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XXXV.—On the primitive cell-layers of the embryo as the basis of genealogical classification of animals, and on the origin of vascular and lymph systems

E. Ray Lankester M.A. ^a

^a Exeter College, Oxford

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[FOURTH SERIES.]

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XXXV.—*On the Primitive Cell-layers of the Embryo as the Basis of Genealogical Classification of Animals, and on the Origin of Vascular and Lymph Systems**. By E. RAY LANKESTER, M.A., Fellow and Lecturer of Exeter College, Oxford.

A "NATURAL" classification in modern zoology—in the zoology which recognizes in the various forms of living things the expression of one part of the general result proceeding from the continuous operation of physical forces—is a genealogical tree. In this tree, as in a family pedigree, no arbitrary arrangement is admissible, no association or separation of organic forms in harmony with theories of types, or with reference to symmetry and the vested interests of subkingdoms, classes, and orders. The simple questions are:—Have we grounds for believing this lot of forms to have a common ancestry with that lot? Which of these, again, give evidence of closer kinship? and which represent diverging lines of descent?

The evidence at our disposal for answering these questions satisfactorily, with regard to the innumerable varieties of plants and animals, is at the present time small indeed, but is increasing with great rapidity.

The fact that we are able to classify organisms at all in accordance with the structural characteristics which they present is due to the fact of their being related by descent; and the

* The substance of the following pages formed part of a course of lectures on the classification of animals, commenced in the University Museum, Oxford, during Michaelmas term, 1872.

classifications in vogue before the recognition of the origin of organic forms by descent may be regarded as unconscious attempts to answer the questions above put before they had been rightly formulated.

The chief means which the naturalist at present possesses of making out the genealogical tree of the animal kingdom lie in the fact that the individual animals living at the present day, in the process of reproduction, revert to the original simple condition (or nearly so) from which they have in the course of long ages been evolved as specific forms. The doctrine of evolution teaches us that at a certain period in the history of this planet such albuminoid substances as protoplasm came, by gradual building-up, into existence. From such protoplasm, by slow continuous development, due to its properties of heredity and adaptation, all living forms have proceeded by direct descent. Strangely enough, a simple spheroid of protoplasm (nucleated or not) is the form under which the detached reproductive particle of each living organism makes its appearance, and from such a spheroid every individual living thing has been more or less directly developed within the space of a few days or weeks. In passing from this simple condition to its adult form the individual goes through a series of changes, which are now explained by what may be termed "the recapitulation hypothesis," which supposes that the individual organism in thus developing repeats more or less completely the successive series of forms which its ancestry has presented in the course of past ages; in fact the development of the individual is an epitome of the development of the species. This tendency to recapitulate, which is the fullest expression of the phenomenon termed heredity, is liable to be masked in its effects in two chief ways, due to adaptation—namely, the tendency to develop directly to the adult form without exhibiting any ancestral phases, and the tendency to develop evanescent organs for the temporary wants of the young organism. The discrimination of the appearances due to these distinct factors is the task of modern embryology. It is clear that in proportion as this can be effected we have in our hands in the recapitulation hypothesis the means of determining the pedigree of all organisms.

Comparative anatomy (the morphology of adult organisms), so far as it establishes identity of structure in certain groups of organisms, widens the significance of a developmental history worked out in *one* member of such a group, and furnishes suggestions of the highest value in the disentanglement of the hereditary and adaptational factors of such a history.

The remains of extinct forms have a specially suggestive value; but palæontology as a whole, taken in connexion with

the study of geographical distribution, furnishes, with regard to such groups of organisms as have been preserved in the condition of fossils, a distinct and independent mass of evidence, enabling the naturalist to sketch out parts of the genealogical tree, thus supplementing and independently reiterating the conclusions drawn from embryology.

It is only within the last ten, or, we may almost say, the last five years that the development of animals, especially of the Invertebrata, has begun to be studied with the requisite minuteness. Stimulated by the Darwinian theory and the recapitulation hypothesis, naturalists are beginning to apply the highest powers and new methods* of examination to the study of the development of all kinds of organisms, so as to trace out cell by cell the complete history of the elaboration of the complex adult from the simple ovum. It is only now that the first changes in the egg (the first dispositions of the embryonic cells) are becoming known in a sufficiently widely varied series of forms to enable the naturalist to form generalizations. It is only by slow degrees that those species are being found out which conserve precious records in their pregnant infancies, often not even hinted by the uneventful life-histories of their nearest congeners. A commencement only has been made, but one of great promise, by the researches of Fritz Müller ('Für Darwin'), Weissman†, Kowalewsky‡, Ed. van Beneden§, Hæckel||, and others, from which we may, I think, draw conclusions of the greatest importance for genealogical classification.

It would not be surprising if the facts of development were to lead to another primary grouping of the animal kingdom than that indicated in the four Cuvierian types or the six or seven types now generally adopted, or should assign to those great divisions unequal significance. They are confessedly groupings based upon the anatomy of the adult or-

* The method of hardening the developing egg, imbedding it in a matrix, and then cutting thin sections, has only quite recently been applied to Invertebrata, chiefly by Russian naturalists.

