OBSERVATIONS *on the* DEVELOPMENT *of the* POND-SNAIL (*Lymnæus stagnalis*), *and on the* EARLY STAGES *of other* MOLLUSCA.

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(With Plates XVI and XVII.)

§ 1.—SOME OF THE DEVELOPMENTAL PHENOMENA OF MOLLUSCA.

Four years since, I determined to make a study of the developmental phenomena of a series of Mollusca, with the view of ascertaining from the minute comparison of a number of cases what phenomena might be common to the group, or be considered as indicating ancestral conditions inherited from common ancestors.

The success which had attended Fritz Müller's investigation of the Crustacea, and his celebrated "recapitulation hypothesis," according to which we have, in the development of every individual organism, a more or less complete epitome of the development of the species, so that the series of changing forms passed through between ovum and adult form are but a series of dissolving views or portraits (often very much marred) of its line of ancestors—this, I say, led me to hope that materials might be found in the developmental history of the Mollusca for constructing their genealogical tree. During the past fifteen years but little has been done in the study of the embryology of the Mollusca, and it was therefore to be expected that the application of improved methods of investigation and new hypotheses would yield valuable results. The result of my study of the development of the Lamellibranch *Pisidium* and of the Gasteropods *Aplysia, Neritina, Tergipes* and *Polycera,* are now in course of publication elsewhere.

I have also, during this spring, completed the examination of the development of the Cephalopod *Loligo* from an early stage of the ovarian egg up to the escape of the embryo from the egg-jelly, which, together with less complete accounts of the development of *Octopus* and *Sepia,* I hope soon to see published. Before proceeding to give here an account of observations on *Lymnæus* which I carried out during July in the laboratory of Exeter College, Oxford, I may briefly summarise the chief results of my previous observations, which are remarkably confirmed by the facts to be subsequently related in regard to *Lymnæus*.

Kowalevsky, in his account of the development of *Amphi-*

oxus and of *Phallusia,* pointed out that the inner series of cells which give rise to the alimentary canal in those animals take up their position as the result of an invagination of part of the wall of an original multicellular sac. I found the same mode of origin for the primitive alimentary canal or endoderm of the Lamellibranch *Pisidium,* of the Pulmonates *Limax* and *Lymnæus,* of the Nudibranchs *Tergipes* and *Polycera.* This led me to compare the early development of members of other groups of the animal kingdom, the Planulæ of Sponges and Cœlenterates, the frog's embryo with Rusconian anus, &c., and I was thus led to infer that in this simple double-walled sac, composed of ectoderm and endoderm, we have the transitory indication of a primæval ancestor of all the higher groups of the animal kingdom, whose essential structure is permanently retained in the corals and polyps (Cœlenterata), but is in the course of development improved upon by the evolution of a body-cavity, and an additional third or intermediate mass of embryonic cells, giving rise to muscular and vascular structures in worms, molluscs, arthropods, star-fishes, and vertebrates. I proposed to call this developmental form the Planula, its immediate predecessor (the multicellular sac) a Polyblast, and indicated three large divisions of the animal kingdom—Homoblastica, Diploblastica, and Triploblastica—corresponding respectively to a lower stage than the Planula, to the Planula itself, and to a higher development of the essential Planula-structure.[1]

Almost simultaneously Professor Haeckel, of Jena, arrived at similar conclusions, which he first made known in his 'Monograph of the Calcareous Sponges,' and subsequently developed in the essay entitled "The Gastraea-Theory," which has been translated by Professor Perceval Wright for the April and July numbers of this Journal. The terms Gastrula and Gastraea, introduced by Professor Haeckel, are preferable to the term Planula which I had adopted; and I may further take this opportunity of admitting to some extent the justice of his criticisms on my use of the term Triploblastica. It appears to me more and more certain that (as he has definitely pointed out) the third layer, or those masses of cells which in the embryos of Triploblastica are regarded as belonging to such a layer, are phylogenetically derived either from one or other of the two primitive cell-layers, and only appear by suppression of the historical steps of development as an intermediate and independent layer. Nevertheless, the fact that they do so appear, and that there

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[1] 'Annals and Mag. Nat. History,' June, 1873.

is a *third* plane of development really brought about by the formation of a body-cavity, seems to justify the use of the terms Diploblastica and Triploblastica. The latter corresponds essentially with Haeckel's Metazoa. With regard to the difference between Professor Haeckel and myself as to the relation of the body-cavity and the water-vascular system, I must at present maintain the view expressed in my essay. The difference is not so great as Professor Haeckel appears to believe. I do not accept his existing groups of acœlomatous worms as such, for in the Planarians and Cestods there appears to me to be evidence that the ramifications of the water-vascular stems are to be regarded as corresponding to a commencing body-cavity. The terminal portions of those stems, which open to the exterior, on the other hand, are, as I pointed out in the essay referred to, to be regarded as something distinct—an involution of the epidermic layer subsequently developing into the segmental organ. It does not by any means follow that the body-cavity is *primitively* open to the exterior, a view which Professor Haeckel has by misapprehension attributed to me. It will not, however, be useful to discuss this matter further without reference to renewed investigation of the facts.

A second and third phase in the development of the Mollusca, which have long been known, and which may or may not make their appearance in any particular case, are (what may be called) the Trochosphere and Veliger forms, the former an early condition of the latter. Both are well known and characteristic of various groups of Worms and Echinoderms, and the latter is seen in its full development in the adult Rotifera and in the larval Gasteropoda and Pteropoda. The identity of the velum of larval Gasteropods with the ciliated discs of Rotifera seems to admit of little doubt, and it would be well to have one term, *e.g.* velum, by which to describe both. The Trochosphere is the earlier, more or less spherical form in which the velum is represented by an annular ciliated ridge, and which is sometimes (*e. g. Chiton*) provided with a polar tuft of long cilia.

The cell, polyplast (morula), gastrula, trochosphere, and veliger phases of molluscan development are not distinctive of the molluscan pedigree; they belong to its præ-molluscan history. The foot, the shell-gland, and the odontophore are organs which are distinctively molluscan—the last characteristic of the higher Mollusca only—the other two of the whole group, and their appearance must be traced to ancestors within the proper stem of the molluscan family tree. The foot is essentially a greatly developed lower lip.

With regard to the shell-gland, which has not up to the present moment been recognised by any observers, my studies have yielded most interesting results. This organ appears to have a very wide distribution among the different classes of Mollusca, and to be present even in the most remote members of the group—the Polyzoa and Brachiopoda.

I do not propose here to give a detailed account of this

Fig. 1.

