* *Gonyleptus.*
	6. Acarina . .	*Hydrachna.* *Demodex.*
	Branch B.	BRANCHIOPULMONATA.
	1. Xiphosura .	*Limulus.*
	2. Eurypterina .	*Pterygotus.* *Slimonia.*
	3. Trilobitina .	*Phacops.* *Ilenus.*
	Appendix.	METARACHNÆ.
	1. Linguatulina .	*Linguatula.*
	2. Tardigrada .	*Arctiscon.* *Macrobiotus.*
	3. Pycnogonida .	*Pycnogonum.* *Phoxochilidium.*

CLASSES AND ORDERS OF THE MOLLUSCA.

Branch A. **EUCEPHALA.**

Class.	*Order.*	*Examples.*
	GRADE A. **Lipoglossa.**	
SOLECOCMORPHA	. . . . .	*Neomenia.*
	GRADE B. **Echinoglossa.**	
I. GASTROPODA	GRADE *a. AMPHOMŒA.*	
	1. Polyplacophora	*Chiton.* *Chitonellus.*
	GRADE *b. COCHLIDES.*	
	1. Autocochlides	*Patella.* *Buccinum.*
	2. Natantia .	*Atlanta.* *Pterotrachea.*
	3. Cryptocochlides	*Aplysia.* *Eolis.*
	4. Pulmonata .	*Limax.* *Limnæus.*
II. CEPHALOPODA	GRADE *a. PTEROPODA.*	
	1. Thecosoma .	*Hyalæa.* *Criseis.*
	2. Gymnosoma .	*Clio.* *Pneumodermon.*
	GRADE *b. SIPHONOPODA.*	
	1. Tetrabranchia .	*Orthoceras.* *Nautilus.*
	2. Dibranchia .	*Spirula.* *Loligo.*
III. SCAPHOPODA	. . . .	*Dentalium.*

Branch B. **LIPOCEPHALA.**

I. TENTACULIBRANCHIA (Bryozoa)	Branch *a.* HOLOBRANCHIA.	
	Grade *a. Ectoprocta.*	
	1. Phylactolæma	*Lophopus.* *Plumatella.*
	2. Gymnolæma .	*Paludicella.* *Flustra.*
	Grade *b. Entoprocta.*	
	Pedicellinea .	*Pedicellina.* *Loxosoma.*
	Branch *b.* PTEROBRANCHIA.	
	Podostoma .	*Rhabdopleura.*

Class.	*Order.*	*Examples.*
II. SPIROBRANCHIA (Brachiopoda)	1. Ecardines	*Discina.* *Lingula.*
	2. Testicardines	*Terebratula.* *Spirifer.*
III. LAMELLIBRANCHIA	1. Asiphonia	*Arca.* *Unio.*
	2. Siphonata	*Venus.* *Teredo.*

CLASSES OF THE GEPHYRÆA.

I. ECHIURIDÆ.	*Echiurus.* *Bonellia.*
II. PRIAPULIDÆ	*Priapulus.* *Halicryptus.*
III. SIPUNCULIDÆ	*Sipunculus.* *Aspidosiphon.*
IV. PHORONIDÆ	*Phoronis.*

SUBDIVISIONS OF THE NEMATOIDEA.

I. NEMATOIDEA	1. Ascaridæ	*Ascaris.* *Oxyuris.*
	2. Strongylidæ	*Strongylus.* *Cucullanus.*
	3. Trichinidæ	*Trichocephalus.* *Trichina.*
	4. Filaridæ	*Dracunculus.* *Spiroptera.*
	5. Mermithidæ	*Mermis.* *Sphærularia.*
	6. Gordiidæ	*Gordius.*
	7. Anguillulidæ	*Tylenchus.* *Rhabditis.*
	8. Enoplidæ	*Dorylaimus.* *Enchelidium.*
	9. Chætosomidæ	*Chætosoma.* *Rhabdogaster.*

CLASSES and ORDERS of the VERTEBRATA.