† Embryology of the Diptera (Zeitschr. für wiss. Zool. 1865-66).

‡ A series of papers, in the Memoirs of the Imperial Academy of St. Petersburg (1867-71), on the development of Ctenophora, Ascidia, *Amphioxus*, *Sagitta*, *Euaxes*, *Lumbricus*, *Apis*, and *Hydrophilus*.

§ A series of papers on the development of the *Gregarina* of the lobster and of various Crustacea (*Nebalia*, *Mysis*, *Sacculina*, &c.), in the Bulletins of the Belgian Academy, 1869-72. Also prize memoir, in the same Academy's Transactions, on "The Signification of the Parts of the Egg."

|| Monograph of the *Monera*, *Jenaische Zeitschr.* 1868; *Generelle Morphologie*, 1867; The Organization of the Sponges and their Relationship to the Corals, *Jenaische Zeitschr.*, and *Ann. & Mag. Nat. Hist.* 1870, v. pp. 1 & 107.

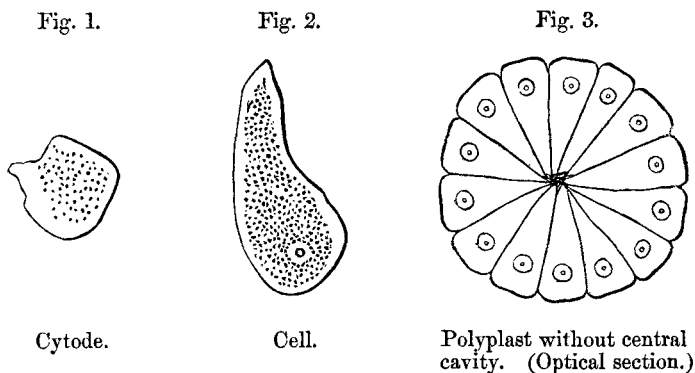
ganism ; and therefore necessarily there has been a tendency in forming them to attach great importance to distinct plans of structure due to a secondary adaptation, whilst the fundamental community of organization has been ignored with something like intention. Von Baer's coincidence with Cuvier in his establishing four modes of development, marking out groups of the same value as the latter's "embranchements," is due to the fact that fifty years ago the condition of biological science did not allow even the great philosophic student of embryology to go more deeply into the problem. He pointed out four modes in which the later adaptation of animals may proceed ; but he was unable at that time to bring into consideration the details of the previous stages of the history. It was under his immediate influence that the invaluable memoirs of Kowalewsky have been produced.

It is, then, to be borne in mind that the four types of Baer and Cuvier represent essentially four modes of mechanical adaptation, and might be assumed, as, indeed, in some cases they are, by organisms exhibiting divergent characters of an earlier and more fundamental character. The doctrine of "unity of type," which has from time to time been put forward by opponents of Cuvier, seems to be in closer agreement with the facts made known by recent embryological study than the more widely received dogma of a plurality of types. Already the most eminent of German anatomists, Professor Gegenbaur, has, in the second edition of his *Comparative Anatomy* (1870), adopted an arrangement of the seven great divisions of the animal kingdom which indicates this inequality in their relative value as branches of a genealogical tree. Whilst the Protozoa stand at the base of the main trunk, and the Coelenterata diverge from this as a primary branch, the Mollusca, Vertebrata, Arthropoda, and Echinodermata are depicted as springing as four distinct secondary branches from the primary branch, represented by the heterogeneous and feebly marked group Vermes. This filiation of the five highest groups of the animal kingdom is supported on grounds which are chiefly anatomical ; and in the pages of this inestimable book facts are continually pointed out tending to demonstrate the homogeneity of the various organs of all these large groups—in short, exhibiting them as modifications of one type.

The early history of the developing embryo tends conclusively to establish this mode of representing the main features of the family tree of the animal kingdom ; whilst, further, the hypothesis of unity of type (which is to be preferred as a preliminary hypothesis on account of its greater simplicity as compared with that of a plurality of types) is, in

its application to the five higher groups of animals, continually receiving new support from observation, and seems likely to lead into most productive lines of research.

The early changes in the developing spheroid of protoplasm leading to the formation of organs may be summarily stated as follows, so as briefly to put in view the fundamental characteristics which they present in different groups of the animal series.



A. The reproductive spheroid is a non-nucleated particle of protoplasm (*Cytod*, Hck.), which either acquires a nucleus and becomes a true cell (Hck.), or remains in the non-nucleated condition; this latter condition characterizes the Monera or Protozoa homogenea, whilst the former is what is observed in all the other groups commonly classed as Protozoa (from which, however, the Spongida are excluded, since they appear in the next section). By differentiation of the primitive substance of the plastid (cell or cytode), *without fission* of the original mass, a cuticle and cuticular appendages, muscular fibrous layers, cilia, contractile cavities, and, by the segmentation of the nucleus, a reproductive germ- or sperm-mass may be former. Division of the primary spheroid, when it does take place, gives rise to new and separate individual spheroids, or to a loosely aggregated colony of such spheroids, to be termed a *polyplast*. In this polyplast there is no arrangement of the units into definite layers.