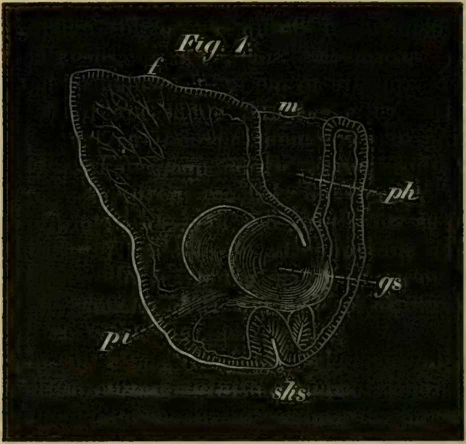

Diagram of an embryo of *Pisidium pusillum*. *f.* Foot. *m.* Mouth. *ph.* Pharynx. *gs.* Gastrula-stomach (now bilobed). *pi.* Pedicle of invagination (terminal intestine). *shs.* Shell-gland.

Fig. 2.

Diagram of an embryo of *Pleurobranchidium*. *f.* Foot. *ot.* Otocyst. *m.* Mouth. *v.* Velum. *ng* Nerve-ganglion. *ry.* Residual yelk-spheres. *shs.* Shell-gland. *i.* Intestine.

organ, but shall refer to the woodcuts (figs. 1 and 2) as illustrating its position and character in the embryos of *Pisidium* and of *Aplysia* (*Pleurobranchidium*) respectively. The gland (*shs*) under certain circumstances, connected with an arrest of regular development, becomes filled with a chitinous plug in the case of the *Aplysia* embryo. When at Messina, during May of this year, I found that Dr. Herman Fol had discovered the same shell-gland in embryo Pteropods, and, strangely enough, he had found the same plugging with a chitinous secretion in specimens abnormally developed. I have observed the same "shell-gland" in an early stage of *Neritina*, and, as will be seen below, it has a very well-marked development, accompanied by occasional plugging with a chitinous material, in *Lymnæus*.

The position of the gland in *Pisidium*, and its relation to the pair of calcareous valves which develop on either side of it, suggests that it may in the Lamellibranchs be represented in adult life by the ligament; but this connection I have not been able to demonstrate; on the other hand, in *Aplysia*, *Neritina*, *Lymnæus*, and the Pteropods, it certainly disappears—is, in fact, an evanescent embryonic structure.

One naturally turns, after detecting this organ in Lamellibranchs, Gasteropods, and Pteropods, to the classes which have been (I think a little invidiously) separated as Molluscoida from the other Molluscs—I mean the Brachiopoda and the Polyzoa—to see if in them any trace of the shell-gland can be found. I do not know, at the present moment, of any such organ having been as yet observed in the young stages of Polyzoa. But in a very strange form, which must be classed with the Polyzoa, there is such an organ, occupying exactly the required position.

Loxosoma neapolitanum was described first by Keferstein, and subsequently by Kowalewsky, from whose memoir the accompanying woodcut (fig. 4) is taken. The large gland of attachment (*shs*) appears to me to be very probably the homogen of the shell-gland. Further, in the Brachiopoda we have a gland developed at the same point in many forms, appearing at a very early stage in *Terebratula* and *Trebratulina*, and well known as enabling the animal to fix itself by means of its pedicle. The position of this gland corresponds accurately with that of the shell-gland in the embryo *Pisidium*, *Aplysia*, and *Lymnæus*. Hence I consider that we have evidence for considering this organ as one common to Polyzoa, Brachiopoda, Lamellibranchia, Gasteropoda, and Pteropoda.

A question which at once presented itself after the general presence of this organ had been ascertained was this—Does it correspond in any way to the sac in which the internal shell of *Limax*, and, further, that in which the pen of the

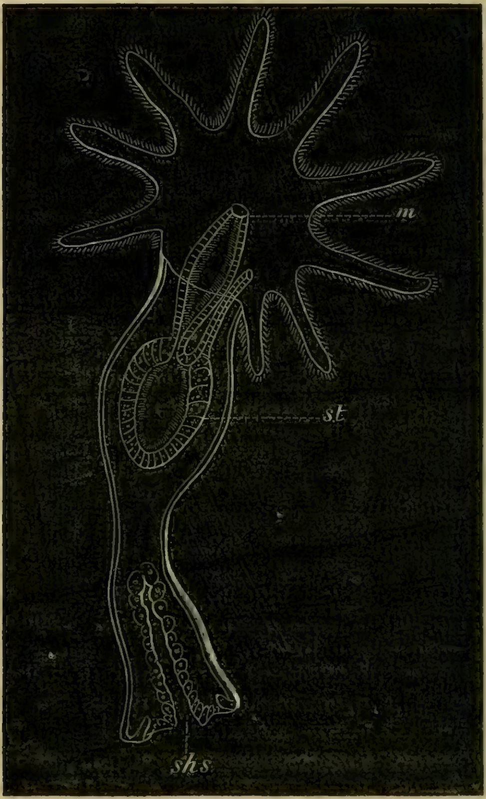

Diagram of *Loxosoma*. *m.* Mouth. *st.* Stomach. *shs.* Shell-gland.

Dibranchiate Cephalopods, is developed? These two heads of the question must be kept apart.

We know, among *Aplysia* and its allies, and, further, in *Spirula*, of *external* shells which have become internal, or, we should better say, *enclosed*, by the overgrowth of the surrounding folds of the mantel. That is apparently the individual history of the concealed shell of *Aplysia*, and probably is that of the concealed nautiloid shell of *Spirula* also; and, consequently, it may be inferred that such is also the genealogical history of those shells.

But the development of *Limax*, &c., has been sufficiently studied by Gegenbaur (' Zeitschr. f. Wiss. Zool.,' Bd. iii), and Schmidt (' Archiv f. Anatomie,' 1851), to show that in these animals the shell is from the first formed in a sac. In fact, we should only have to retain the shell-gland of the allied pulmonate *Lymnæus*, in adult life, in order to produce precisely the required internal shell of *Limax*. It seems, therefore, very probable that the shell of *Limax* is identical with the plug of the shell-gland, which has so wide a distribution among the embryos of Mollusca. At the same time further knowledge of the development of *Limax* and other Pulmonata, is necessary for a satisfactory conclusion on this point.