Branch A. **UROCHORDA.**

Class.	*Order.*	*Examples.*
I. LARVALIA	. . .	*Appendicularia.* *Kowalewskyia.*
II. SACCATA	1. Ascidiæ.	*Ascidia.* *Clavellina.* *Botryllus.*
	2. Luciæ.	*Pyrosoma.*
	3. Thaliacea	*Salpa.* *Doliolum.*

Branch B. **CEPHALOCHORDA.**

I. LEPTOCARDIA.	. . .	*Amphioxus.*

Branch C. **CRANIATA.**

Grade A. Cyclostoma (Monorrhina).

I. HYPEROTRETA.	. . .	*Myxine.* *Bdellostoma.*
II. HYPEROARTIA	. . .	*Petromyzon.*

Grade B. Gnathostoma (amphirrina).

Subgrade A. *Heterodactyla branchiata.*

I. PISCES
II. DIPNOI } (See separate Lists).

Subgrade B. *Pentadactyla branchiata.*

I. AMPHIBIA (See separate List).

Subgrade C. *Pentadactyla lipobranchia.*

Branch A. Monocondyla.

I. REPTILIA
II. AVES . } (See separate Lists.)

Branch B. Amphicondyla.

I. MAMMALIA (See separate List).

DIVISIONS OF THE HETERODACTYLA.

CLASS I.—PISCES.

Subclass.	*Order.*	*Examples.*	
I. SELACHII	1. Squali	*Heptanchus.* *Squatina.*	
	2. Raii	*Raia.* *Torpedo.*	
II. HOLOCEPHALI		*Chimæra.* *Callorhynchus.*	
III. GANOIDÆ	1. Sturiones	*Acipenser.* *Polyodon.*	
	2. Polypterini	*Polypterus.* *Calamoicthys.*	
	3. Lepidosteini	*Lepidosteus.* *Palæoniscus.*	
	4. Amiadini	*Amia.*	
	5. Cephalaspidæ	*Cephalaspis.* *Pteraspis.*	Extinct.
	6. Placodermi	*Pteriethys.* *Coccosteus.*	
	7. Acanthodini	*Acanthodes.* *Diplacanthus.*	
	8. Pycnodontidæ	*Pycnodon.* *Ptatysomus.*	
	9. Cælacanthini	*Cælacanthus.*	
	10. Dipterini	*Holoptychius.* *Osteolepis.*	
IV. TELEOSTEI	Branch A. *Physostomi.*		
	1. Abdominales	*Clupea, Salmo, Esox, Cyprinus, Silurus, Mormyrus.*	
	2. Apodes	*Muræna, Conger.* *Gymnotus.*	
	Branch B. *Physoclisti.*		
	1. Anacanthini	*Gadus.* *Pleuronectes.*	
	2. Pharyngognathi	*Belone.* *Labrus.*	
	3. Acanthopteri	*Perca, Trigla, Zeus, Cyclopterus, Lophius.*	
	Branch C. *Plectognathi.*		
	1. Plectognathi	*Ostracion.* *Diodon.*	
	Branch D. *Lophobranchi.*		
	2. Lophobranchi.	*Syngnathus.* *Hippocampus.*	

CLASS II.—DIPNOI.

Subclass.	*Order.*	*Examples.*
	1. Monopneumones.	*Ceratodus.*
	2. Dipneumones .	*Protopterus.* *Lepidosiren.*

SUBCLASSES AND ORDERS OF THE
PENTADACTYLA BRANCHIATA.

I. LISSAMPHIBIA	1. Urodela .	*Proteus.* *Salamandra.*
	2. Anura .	*Rana.* *Dactylethra.*
II. PHRACTAMPHIBIA	1. Labyrinthodonta	*Archegosaurus.*
	2. Gymnophiona	*Cæcilia.* *Siphonops.*

CLASSES AND ORDERS OF THE
LIPOBRANCHIA MONOCONDYLA.