The organisms whose mode of growth is thus described may be distinguished as HOMOBlastica.

Notes to A.—The stock of the Homoblastica thus coincides with the Protozoa with the exclusion of the Sponges, and contains the following chief groups, the genetic affinities of which must be hereafter discussed:—1. *Homogenea* (embracing

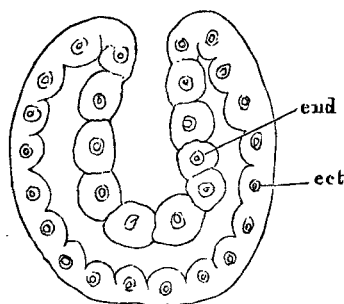
Häckel's *Monera* as *Nuda* and the Foraminifera as *Testacea*); 2. *Nucleifera* (embracing *Amœboidea*, *Gregarinida*, and *Catallacta*); 3. *Radiolaria* or *Cytophora* (embracing the *Heliozoa* or freshwater Radiolaria, and the *Radiolaria* proper or marine forms); 4. *Infusoria* (embracing the *Suctorina* and *Ciliata*, excluding the so-called Flagellate Infusoria, which, it seems, should be referred to the Volvocinean Algæ); 5. *Noctilucida* (*Noctiluca* and *Peridinium*).

We are indebted to Häckel's monograph in the 'Jenaische Zeitschrift' (and translated in 'Quart. Journ. Micr. Sci.' for 1869) for the knowledge of the *Monera* and their reproduction. Prof. Ed. van Beneden, of Liège, has given a valuable account of the development and structure of a *Gregarina* from the lobster (Quart. Journ. Micr. Sci. 1870 & 1871), from which it appears that the reproductive spheroid appears first as a *cytode*, and subsequently acquires a nucleolus and nucleus, whilst considerable tissue-differentiation also goes on, though the unicellular condition is maintained. The high differentiation of the Ciliate Infusoria is thus no evidence against their unicellular character.

The development of the Radiolaria is not properly known in any case. Häckel, in his great monograph, and more recently Cienkowski (Schultze's Archiv, 1871, and Quart. Journ. Micr. Sci., Oct. 1871) have given some account of the formation of spores, which demonstrate the central capsule to be reproductive like the nucleus in other groups. If the yellow cells should prove to be parasitic, as Cienkowski suggests, then, as in colonies of *Monera* or *Catallacta*, all the units, with the exception of the central reproductive body, would be of coordinate value.

B. The reproductive spheroid is at first a nucleated particle of protoplasm; in some cases it develops from a non-nucleated stage. In many cases the nucleus disappears before fertilization. Division of the spheroid then gives rise to a *polyplast*. By the growth of this polyplast either a hollow sphere bounded by a single layer of cells is produced, into which a portion of its own wall becomes invaginated or tucked, as by the adjustment of a

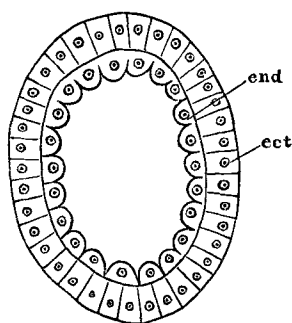
Fig. 4.



Planula formed by invagination of a part of the wall of a polyplast with central cavity. (Optical section.)

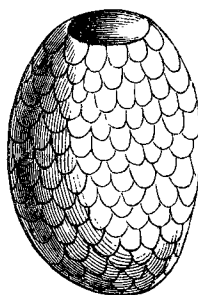
woven nightcap from its pulled-out to its cap-like condition, or the cells arrange themselves in two definitely marked

Fig. 5.



Planula, without orifice,
formed by direct growth.
(Optical section.)

Fig. 6.



Planula with orifice, which
has broken through.
(Surface view.)

layers, the inner of which bounds a cavity which subsequently, by a breaking through at one pole, communicates with the exterior. In either case the result is an organic form characterized by being constructed of two layers of cells, the inner of which lines a cavity opening to the exterior. This cavity is the primitive gastric cavity; and the organic form thus characterized may be known as the *Planula**.

The production of such a *Planula*, recognizable under extreme modifications of non-essential general shape (one of the most common causes of which is the admixture of a large mass of secondary yelk with the original egg-cell), is common to the developmental history of all animals above the Protozoa. But after this there is a divergence; for whilst there is a further development of primitive cells in the Vermes, Mollusks, Echinoderms, Arthropods, and Vertebrates, in the Coelenterata (including herein the Sponges) these two layers of cells, the endoderm and ectoderm, remain throughout life as the basis of further histological differentiation, even though in the larger forms the ectoderm may largely develop deep layers of a special muscular or skeletal nature. The series of forms thus branching off from the genealogical tree may be termed DIPLOBLASTICA.

The endoderm and ectoderm of the polypes and corals was recognized first by Professor Huxley, who at the same time

* It may be advantageous to use the term *Gastrula* for that condition of the *Planula* when the orifice is present, as Hæckel has proposed since the above scheme was drawn up.

pointed out the similarity of these layers to the two primitive layers of the Vertebrate embryo.