The further question as to the identity of the shell-gland and its plug with the pen-sac and pen of the dibranchiate Cephalopods is of very great importance and great difficulty. Professor Gegenbaur, in his 'Grundz. der vergleich. Anatomie,' puts forward the view that the Cephalopoda, on account of their bilateral symmetry and general anatomical relations with the other Mollusca, are to be regarded as the least specialised group of the whole stock; that is, as more closely retaining the characters of the common ancestors of existing Mollusca than do any other forms. If this be so, we should expect to find a representative of the shell-gland in the organization of the Cephalopods, and our attention is immediately directed to the pen-sac and pen of the Dibranchiata. If the shell-gland and pen-sac are identical structures we have a brilliant confirmation of Gegenbaur's view. This was one of the chief matters to which I directed my attention in a recent study of the development of *Loligo*, *Sepiola*, *Sepia*, and *Octopus*. I was anxious to determine the exact mode of the first commencement of the sac in which the "pen" of these cuttle-fish develops. I have only space here to state that it makes its first appearance as a relatively very small circular pit, the sides of which close in above so as to form a shut sac, which enlarges and elongates with the later growth of the embryo. In fig. 3 is given a drawing of a section of a very young embryo (the drawing is cut off so as to omit the yelk-sac and give only the embryonic portion of the specimen) at a stage when the pen-sac is still open, and its lips commencing to close in. Its position and mode of development exactly agree with that of the shell-gland as seen in the other molluscan embryos figured in this paper. We are, therefore, fairly entitled to conclude, from the embryological evidence, that the pen-sac of Cephalopoda is identical with the shell-gland of other Mollusca.

But here—forming an interesting example of the interaction of the various sources of evidence in genealogical biology—palæontology crosses the path of embryology. I think it is certain that if we possessed no fossil remains of Cephalopoda the conclusion that the pen-sac is a special development of the shell-gland would have to be accepted. But the consideration of the nature of the shell of the Belemnites, and its relation to the pen of living Cuttle-fish, brings a new light to bear on the matter. Reserving anything like a decided opinion as to the question in hand, I may briefly state the hypothesis suggested by the facts ascertained as to the Belemnitidæ. The complete shell of a Belemnite is essentially a straightened nautilus-shell (therefore an external shell, inherited from a nautilus-like ancestor), which, like the nautiloid shell of *Spirula*, has become enclosed by growths of the mantle, and, unlike the shell of *Spirula*, has received large additions of calcareous matter from those enclosing over-growths. On the lower surface of the enclosed nautilus-shell of the Belemnite—the phragmacone—a series of layers of calcareous matter have been thrown down forming the guard; above, the shell has been continued into the extensive chamber formed by the folds of the mantle so as to form the flattened pen-like pro-ostracum of Huxley. Whether in the Belemnites the folds of the mantle which thus covered in and added to the original chambered shell were completely closed so as to form a sac or remained partially open with contiguous flaps must be doubtful. In *Spirula* we have an originally external shell enclosed but not added to by the enclosing mantle-sac. In *Spirulirostra*, a tertiary fossil, we have a shell very similar to that of *Spirula*, with a small guard of laminated structure developed as in the Belemnite (see the figures in Bronn, 'Classen u. Ordnungen des Thierreichs'). In the Belemnites the original nautiloid

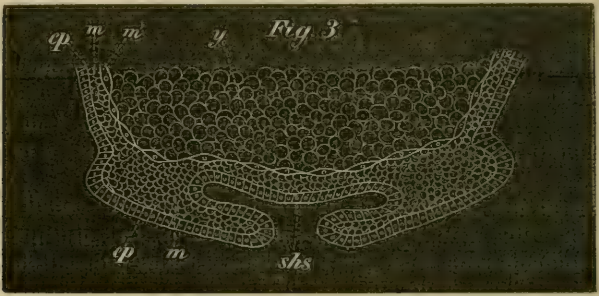

Diagram of vertical right-and-left section through mantle-region of an embryo *Loligo*. *ep.* Epiblast. *y.* Food-yelk. *m.* Mesoblast. *m'.* Deep-layer of cells (query, hypoblast) separating embryo from food-yelk. *shs.* Open pen-sac.

shell is small as compared with *Spirulirostra*. It appears to be largest in Huxley's genus *Xiphoteuthis*. Hence, in the series *Spirula, Spirulirostra, Xiphoteuthis, Belemnites*, we have evidence of the enclosure of an external shell by growths from the mantle (as in *Aplysia*), of the addition to that shell of calcareous matter from the walls of its enclosing sac, and of the gradual change of the relative proportions of the original nucleus, (the nautiloid phragmacone,) and its superadded pro-ostracal and rostral elements tending to the disappearance of the nucleus (the original external shell). If this view be correct as to the nature of these shells, it is clear that the shell-gland and its plug has nothing to do with them. The shell-gland must have preceded the original nautiloid shell, and must be looked for in such a relation whenever the embryology of the pearly Nautilus can be studied. Now, everything points to the close agreement of the Belemnitidæ with the living Dibranchiata. The hooklets on the arms, the ink-bag, the horny jaws, and general form of the body, leave no room for doubt on that point; it is more than probable that the living Dibranchiata are modified descendants of the mesozoic Belemnitidæ. If this be so, the pens of *Loligo* and *Sepia* must be traced to the more complex shell of the Belemnite. This is not difficult if we suppose the originally external shell, the phragmacone, around which as a nucleus the guard and pro-ostracum were developed, to have finally disappeared. The enclosing folds of the mantle remain as a sac and perform their part, producing the chitino-calcareous pen of the living Dibranch, in which parts can be recognised as corresponding to the pro-ostracum, and probably also to the guard, of the Belemnite. If this be the case, if the pen of *Sepia* and *Loligo* correspond to the entire Belemnite shell minus the phragmacone-nucleus, it is clear that the sac which develops so early in *Loligo*, and which appears to correspond to the shell-gland of the other molluscs, cannot be held to do so. The sac thus formed in *Loligo* must be held to represent the sac formed by the primæval upgrowth of mantle-folds over the young nautiloid shell of its Belemnitoid ancestors, and has accordingly no general significance for the whole molluscan group, but is a special organ belonging only to the Dibranchiate stem, similar to—but not necessarily genetically connected with—the mantle-fold in which the shell of the adult *Aplysia* and its congeners is concealed. The pen, then, of Cephalopods would not represent the plug of the shell-gland. In regard to this view of the case, it may be remarked that I have found no trace in the embryonic history of the living Dibranchiata of a structure representing the phragmacone; and further, it is possible, though little importance can be attached to this suggestion, that the Dibranchiate pen-sac, as seen in its earliest stage in the embryo *Loligo*, &c., is fused with the surviving remnants of an embryonic shell-gland. When a zoological observatory has been established in the southern seas, and the embryology of *Nautilus pompilius* worked out, we shall probably know with some certainty the fate of the molluscan shell-gland in the group of the Cephalopoda. By the use of no very great ingenuity it might be possible to conceive of the pro-ostracum alone of the Belemnite as being the plug of the shell-gland, and thus to save the homogeny of the embryonic pen-sac of living Cuttle-fish with the so closely corresponding sac (the shell-gland) of other Mollusca. I will only venture one additional remark of a speculative tendency here, and that is that the siphuncle of the chambered shells of *Nautilus* and *Spirula* is so placed as to suggest an inquiry as to whether it may have any relation to this problematical shell-gland.