CLASS I.—REPTILIA.

Subclass.	*Order.*	*Examples.*
I. CHELONIA .	. . . . .	*Chelonia, Trionyx,* *Emys, Chelys,* *Testudo.*
II. LEPIDOSAURIA	Branch A. *Sauria.*	
	1. Annulata .	*Amphisbæna.* *Chirotes.*
	2. Vermilinguia .	*Chamæleon.*
	3. Crassinliguia .	*Platydactylus.* *Ignana.*
	4. Brevilinguia .	*Anguis.* *Cyclodus.*
	5. Fissilinguia .	*Lacerta.* *Monitor.*
	Branch B. *Ophidia.*	
	1. Opoderodonta	*Stenostoma.* *Typhlops.*
	2. Colubriformia.	*Python.* *Coluber.*
	3. Proteroglypha	*Naja.* *Hydrophis.*
	4. Solenoglypha .	*Vipera.* *Crotalus.*

Subclass.	*Order.*	*Examples.*
III. PTEROSAURIA	1. Rhamphorhynchia .	*Rhamphorhynchus.*
	2. Pterodactyla .	*Pterodactylus.*
IV. DICYNODONTA	. . . .	*Dicynodon.* *Rhynchosaurus.*
V. ORNITHOSCELIDA	. . .	*Megalosaurus.* *Iguanodon.* *Compsognathus.*
VI. CROCODILIA .	1. Teleosauria .	*Teleosaurus.*
	2. Steneosauria .	*Steneosaurus.*
	3. Alligatores .	*Crocodilus.* *Gavialis.* *Alligator.*

CLASS II.—AVES.

1. Saururæ .	*Archæopteryx.*
2. Ratitæ .	*Struthio.* *Apteryx.*
3. Carinatæ .	*Anser.* *Psittacus.*

GRADES AND ORDERS OF THE
LIPOBRANCHIA AMPHICONDYLA.

CLASS MAMMALIA.

Grade A. Cloacalia.

1. Platypoda .	*Ornithorhynchus.*
2. Echidnida .	*Echidna.*

Grade B. Marsupialia.

1. Barypoda .	*Nototherium.*
2. Macropoda .	*Macropus.* *Hypsiprymnus.*
3. Rhizophaga .	*Phascolomys.*
4. Carpophaga .	*Phascolarctus.* *Phalangista.*
5. Cantharophaga	*Perameles.* *Myrmecobius.*
6. Edentula .	*Tarsipes.*
7. Creophaga .	*Dasyurus.* *Thylacinus.*
8. Pedimana .	*Didelphys.* *Chironectes.*

Grade C. Placentalia.

Subclass.	*Order.*	*Examples.*
I. EDENTATA	1. Bradypoda	*Megatherium.* *Cholœpus.*
	2. Effodientia	*Myrmecophaga.* *Manis.* *Orycteropus.* *Dasypus.*
II. UNGULATA	1. Perissodactyla.	*Equus.* *Tapirus.*
	2. Artiodactyla	*Sus.* *Bos.*
	3. Sirenia	*Halicore.*
III. PROBOSCIDEA	Proboscidea.	*Elephas.* *Dinotherium.*
IV. CHELOPHORA.	Hyracoidea.	*Hyrax.*
V. CARNARIA	1. Carnivora	*Canis.* *Ursus.* *Felis.*
	2. Pinnipedia	*Phoca.* *Trichecus.*
	3. Cetacea	*Balœna.* *Squalodon.*
VI. DISCOPLACENTALIA.	1. Prosimiæ	*Cheiromys.* *Lemur.*
	2. Rodentia	*Lepus.* *Sciurus.*
	3. Insectivora	*Erinaceus.* *Talpa.*
	4. Cheiroptera	*Pteropus.* *Vampyrus.*
	5. Simiæ	*Hapale.* *Mycetes.* *Macacus.* *Homo.*