Notes to B.—The difference in the two modes of origin of the *Planula* may be due to the dropping of the invagination-process as a shortening of the developmental process—that is to say, in obedience to the tendency to a *direct* as opposed to a *recapitulative* development. It is, however, to be noticed in connexion with this that in the later development of special organs we have examples where development occurs sometimes by invagination and sometimes by simple accretion, and where the bulk of the developing structure appears to determine the invagination. Such, for instance, is the case with the otocysts or auditory capsules of mollusks. In the Nudibranchiates I have satisfactorily determined that their cavity does not arise by invagination. On the other hand, in the Cephalopod *Loligo* I have found (what was previously suspected but undemonstrated) that the otocyst *is* formed by an invagination, the ciliated canal connected with it being a remnant of its external communication. The development of the nerve-centres also furnishes examples. In *Loligo* I have observed that the cephalic ganglia originate each by invagination and formation of a groove and cavity. In Gasteropods the corresponding ganglia form by simple thickening of the outer layer of cells. The origin of the cerebro-spinal nerve-centre of Vertebrates and certain Tunicates, as compared with that of Arthropods and notably of certain Annelids (*Lumbricus*, and *Euaxes* as described by Kowalewsky), offers the same contrast.

It is remarkable that the origin of the primitive gastric cavity by invagination has been more widely observed in the higher groups, and that in most Cœlenterata as yet studied the cavity is formed directly. There are exceptions to this among Cœlenterata; but in this subject it must be remembered that we have as yet very few adequate observations. Among the higher groups the observations of Kowalewsky have especially established the occurrence of this primitive invagination in *Amphioxus*, in Tunicates, and certain Vermes; my own observations (as yet unpublished) have proved its wide-spread occurrence in Mollusca, viz. in the Lamellibranch *Cyclas pusilla*, in several Nudibranchs (*Polycera*, *Eolis*, *Doris*, *Pleurobranchus*), in the Pulmonates *Arion* and *Limax*. The presence of accessory yolk is what, more than any thing else, appears among the Mollusca to be associated with the suppression of the invagination-process. The anus of Rusconi in the developing Batrachia among Vertebrata represents the orifice of invagination in a somewhat modified condition.

The observations of Miklucho-Macleay*, which have been followed up in a masterly way by his teacher Professor Häckel of Jena, first demonstrated the relationship of Sponges and Cœlenterata. The *Planula*-embryo of a calcareous sponge (*Guancha blanca*) is made known in Macleay's paper; O. Schmidt has figured that of another (*Dunstervillia*). The embryo of *Spongilla*, as described by Lieberkühn, is also a *Planula*.

The retention of the Diploblastic constitution throughout life by the Cœlenterata serves as an important fact in determining the homogenies of the perigastric and canal systems of the corals and medusoids. It is clear enough that they are merely diverticula, or portions of the primitive gastric cavity. As such they can have no homogenetic, but merely a homoplastic, agreement with the vascular and perivisceral systems of higher animals, the origin of which will be pointed out below. The fluid which they contain will also be seen to be of a different nature from chyle or blood, and, in fact, is merely a diluted chyme. In the histological differentiation of Cœlenterata the outer layer of cells gives rise to muscular fibre, and also represents a nervous system; in the case of *Hydra* the fibres are continuous with the large ectodermal cells (Kleinenberg), whilst in others (*Medusæ* &c.) deep-lying cellular elements of the nature of muscular and connective tissue develop from the ectoderm. The endodermal cells are confined to vegetative functions. The origin of generative products will be discussed below.

C. Development having proceeded, as in the Diploblastica, to the production of an ecto- and endoderm, or an epi- and hypoblast, with primitive gastric cavity bounded by the latter, a third layer of cells makes its appearance between these two, whence taking its precise origin is not yet determined. A portion of this middle layer becomes more especially adherent to the ectoderm, another portion more especially to the endoderm. The separation between these two portions of the new mid layer may be complete so as to leave a wide cavity, or it may never be carried to any extent; but whatever extensive cavity or partial channels make their appearance, or whatever mesh-bearing or sponge-like character the mesoblast takes on, so as to produce an imperfect continuity between its more superficial and deeper parts, connected and bound together, it may be, by branched cells—such cavity, channels, or spongy tissue are more or less complete representatives of the *blood-lymph* system. The organisms characterized by the presence of these

* Jenaische Zeitschrift, 1868, p. 221.

three primitive layers of cells, which furnish the original material for further histological differentiation, may be termed **TRIPLOBLASTICA**.