The preceding discussions and speculations have been introduced with the object of rendering more clear the points of interest in the facts of the development of *Lymnæus stagnalis* which are recorded below.

§ 2.—DEVELOPMENT OF LYMNÆUS STAGNALIS.

The well-known egg-jelly of the common pond-snail is to be found on water-plants in most ponds from June to October. The jelly encloses a number of tense capsules, each of which contains one, rarely two, eggs.

Many points of interest in the earliest stages of the deposited egg demand minute investigation with the highest power, and have been entered into in a suggestive rather than a conclusive manner by M. Lereboullet in his extended "Monograph of the Development of *Lymnæus*" ('Annales des Sciences Naturelles,' ser. iv, t. 18, 1862). I shall here only record a few facts tending to show the general disposition of the masses resulting from the segmentation of the primitive egg-sphere, reserving the consideration of the minute structure and relations of the various elements of the yelk for another occasion. The egg-sphere, as laid, has a diameter of about $\frac{1}{220}$ of an inch. By the middle of the third day from its deposition in the warm season it has assumed the form seen in Pl. XVI, figs. 8—12, and is then $\frac{1}{180}$ of an inch in diameter. The intermediate steps are not easy to follow with certainty. It is necessary by sharp pressure or by needles to remove the egg from its envelope, to avoid anything like actual contact with it, and to study it with high powers (250 to 400 diameters) by both transmitted and reflected light. The egg is not a transparent one, and is very easily distorted by manipulation. Osmic acid solution of one per cent. is useful in the earlier but more especially in the later stages of the investigation, and enabled me to preserve specimens permanently.

Formation of the Gastrula.—With the first contractions of cleavage one or two pellucid drops are extruded from the brown yelk-mass, and remain adherent to the axial point of the egg, as in many other molluscs and worms; they are the well-known "Richtungsbläschen," and disappear, becoming detached at a later stage of development. They may serve a useful purpose for the embryologist if they enable him to recognise at any subsequent period when they are present the original pole at which they made their appearance. But it must be borne in mind that such droplets of albuminous matter are occasionally extruded from eggs of the same character as those of *Lymnæus* at other points during later stages in the process of segmentation of the egg-sphere. In Pl. XVI, figs. 2 and 3, lateral and polar views of the egg when exhibiting four divisions are given. In figs. 5 and 6 a series of smaller segmentation cells is seen extending itself so as to surround four larger spheres. The stage intermediate between this and the simple quadripartite form I have not yet observed, nor is it clear from M. Lereboullet's figures whence precisely these smaller cells arise. He figures an egg consisting of four large cells with four little ones surmounting them, but does not demonstrate whence these four smaller cells have originated. I have not seen the egg in this state. If we compare the case of *Aplysia* we find there a series of smaller cells growing over and enclosing two larger segmentation spheres, but the origin of these smaller cells is clear from the beginning; even in the unsegmented egg the pale transparent portion of the egg from which they are formed is distinguishable from the more granular opaque mass which forms the two large enclosed spheres. This is the first point of obscurity in the transition from fig. 3 to fig. 10. It can, no doubt, be readily cleared up by painstaking observation of a large number of eggs. In fig. 4 we have a lateral view of the same egg as that of figs. 5 and 6. The drawing is so placed that the smaller cells are below the large spheres above. This is for comparison with the succeeding fig. 7. At the pole of fig. 4 is seen a clear albuminous corpuscle, undoubtedly of the nature of Richtungsbläschen, sticking, as it were, in the point of intersection of the sectors of the large yelk-masses. It is possible that this is *not* the same corpuscle as that seen in figs. 1 and 2. If it be the same we have this to observe — that whereas in *Aplysia* the Richtungsbläschen escapes from the paler pole of the unsegmented egg, where the smaller enveloping cells are formed, in *Lymnæus* the pole from which the Richtungsbläschen is detached does *not* exhibit the *more* active, but the *less* active, segmentation. Accordingly, the small cells in *Lymnæus* would appear *not* to correspond with the small cells in *Aplysia;* they are not advancing, in the case of *Lymnæus*, to enclose the four larger masses as they do enclose the two large spheres of *Aplysia*, but are growing in the opposite direction. In fig. 7, taking the position of the Richtungsbläschen and the general shape again as a guide, we find the larger cells still left unenclosed by the smaller, which are now sinking in on the lower surface to form the primitive alimentary canal of the gastrula-form seen in the subsequent figures. This interpretation depends upon the assumption of the constancy of the position of the Richtungsbläschen, and also on the marked agreement in form of the embryos when placed as drawn in figs. 4 and 7. If we might disregard this, and invert fig. 6, we should have what would appear to be a much more intelligible mode of formation of the primitive in-pushing of the gastrula of *Lymnæus*. Fig. 4 being inverted, we should, looking at it in the light of fig. 7, and disregarding Richtungsbläschen, see in this stage the gradual extension of the smaller cells over the larger, so as to enclose them, just as certainly does occur in *Aplysia*, and the in-pushing in the base of fig. 7 would be the final result of the growing over and approximation of the circumferential border of the cap of enclosing cells. Unfortunately the embryo or segmented egg-mass in the stage seen in fig. 7 is too opaque to allow of our obtaining evidence on this point from its actual structure. The question as to the *precise* mode of formation of this gastrula, and, indeed, of all gastrula-forms, is one of such very great interest at present that I have not kept silence about the difficulties which this has presented to me, though a little more time and care than I have given to this part of the developmental history of *Lymnæus* would settle the point.[1] In figs. 8, 9,

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[1] M. Lereboullet's account does not help one very much in this part of the history. He figures one embryo as perfectly spherical and composed of "twenty equal spheres." I did not come across such embryos, but they would clearly be later than the stage given in fig. 4, and intermediate necessarily between it and the youngest gastrula-phase, namely fig. 7. In

10, 11, 12, we have various views of the gastrula of *Lymnæus*. In assuming this form the embryo gets rid of a very delicate envelope, which appears to be of a slightly viscid nature, and which, together with the Richtungsbläschen, is now lost. It is seen in a loose detached condition in the stage represented in fig. 7.