In all Triploblastica (Vermes, Echinodermata, Mollusca, Vertebrata, Arthropoda) it appears that of the three layers the outer (*epiblast*) gives rise to epidermic structures, sense-organs, and the great nerve-centres; the mid layer (*mesoblast*) to muscular tissue, skeletal tissue (varieties of connective tissue and cartilage), blood and lymph, and the walls of the cavities in which they are held; the innermost layer (*hypoblast*) to the lining of the gastric or alimentary tract and its diverticula, in the form of glands. The primitive orifice of invagination (mouth of the *Planula*) does not persist, either as mouth or, as has been erroneously supposed, as anus, but becomes entirely closed up, and a new mouth and an anus eat their way into the gastric cavity from the exterior, developing thus pharynx and terminal intestine. The origin of the generative products is, as in the Diploblastica, not ascertained to be *exclusively* from either epiblast or hypoblast. The communication of the mesoblastic blood-lymph-cavity, or a part of it, with the exterior occurs in all Triploblastica, and is accompanied by an ingrowth of the epiblast, which, appearing in the simplest worms as the pair of segmental organs or "ciliated excretory tubes," persists in all the subsequent modifications of the type (Echinoderms, Arthropods, Mollusks, Vertebrates).

Notes to C.—The above generalization must be understood as resting on a limited number of facts, which, however, are being daily increased in number. Attention has been already drawn in the notes to B to the frequent masking of the *Planula* stage and invagination-process in this group as well as in the preceding one. In the early stages of development of the few Vertebrata as yet carefully studied (viz. a few fish, Batrachia, and the common fowl) it is only in the Batrachia that evidence of the invagination, and that in a modified condition (see Stricker's valuable paper in 'Zeitschr. für wiss. Zoologie,' vol. xi., 1861), is obtained. It is yet a question, on which there is a considerable divergence of opinion, supported in each case by careful observation, whether the mesoblast has uniformly the same essential origin in the various groups of the Triploblastica. The hypothesis that it has is justifiable in the present condition of knowledge as the simplest. We have to look for a reconciliation of the opinions based upon interpretation of observations carried out with different animals, which variously point to the derivation of the mid layer from cells of the epiblast, from cells of the hypoblast, from original cells of the primitive polyblast, or from a new cell-formation in the yolk

distinct from the cleavage-process (free-cell formation). A further comprehension of the accompanying conditions and mode of carrying out of the *suppression* of steps in the historical epitome of the individual's development will, more than any thing else, tend to this result. The non-identity of the mouth in Diploblastica and Triploblastica is one of the most curious divergences which a comparison of the two groups brings out.

There is on the whole a satisfactory concordance of testimony with regard to the chief tissues and organs to which the three layers respectively give rise, if we except the generative products. The hypoblast of the Triploblastica retains the characters and significance of the Diploblast's endoderm. The fundamental properties of the latter's ectoderm (musculo-sensorial layer of Kleinenberg) become distributed between the tissues differentiated from epiblast and mesoblast—a fact which, whether rightly or wrongly, suggests the ectoderm as the true source of origin of the mesoblast; and, in the case of the earth-worm, Kowalewsky's researches demonstrate this origin conclusively.

That the generative products arise from cells of the ectoderm in *Hydra* is certain, from Kleinenberg's careful observations. Häckel, on the other hand, has found them derived from the endoderm in certain Medusæ and in Calcareous Sponges, whilst Allman makes the same statement as to some Hydroid polyps. That the ovaries and testes in higher animals arise from the outer layer is not inconsistent with the fact that they may first definitely appear within the limits of the mesoblast. An ingrowth and intercalation of the cells of the epi- and mesoblast at an early period, such as Waldeyer has pointed to, sufficiently explains the position of the vertebrate ovary and testis, even though they be developed from the epiblast. The position of the generative masses of Oligochæteous Annelids in their earliest phase, as buds of the tissue in immediate contact with the nerve-cord, to which I have drawn attention in *Chaetogaster** and *Tubifex*†, is in complete agreement with the view of their derivation from cells of the epiblast, when considered in the light of Kowalewsky's admirable demonstration of the ingrowth of the epiblast to form the ganglion-chain of *Lumbricus* and *Euaxes*.

A true blood-system, or blood-lymph-system as it is better to call it in view of the present signification of words, is only possible where a mesoblast is developed—that is, in the Triploblastica. In all Triploblastica it is represented by lacunæ or channels, or by mere wide-setting of the cellular elements

* Quart. Journ. Microsc. Science, July 1870.

† Ann. & Mag. Nat. Hist. 1871, vii. p. 90.

of the mesoblast, between and around which the movement of a fluid, so-called lymph, is possible.

A blood-lymph-system or series of channels appears in its simplest form in the flat-worms, where the main portion of those channellings in the mesoblast, sometimes spoken of as "water-vascular system," must be regarded as the commencing differentiation of the blood-lymph vascular system. The true nature of these channels is well seen in a transverse section, such as that of *Bothriocephalus* given by Landois (Zeitschr. f. Zool. 1872), or such as that of the Planarian *Bipalium* to be described by my friend Mr. Moseley, who assigns to them the same importance as is done here. The channels of the water-vascular system in these cases are seen in section to be intersected by long branching cells; they are, in fact, only partial excavations of the mesoblastic tissue. Such excavation, carried to a greater extent and widened out, ultimately forms the "perivisceral space" seen in many Nemerteans, and in all the Gephyrea, Chætopoda, Echinodermata. When parts of this excavation remain shut off from parallel parts, and either communicate or do not communicate with the larger sinus-like spaces, the conditions are given for the further modification of this primitive vascular channelling into distinct blood-vessels, lacunæ, and pericardial sinus-system, as in Mollusks, or into a closed vascular system lying within a perivisceral sinus, as in Chætopoda, or (no perivisceral sinus being apparent) into closed vessels containing hæmoglobin surrounding organs, as in some leeches, or, lastly, into great sinus-spaces opening through a "lymph-system" into a closed system of blood-vessels, as in Vertebrates.