The gastrula of *Lymnæus* has been figured and described by Lereboullet, who takes the fossa and orifice of invagination for the rudiment of the adult's mouth. I believe, however, that this is a mistake, and that the orifice of invagination in *Lymnæus* closes up, as I have observed, in the gastrula of the Lamellibranch *Pisidium*, and in that of *Limax* and of *Polycera*, *Tergipes*, and *Doris*.

The Lymnæus-gastrula has the same curious cushion-like form as observed in the Nudibranchs. The orifice of invagination, in its most strongly marked period of development, is a long, trough-like depression, running from one side of the cushion towards the middle, and there sinking deeply into the substance of the mass. Accordingly, as it is turned this way or that, the extent and direction of the orifice presents apparent differences, which are, however, merely apparent.

The figures will give a more correct notion of these appearances than any description.

Besides, by Lereboullet, who did not appreciate its true character, the gastrula of *Lymnæus* has been figured diagramatically by Professor Haeckel in his Gastræa-theory. (See Pl. VII.)

I have elsewhere distinguished two classes of gastrula forms, according to the mode of their development, namely, "invaginate gastrulæ" and "delaminate gastrulæ," the latter forming by an internal movement of stratification in a mass of embryonic cells, and not by a process of involution. The Lymnæus-gastrula is clearly an "invaginate" one; but amongst invaginate gastrulæ we may distinguish those which are formed by emboly (the growth inwards of a number of small cells), and those formed by epiboly, in which large cells remain, as it were, stationary, and are grown over by smaller cells. These terms are adopted from Selenka, who has given a very valuable account of the development of *Purpura lapillus* in the 'Niederlandisches Archiv für Zoologie,' Bd. I, July, 1872.

I am obliged to leave for further inquiry the interesting

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this there is certainly not much if any difference in the size of the component cells, those in the apex of the pyramid being only apparently larger on account of their prominence.

question as to whether the invaginate gastrula of *Lymnæus* forms by emboly or epiboly, or has an intermediate character.

The Trochosphere.—The orifice of invagination of the gastrula now closes up, and its shape commences to undergo a change due to the development of a kind of equatorial ridge, the earliest rudiment of the velum. At the same time the movements of rotation of the embryo commence. The phase in which there is as yet no trace of the mouth, and in which the gastrula's orifice of invagination has disappeared, is not figured in the plates accompanying this paper; but I may refer to Lereboullet's pl. xii, fig. 36, for a good drawing of that particular phase, though the French naturalist does not recognise the significance of his illustration, since he believes that the Gastrula's orifice becomes the mouth.

The movements of rotation in the embryo *Lymnæus* are caused by very short cilia, which it is not difficult to see even with a quarter-inch (English make), after the embryo has been treated with osmic acid. These cilia have entirely escaped M. Lereboullet, who says, "J'ai cherché en vain la cause de ce mouvement qu'on attribue généralement à des cils vibratiles. Je puis affirmer que ces derniers n'existent pas, et qu'ils ne se voient jamais, à aucune epoque de la vie embryonnaire, sur toute la surface de l'œuf."

With a No. 10 *à* immersion Hartnack the cilia can be observed, even in the early period, when rotation first begins; later they are obvious enough in the region of the velum.

The phase which the embryo now enters upon with a distinct circumferential ciliated band is that which I have designated in the introductory remarks above as the trochosphere. In the earliest of the forms referable to this phase (Pl. XVI, fig. 13) the embryo has a very peculiar outline when viewed from the oral pole, the ciliated band appearing to commence its development in connection with the two lobe-like outgrowths right and left of the mouth. The remaining figures on Pl. XVI give various views of later trochospheres. The movements of rotation are now very rapid, and vary around two axes at right angles to one another, so that it is difficult to get a correct notion of the actual superficial form of the embryo. The figures supply such information as I can give.

The changes in the histological elements of the embryo from the earliest gastrula-form (fig. 7) to the latest trochosphere are no less marked and important than the changes in external shape. I am not prepared to give a detailed account of those changes, but can only draw attention to some general features.

The invaginated cells or segmentation-products, which form the endoderm or primitive alimentary sac of the gastrula, are not at first distinguishable through the walls of the widely excavated pyramidal embryo. But as the wide orifice narrows to a slit, the two sets of cells become clearly distinguishable, a result due, not merely to the clearing-up of the outer cells, but also to the gradual assumption of a specific character—globular form, dark granulation, and high refrangibility—by the invaginated cells. During the whole of the later development, as far as I have watched it in *Lymnæus*, the gastrula's endoderm-cells are undergoing modification, resulting at last in the separation of a pellucid material from a more superficial granular matter, which appears ultimately to give rise to a cellular network (Pl. XVII, fig. 22). The minute history of the changes in these cells would be an important matter to determine, since it appears that the history of other invaginated gastrula-endoderms is not so simple as one might suppose beforehand. They are by no means simple masses of formative protoplasm, which merely multiply by division, but appear in many cases to contain other elements analogous to the nutritive yelk (whence obtained is not clear), which in earlier stages have accumulated in each endodermal cell. Each endodermal cell then appears to play a part analogous to that of a whole ovum in its early stages, segregating and giving rise to new cells by endogenous formation. A process of this sort appears to go on in the gastrula-endoderm of *Pisidium* as well as in that of *Lymnæus*, and probably also in the "residual yelk-spheres" of Pleurobranchidium. An important histiological arrangement seen in the specimen (Pl. XVI, fig. 14) is the connection of the endodermal mass of cells with those forming the body-wall by means of long processes. This is seen again in a later phase in Pl. XVII, fig. 19. The processes appear to be actual filaments of the cell-substance of the endodermal cells.

In the trochosphere so far the shape is nearly spherical, excepting for the raised ciliated ridges, which together make a heart-shaped outline on the surface of the embryo, the indentation of the heart being occupied by the mouth.

The Veliger-phase.—In fig. 1 of Pl. XVII we have a somewhat more advanced stage, and in figs. 2, 3, 4, 5, 6, the definite Veliger-phase is attained. In the Veliger the area of the velum has a definite development, occupying relatively the same position and having something of the same relative size as the wheel-apparatus of a Rotifer. Moreover, in the Veliger the foot takes on a large relative growth, so as to form a projecting lobe; at first it is simple, but soon becomes, what is exceedingly important, bilobed. This bilobed condition of the foot need but be carried a very little further than it is in the Lymnæus-veliger, and we should have the Pteropod-veliger, with fully developed velum and two epipodial "wings," such as I had the opportunity of examining last spring at Messina through the kindness of Dr. Herman Fol.

In fig. 1 some interesting features are exhibited which happened to be unusually well-presented by the particular specimen from which the figure is drawn. The letter *g* indicates the spot at which the gastrula's orifice of invagination has closed up, and the delicate pedicle of tissue (*p i*) extending from this to the enlarged gastrula-endoderm-cells is the "pedicle of invagination," precisely similar to the pedicle formed in the same way in the Lamellibranch *Pisidium* (for an account of which I must refer to the forthcoming volume of the 'Philosophical Transactions'). The thickened superficial tissue to the left of the closed orifice of invagination is the shell-disc—the earliest commencement of the mantle area. This again will be seen from the woodcut (fig. 2) to have its equivalent in other molluscs, and has, indeed, been especially described by Paul Stepanof in his account of the development of the pulmonate *Ancylus fluviatilis.* The further development of this region has, however, escaped him and all other previous observers. It is as a pushing in from this shell-disc that the shell-gland to which I have referred in the introduction, and which is seen in Pl. XVII, figs. 11, 12, 13, 14, and 17, is developed.

The Shell-gland.—The shell-gland—a name which suggests itself merely from the position of the gland, and not from any necessary functional connection with the formation of the shell—was seen figured and described by Lereboullet in his account of the development of *Lymnæus.* Lereboullet accurately described it at one period of its growth as a hollow cone, truncated and closed at its deeper extremity. He regarded it as the anal portion of the alimentary canal, and consequently termed it the "anal cone." From this it follows that he had failed to detect, as his figures also show to be the case, the "pedicle of invagination" and the true commencement of the terminal part of the alimentary tract. If we follow the shell-gland through the various figures on Pl. XVII, in which, it appears, we shall find that occupying at one time a very prominent position, and pushing its way right up into the central mass of gastrula-endoderm-cells, it subsequently dwindles, and very rapidly disappears *altogether*, as the shell forms and the mantle-area becomes raised up as a convex dome with margin distinctly projecting to form a rudimentary mantle-flap. The drawings (Pl. XVII, figs. 11, 12) represent the shell-gland in its most strongly marked condition, the conical lumen of the gland being filled by a highly refracting chitinous substance. Curiously enough, the cases in which this occurs appear to be abnormal. In a mass of eggs which have for the most part advanced to the stage seen in Pl. XVII, fig. 10, two or three may be found which have hung back, and have an abnormal proportion of foot, mantle-flap, &c., besides being much smaller than the further advanced normal specimens. Such retarded specimens frequently exhibit the condition of the shell-gland figured in figs. 1 and 12. Not only is there this plugging of the gland, but the commencing shell (not at this period calcified, but entirely of a horny composition) is thick and rough as compared with the normal shell of the same size, and sometimes the plug is united to the disc-like shell, so that the two can be picked out by careful teazing as a separate plate and handle. In the introductory remarks above I have referred to my observations on *Aplysia* (*Pleurobranchidium*), where I found a precisely similar condition accompanying a retarded development.

The Velar Area.—Let us now return to the velum for the purpose of tracing its development, and that of the velar area. It is an extraordinary fact that the existence of a velum in the embryos of Pulmonata has been denied, and its absence is at this moment mentioned in so authoritative a work as Bronn's ‘Thierreich’ as characterising the young stages of that group. Pouchet, who appears to have seen it in the trochosphere-phase of *Lymnæus*, and whose figures are copied in Bronn's plates, traces it to the free edge of the mantle, for the first rudiment of which he mistakes it. Lereboullet appears to have missed it altogether. The fact is, as will be seen from the figures in Pl. XVII, that it not only is well developed in the youngest stages of *Lymnæus*, but persists in an altogether exceptional way, and is actually *retained in the adult*, having become the lip-like masses which are known in *Lymnæus* as the “subtentacular lobes.” The margin of the velum is easy to trace in the Veliger-phase of *Lymnæus* on account of the large, granular, epidermic cells of a yellowish-brown colour which compose it. When the embryo passes from the Veliger-phase to the definite molluscan phase with creeping foot, with mantle-flap and eye-tentacles, the cilia no longer predominate on the velum, but it remains as a well-marked ridge swelling out into a pair of lobes, one on each side of the mouth, and terminating bluntly on each side at the back of the head (Pl. XVII, figs. 7 and 10).

At the same time during the Veliger-period in which the foot commences to assume a bilobed form, a conical eminence appears on each side within the heart-shaped velar area. These two eminences are the eye-tentacles, and rapidly grow so as to overshadow the margins of the velum. In this phase of the development, as the embryo rotates, it often presents itself in the position seen in Pl. XVII, fig. 6, in which the foot is stretched in front, and the velar area with the growing eye-tentacles, and the mouth placed centrally, complete the rest of the visible part of the Veliger. The dark coloured margin of the velum itself is seen forming a curious saddle-shaped cincture placed transversely. It is easy enough to demonstrate that the velum actually persists in adult life by comparing such embryos as figs. 7 and 10 with full-grown Lymnæi. The fact that some of the Pulmonata thus retain this larval organ in the adult condition is important, because, so far as I know, no other mollusc has been shown to do so; and, in fact, no other organism which possesses a velum in its younger phases of development, such as the Echinodermata, Nemerteans, Gephyreans, and Chætopodous Annelids, with the exception of the Rotifers. Parts of the prostomial region in some of the Chætopodous Annelida may perhaps be traceable to the larval velum, as are the sub-tentacular lobes of *Lymnæus*.

The retention of the velum and the strongly bilobed character of the young foot mark the Pulmonata as an archaic group of odontophorous Mollusca. The presence of these archaic features is in accordance with the generalisation that such features may be looked for in the fresh-water representatives of large sea-dwelling groups, other examples being found in the fresh-water Radiolaria, in *Hydra* and *Cordylophora,* and in the living Ganoid fishes.

Nerve-ganglion.—Within the velar area coincidently with the commencing development of the eye-tentacles a bilobed mass of cells commences to develop, apparently from a local multiplication of cells belonging to the epidermic layer. They form a conspicuous mass, and enter into connection with the pharyngeal mass (figs. 8, 17, 23 *ng*). This is the supra-œsophageal nerve-mass, and it is to be noted that its mode of development is identical with that which I have elsewhere described in *Aplysia.*

I have no details to record with regard to the development of the eyes; but with regard to the otocysts may draw attention to the fact that they are absent in the stages studied by me, though in a corresponding period of development in the Nudibranchiata they have attained a high degree of perfection. This I imagine may be explained by the relatively smaller importance of the auditory organ in the adult *Lymnæus* than in the Sea-slugs, and their near allies the free-swimming snails (Heteropoda).