The orifices of the water-vascular system of the Planarians, Cestodes, and Trematodes are, no doubt with reason, looked upon as representing exactly the orifices of the "segment-organs" of the Chætopoda; but we have no warrant for assuming that more than the aperture and a first portion of the "canal" in the flat-worms corresponds with the little trumpet-mouthed tube which hangs freely in the large perivisceral space of a Chætopod, or such a leech as *Branchiobdella*. The observed facts of development are not conclusive as they at present stand as to the origin of the segmental organ of Chætopoda. Kowalewsky derives them from the middle layer in the case of *Euæzes*; but in view of the difficulties of the observation, and of adverse considerations furnished by the facts of development of apparently homogenous parts in Mollusks and Insects, an argument cannot be based upon their mode of development; nor do the facts of development at present established lend themselves to the decision of the question whether the flat-

worms possess in their vascular system the commencement of a body-cavity. The most conclusive evidence which can be adduced on the matter is the analogy of such a mollusk as *Phyllirhoë*, where, as in other Mollusca, the perivisceral cavity is developed only as a series of sinuses, of which the pericardium is one, or where, as we may say, the perivisceral space is *reduced* to the *pericardium*. This pericardium is produced at one end into a tube or canal ciliated at one part, which opens to the exterior. The ciliated tube represents a segment-organ, as must be admitted for the renal organ of Mollusca generally, and especially for the so-called "hearts" or "oviducts" of Brachiopoda. In *Phyllirhoë* we have, it seems to me, as in the flat-worms, the imperfect channellings and spaces of a "parenchymatous" body placed in relation with the exterior by the segment-organ, the wall of which is not discontinuous with that of the channels. It is when the perivisceral space becomes large and expanded that the segment-organ floats in it with a trumpet-like inner orifice; on the other hand, when the blood-lymph-space is *canal-like*, then the segment-organ is merely its continuation to the exterior.

Ciliation and contractility, both exhibited by the "water-vascular system" in Trematodes, are both familiar characters of the perivisceral space when developed on a more capacious scale. Contractility is of course in the nature of the case, the walls of the perivisceral space being muscular. Cilia occur in the perivisceral cavity of some Chætopoda and in that of Gephyrea, in the primitive mesoblastic cavity of the developing Lamellibranch *Pisidium* and of *Aplysia*, also in the peritoneal (perivisceral) space of the frog.

The condition of the vascular system in different genera of leeches is instructive, tending, as it seems, to bridge over the gulf between a simple perivisceral primitive blood-lymph-space and the more complicated differentiations of lymphatic systems, pleuro-peritoneal cavity, and blood-vascular system to which it simultaneously gives rise in higher organisms. The blood-lymph-space exists in the common leech as four chief longitudinal canals, in one of which the nerve-cord lies. The apertures of the segment-organs lead into closed pouches, whose cavity is also to be reckoned to the blood-lymph-space, though not in continuity with its longitudinal portions. In other leeches (e. g. *Branchiobdella*), whilst two of the longitudinal canals are retained, excavation is carried on in the mesoblastic parenchyma in such a way as to leave the segment-organs floating trumpet-like in a great perivisceral sinus, in which also the nerve-cord lies. The longitudinal canals may, as in *Hirudo*, contain a liquid impregnated with hæmoglobin, and remain closed from

communication with the rest of the blood-lymph-system. This is very generally the case in Annelids; not so, however, in the Gephyrean *Sipunculus*, where the tentacular vessel communicates periodically with the perivisceral space. In Vertebrates the hæmoglobin-bearing or respiratory system and the lymph-bearing sinus-system communicate at various points, so that the fluid in the former is complex, being comparable to the respiratory fluid of an Annelid *plus* its perivisceral fluid. It is hence hæmo-chyle or blood-lymph, if we limit the significance of "blood" to that which it really connotes, namely the *red* part of the vascular fluid. If such a nomenclature be admissible, viz. the limitation of "blood" to the respiratory element, then the fluid in the closed vascular system of Annelids would be blood, the perivisceral fluid lymph; the perivisceral fluid of *Glycera* with its red corpuscles would be blood-lymph or hæmo-chyle; the circulatory fluid of Mollusca and Arthropods would also be hæmo-chyle, since there is no separation of a respiratory element in separate vessels, and in exceptional cases (*Solen*, *Planorbis*, *Chironomus*, *Chirocephalus*, *Daphnia*) hæmoglobin does appear in the common circulatory fluid; the fluid of the pleuro-peritoneal cavity, lymphatic canals, and vessels in Vertebrates would be "lymph," and its corpuscles, *derived, as throughout the triploblastic series, from the proliferation of the connective-tissue corpuscles lining the walls of the lymph-spaces*, would be lymph-corpuscles or leucocytes; the fluid in the arteries and veins, on the other hand, would be blood-lymph or hæmo-chyle, being lymph added to other liquid and corpuscular elements, the latter of which are respiratory and impregnated with hæmoglobin, whence they may be termed "pneumocytes."