Mantle-flap and lung.—In Pl. XVII, fig. 8, a stage in which the shell-gland has disappeared, and the shell itself (*sh*) is already projecting like a watch-glass from the aboral pole of the embryo, the edge of the mantle first becomes raised up and definitely emarginated. Following this through figs. 7 and 10, we find its rim becoming more and more detached or lengthened, until in fig. 18, on the right-hand side, a considerable space is overhung by this marginal flap. It is here that the lung develops as a simple recess covered in by the mantle-flap. In the specimen drawn in fig. 18 the rudiment of the heart is also seen (*h*), and other organs in connection with the enlarged border of the mantle, viz. the tubular dark-coloured body opening to the exterior (*n*), which I take to be the young kidney, and the prolonged delicate terminal portion of the alimentary canal, which still ends blindly (*cr*).

Alimentary canal.—The fact that the alimentary canal ends blindly in so late a stage of development as that of fig. 18 should have made clear to M. Lereboullet that he was wrong in interpreting the shell-gland as an anal cone; but it must be admitted that to follow out fully the development of the alimentary canal is exceedingly difficult, even as far as its general contour is concerned, still more so when a histological and histogenetic point of view is attempted. In fact, here, as in all the embryologies which have been attempted, the dark point is in connection with the middle portion of the alimentary canal. If we knew with certainty whence and how its cellular elements are developed in all types which have been studied, we should have little difficulty in reducing the facts of development of the whole animal kingdom to satisfactory order.

We have seen that there results from the gastrula-invagination an outer cellular body-wall, from the elements of which the epidermic and muscular structures of foot, velum, mantle, and shell-gland, develop, and an inner invaginated sac composed of larger cells, supported on a short pedicle (the cells of which are *not* large and granular, but scarcely distinguishable), the pedicle of invagination.

The sac composed of large cells very early becomes constricted, so as to present two lobes, as seen in Pl. XVII, fig. 1. In looking at the figures in Pl. XVII it must be remembered that the specimens are often compressed, and that only an optical section or partial view can be given of the various parts; hence the mass of large cells (the gastrula-endoderm) is frequently distorted. The lobes appear at first to lie right and left, the pedicle being in the median plane.

The pharynx now commences to develop with the in-pushing of the mouth from the body-wall, and gradually extends downwards into the mass of endoderm-cells, so as to be partly concealed by them (figs. 8, 11, 17 *ph*). At the same time the cells in the pedicle of invagination differentiate. The pedicle assumes a tubular character, and its parietal end becomes bent round, so that the tube terminates as a shortly reflected cæcum. Whilst the pharynx and the intestinal portion of the alimentary canal are thus differentiating, changes have been going on in the gastrula-endoderm-cells, to which changes I have already alluded. In place of a bilobed group of large granular cells we now have a net-work of fine granular filaments with nuclei at intervals completely enclosing and surrounding on all sides pellucid, highly refracting spheres (fig. 22). Moreover, a tunic of fusiform cells, of the same character as the elementary muscular cells which are seen in other parts of the embryo, has spread itself over the whole of the alimentary tract (fig. 17, *tge*). They are closely fitted to the pharynx and rectum (figs. 21, 22), and also extend over the pellucid spheres and their granular network, whence they send branches to the similar cells lining the body-wall (figs. 17, 22). Whence has this tunic developed? At the pharyngeal end the cells are clearly continuous with those of the body-wall, and at the rectal end also; but those enclosing what was the gastrula-endoderm are probably developed from the processes which the invaginate gastrula-cells send to the body-wall, even in the trochosphere stage of development, as seen in Pl. XVI, fig. 14. If this is the case the musculature of the terminal portions of the alimentary canal will have been developed, like the musculature of the body-wall, from the ectoderm of the gastrula, whilst the musculature of the middle portion of the alimentary canal and its appendices will have been developed from the gastrula's endoderm.

We have, however, yet to see what eventually comes of this middle group of cells—the histologically changed, but in coarser features unchanged, bilobed group which formed the gastula's stomach. I have failed to penetrate to the centre of this mass of cells in earlier phases, and can, therefore, not explain how the structure to be described comes about. What can be observed is this, that as soon as the pharynx and its appendix, the odontophore's sac, becomes well marked, and the tubular structure with epithelial lining in the pedicle of invagination is clearly visible, then a little compression and manipulation renders clear the continuation of a tube-like structure with walls formed of small cells from pharynx to intestine, traversing the mass of large pellucid cells (Pl. XVII, fig. 21). This tubular structure is undoubtedly to be regarded as the so-called stomach of the adult *Lymnæus*. The metamorphosed gastrula-endoderm-cells now lie on each side of it as a pair of grape-like bunches, and long after it has become well-defined these two agglomerations of pellucid spheres, with their enclosing network and mesoblastic coat (the tunic of fusiform cells), remain. They are apparently eventually *absorbed* as nutritive matter by diverticula of the alimentary canal, which give rise to the liver, they themselves not giving rise subsequently to any permanent tissue. Now, it is a most important question whether the cell-elements which build up the so-called "stomach" (the middle piece of the alimentary canal) arise in any way from the large gastrula-endoderm-cells, or from the pharyngeal in-pushing, or from the intestinal pedicle of invagination. If from this last, they would just as much, as if they arose from the material of the central mass of gastrula-endoderm, be traceable to the invaginated cells of the gastrula-phase. On the whole, it seems probable that this is their origin; but the matter is still obscure. The analogy of other Mollusca does not take us very far towards a clearing up, for in all cases that I have studied the exact mode of origin of the middle portion of the alimentary canal is equally obscure. It is, however, interesting and of considerable importance for a true understanding of the matter, to note that in this case of *Lymnæus* we have a large proportion of the material which at one time formed the wall of the gastrula-stomach left outside the permanent alimentary canal and absorbed as a kind of food-yelk. The case of *Pleurobranchidium*, of which an embryo is represented in the woodcut, is, in a measure, parallel to this, for the two large nucleated spheres (*ry*) are that portion of the original cleavage-product of the egg which are overgrown or invaginated by epiboly. Hence they represent the gastrula-stomach, and, as in *Lymnæus*, a middle intestine appears *between* them without our being able to determine whence it takes its origin; possibly it is from some of the material of these very cells, but they remain unembraced by the walls of the alimentary canal so formed, and gradually dwindle by the absorption of their material. In *Pisidium,* again, we have in the earlier condition a still closer agreement with *Lymnæus,* for there a very definitely marked, bilobed gastrula-stomach is formed by invagination (see woodcut, fig. 1). But in *Pisidium,* too, after this epoch, a great change comes over the cells forming the wall of the gastrula-stomach, its cavity becomes constricted, narrowed, and contorted, and apparently a new mid-portion of the alimentary canal is formed with separation of nutritive and formative elements from the original gastrula-endoderm-cells. Therefore it seems that the history of the development of the gastrula-stomach into the permanent middle intestine is by no means a simple one. It, in fact, involves the whole question of the part played by the so-called nutritive elements of the original egg-yelk, and we may expect gradations between the developmental processes of a simple unencumbered egg-cell (free from yelk-granules), such as that of the Nematoid *Cucullanus* (in which I should anticipate that the primitive alimentary canal would be directly enlarged so as to form the adult one), and those of the eggs of Cephalopods and birds, in which the egg-cell is well-nigh lost in an excess of superadded nutrient material.