As an illustration of the point which I wish to urge—viz. that the various vascular and sinus systems of Triploblastica are not to be regarded as important differentiations, but are rather parts of one and the same primary blood-lymph-cavity slightly modified or isolated—let me point to two facts. First, among polychætous Annelida we have generally a closed vascular system and a perivisceral space; in *Glycera*, however, the shutting off of a part of the blood-lymph-space as a closed system does not occur, but we have only the one great perivisceral chamber, with pneumocytes added to its corpuscular contents, this change being unaccompanied by any other great structural modification; and it is a fact that "anangian genera" occur in the same family with others possessing the closed set of vessels, *e.g.* Aphroditacea. Secondly, in a parasitic crustacean as yet undescribed, discovered by Prof. Edouard van Beneden of Liège, there is developed a closed vascular system lying within the regular blood-sinuses, and

containing, as in the case of Annelids, hæmoglobin. The exceptional development of such a subdivision of the blood-lymph-space, unparalleled throughout the whole group of Arthropoda, is additional evidence in favour of the view that the primitive blood-lymph-space readily lends itself to the development of variously distributed and communicating vascular systems, even systems as special as the ambulacral and respiratory systems of Echinoderms.

The relation of the segment-organs to the primitive blood-space has already been spoken of. There is considerable ground for regarding it as constant throughout the Triploblastica, as the blood-lymph-space itself is constant. It appears under various modifications as a canal, often ciliated and funnel-like, forming a communication between part of the blood-lymph-space and the exterior—as, for example, the brown tubes and the cloacal tree of *Gephyrea*, the organ of *Bojanus*, the Fallopian tubes and seminal ducts of sharks, and more doubtfully in Echinodermata and Arthropods.

The Triploblastica not only exhibit this unity of type as regards their chief viscera, but there are certain regions of the body which must be considered identical in all; especially must the prostomium or region in front of the mouth, the axis of anterior growth, where it is persistent, be held to be homogenous throughout the series. It is in relation with this "head-flap" that the primitive nerve-centres are developed and always make their appearance as the great sensorial ganglion-masses. Already in the free-swimming larvæ of some Diploblastica, such as *Actinia*, the prostomium is indicated, having a necessary mechanical relation to bilateral symmetry when the mouth is placed anteriorly and locomotion is parallel with the alimentary axis, though here we must not overlook the distinct character of the Diploblastic and Triploblastic mouths. The large primitive tentacle of the young *Actinia* is a prostomium, and only loses its superior overhanging character as regards the mouth when the animal, abandoning locomotive habits, fixes itself and develops other processes around the mouth which soon equal the first in size. The prostomium in Triploblastica is liable to be suppressed altogether in the course of individual development, the mouth becoming terminal or other modifications arising; but where it does appear it constantly carries the chief organ of sight, whilst the auditory sac is prostomial in Turbellarians, but metastomial in Tunicates, Vertebrates, and Mollusca.

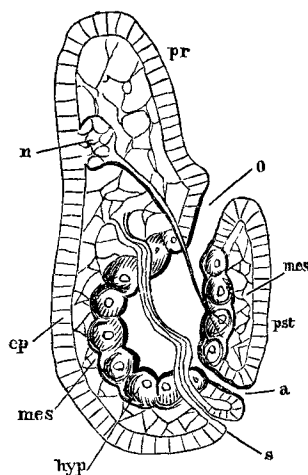
The production of individuals of an increased complexity of organization among Triploblastica, by the linear aggregation of zooids, produced by budding in the posterior or metastomial

axis of growth (tertiary aggregates of Herbert Spencer) among Annelosa, and probably (though not according to Spencer) among Vertebrata, and even some Mollusca—the process occurring at a very early period and its results being *obscured*, or even *entirely resolved*, by later “integrating” development in the two latter cases—does not affect the prostomium, which always has an axis of *anterior* growth. When a zooid-segment of a linear tertiary aggregate develops a prostomium or axis of anterior growth, the chain necessarily breaks at that point (*Microstomum*, *Tænia*, *Naididæ*, *Syllidæ*). The segmentation of the prostomial axis in Arthropoda and some Annelids, which has an appearance of being a zooid-segmentation comparable to that of the metastomial axis, on account of the identity in the character of the appendages with

those of the metastomial axis, has yet to be explained. It may be suggested that it is due to a distinct breaking up of this axis like the posterior one into zooid-segments or zoonites: there is much against this supposition (see Trans. Linn. Soc. 1869, “On *Chaetogaster* and *Æolosoma*”). Much more likely, it seems, is the explanation that the oral aperture shifts position, and that the ophthalmic segment alone in Arthropoda represents the prostomium, the antennary and antennular segments being aboriginally metastomial and only prostomial by later *adaptational shifting of the oral aperture*.

The assumption of such a shifting of the oral aperture is fully warranted by what has been demonstrated in the case of Vertebrata through Kowalewsky's researches on *Amphioxus*. It is certain from those observations that the mouth of *Amphioxus* is the first gill-slit or pharyngeal perforation of the left side, and has no relation to a mouth such as that which appears at an earlier phase of development in the allied Ascidian larva, which latter mouth is that of Vermes generally. *Amphioxus*, then, and the Vertebrata have a new oral aperture, the old one having been gradually suppressed. Comparative

Fig. 7.



Archiscollex (optical section):
pr, prostomium; *pst*, metastomium;
o, mouth; *a*, anus; *s*, segmental or excretory aperture;
cp, epiblast; *n*, nerve-centre; *mes*, mesoblast; *hyp*, hypoblast.

osteology and the embryology of higher Vertebrata have long made it clear that the vertebrate mouth belongs to the series of visceral clefts; but the significance of this in the comparison of Vertebrata and Invertebrata has yet to be fully appreciated. The identification of the neural and hæmal aspects of Vertebrata and Vermes, in the light given by this demonstration of Kowalewsky's as to the distinct character of the mouth in the two cases, must lead to most valuable results*.

The triple basis of histological differentiation, the nerve-centres, the alimentary tract, the blood-lymph-spaces, the segment-organs, the prostomial and metastomial regions being recognizable as homogenous under varied adaptative modifications throughout the Triploblastica, is it not probable that other parts may still further exhibit that unity of type of the included groups which forms our hypothesis? Whilst it is necessary always to be on guard against mistaking homoplastic agreements such as clearly must and do exist† for homogenetic agreements, yet, since the working hypothesis must be that of uniformity, as the simpler, we ought to assume homogeny or unity of type as explaining similarity in organs until research proves it necessary to regard this or that particular case as due to coincidence of adaptative causes. Hence it may fairly be suggested that the appendages of Triploblastica, appearing under two chief forms as locomotive and respiratory, (external gills) are homogenous throughout the series.

Such an hypothesis opens a very large field for discussion; but within certain limits it will not, perhaps, meet with strenuous opposition. The gills of Mollusca generally, of Brachiopods, the tentacles of Polyzoa, and the gill-tufts of Annelids—again, the locomotive appendages of Annelids and Arthropods—or, again, the external gills of Vertebrata (embryo Selachians, Batrachians, &c.) and those of Annelids, offer themselves as likely enough to prove homogenous; but since many further embryological inquiries have to be made, and no doubt will be made in consequence of these possibilities presenting themselves to the imagination of many students of embryology, it will not now be useful to discuss them upon the limited evidence at hand.

Note.—Professor Hæckel, in the final part of his newly published splendid monograph of the calcareous Sponges, has entered into speculations on the significance of the polyplast and planular stages of development and the development

* I am indebted to my friend Anton Dohrn for first drawing my attention to some of the legitimate consequences of Kowalewsky's observations as to the mouth of *Amphioxus*.

† Ann. Nat. Hist. 1870, vol. vi. ("On the use of the term Homology").
Ann. & Mag. N. Hist. Ser. 4. Vol. xi.

of a body-cavity, which are of the utmost value. He adopts a more detailed nomenclature than I have used here, and does not take the same view of the water-vascular system of flat-worms as I have done; but to some extent there is naturally coincidence, due to the fact that the material here used in the form of facts has been mainly drawn from his other writings and those of other German and Russian embryologists. I have not attempted to discuss Professor Hæckel's views nor referred to his terms, chiefly because the substance of this paper was drawn up before the 'Kalkschwämme' appeared.

XXXVI.—On a new Australian Species of Thyrsites.

By Prof. FREDERICK M'Coy.

THE common Barracoota of the Cape seas is very abundant in the Melbourne market from the adjacent coast, and has long been known; but an equally large and important species for food is brought in great quantities from Tasmania to the Melbourne fish-shops, usually split open and dried; and, as far as I can see, it has been overlooked by naturalists. It is easily distinguished at a glance from the *Thyrsites atun* or Barracoota by the much greater depth of the body, fewer finlets, shorter dorsal, larger teeth, and double lateral line; but the mode of preparation usually obscures the still more striking character of the ventrals being almost absent, or at least very minute and rudimentary. I subjoin a description of the species.

Thyrsites micropus (M'Coy).

D. 17 | 4+12 | VI. A. 2+11. IV. V. 1+1 (bifurcate).
P. 14. C. 22½.

Height of body five times in total length to centre of caudal fin; head four times to end of lobes of caudal. Lower jaw projecting in advance of the upper; diameter of orbit one fifth the length of the head, and one half the length of the muzzle. Ventrals each with one spine and one bifurcate ray, slightly in advance of base of pectorals; about one third the diameter of the eye in length. Lateral line bifurcate: upper branch extending from a little above the operculum, a little below the dorsal line, as far as the third finlet; lower branch coming off from upper one under base of fifth dorsal spine, and descending with an abrupt curve nearly to the middle of the side, continuing nearly straight to opposite middle of anal fin, from which to middle of tail it describes three upward undulations.