Wherever these nutritive yelk-elements come in they derange and obscure the usual processes of cell-growth; in the earliest stages they give a paradoxical twist to the multiplication by fission of the primitive egg-cell, later to the mode of formation of the hypoblast or gastrula-endoderm, and finally, to the mode of development of middle intestine and liver from this last, whilst they may even have something to say to the development of other organs in which their too ready offer of nutritional assistance is accepted.

The later development of the alimentary canal, the breaking through of the anus to the exterior, and of the pharynx to the stomach or middle intestine, I have not followed, nor have I observed the development of the liver and absorption of the two masses of pellucid cells which Lereboullet has described, since I have not pursued the embryos to that phase. I may, however, here mention that in the Cephalopod *Loligo* I have determined, by means of transverse and longitudinal sections, that the great mass of "unorganised" yelk enclosed by the embryo is in that animal gradually absorbed, whilst the growth of a pair of diverticula from the alimentary canal proceeds, which diverticula penetrate the unorganised yelk, and, filling up the position once occupied by it, become the two lobes of the Cephalopod liver. This process is probably a general one throughout the animal kingdom, with variation in non-essentials.

Muscular layers and muscles.—I have above spoken of fusiform cells arranged as a layer on the inner surface of the body-wall, and as surrounding the alimentary canal and bilobed mass of pellucid cells. These represent the mesoblastic elements of the embryo. I have not been able to find in the early stages of *Lymnæus* a layer or group of undifferentiated embryonic cells lying definitely between the gastrula's body-wall and stomach; such a layer would be a mesoblast. It is possible that there are some such loosely placed cells during a particlar phase of the development, just as there are in *Pisidium,* but they are derived either from the enclosing ectoderm or the invaginated endoderm in the first instance. The appearances are strongly in favour of the fusiform cells which lie in apposition to the epidermic cells of the body-wall, being derived from ectoderm or epiblast cells. The most noticeable groups develop at the circumference of the shell-gland (Pl. XVII, fig. 8 *mu*). The processes which pass from the gastrula-endoderm-cells to the body-wall appear (fig. 19), eventually to become muscular, but whether they should then be attributed to the latter or the former is doubtful. The term Triploblastic is applicable to *Lymnæus* and to other molluscs in which there is no definitely constituted layer intermediate between the gastrula's ectoderm and endoderm, since in it and them, as in all the groups filiated to Vermes the musculature has not only relations to the outer world and to the gastric space, but to a third interposed space—the hæmolymph cavity—in which a vascular system and blood-lymph spaces develop.

It is clear (and in saying this I am qualifying, though not recalling, what I have stated in my essay in 'Ann. and Mag. Nat. History,' June, 1873) that a mesoblast or third intermediate layer must *either* be derived from epiblast or hypoblast (either or both), and so cannot be spoken of as of coordinate value with those two layers; *or,* on the other hand, it must be a separate entity originating simultaneously with the epiblast and hypoblast from the egg-cell or its segmentation products. The latter case is one which certainly has not been usually contemplated in the use of the term "mesoblast" or "middle layer," and there is very small warrant for assuming it as expressing the historic or phylogenetic mode of origin of the layer in question. It is possible that in some cases, when the gastrula's ectoderm and stomach-wall are differentiated by invagination, a certain number of the primitive segmentation-cells should remain involved, neither in the one nor the other, but lying intermediately, thus forming a simultaneously differentiated mesoblast, but even then we should be able to trace such cells to an earlier connection with the cells of either epiblast or hypoblast. In point of fact, such cases have not been brought forward from actual observation for discussion.

Thus, then, the term mesoblast and its correlative term "triploblastic" have not reference to the existence of an embryonic layer of co-ordinate value with the two primary layers, but to a disposition and growth of some of the early structural elements of the higher animals in and around a strongly marked space separating the two primary layers.

Summary.—The observations of fact which have been brought forward above are to a large extent disjointed, and even as far as concerns the period of development to which they refer, very far from exhaustive. They must rather be regarded as suggesting the desirability of more detailed and long-continued study.

As evidence of the value which may be assigned to them, I shall quote the summary of the development of the water-Pulmonata, given by Keferstein in Bronn's invaluable 'Thierreich,' followed by a statement of the points in which my observations traverse or supply important omissions in that summary.

Keferstein says (p. 1230 of the third volume of the above-named work):

"The Pulmonata of fresh waters exhibit the closest agreement with the Prosobranchiata, excepting that in them *all trace of a velum is wanting* (A). We possess very numerous and elaborate memoirs on the development of *Limnæus*, especially by Stiebel, Dumortier, Pouchet, Karsch, Warneck, Lereboullet, &c.; on that of *Planorbis* we have the researches of Jacquemin, &c.; so that the facts are here accurately known. We confine ourselves in the following remarks to *Limnæus*.

"Two hours after the egg is laid its cleavage commences, as a consequence of which at once one or two so-called Richtungsbläschen are pushed out by the contraction of the yelk, and then a first circumferential cleft extends itself round the spherical egg-mass. The germinal vesicle is no longer visible in the impregnated yelk; but shortly before the equatorial cleft is formed a clear speck is visible in the yelk, which, according to Warneck, becomes biscuit-shaped, and finally divides into two clear specks, of which one is found in each half of the cleft yelk-mass. These clear specks are undoubtedly true nuclei of the cleavage spheres, but no connection between them and the germinal vesicle could be demonstrated. These nuclei divide again, and at the same time the yelk is seen to fall into four masses by the formation of a second cleft. According to Lereboullet all the cleavage-spheres fuse themselves into a homogeneous mass before each new segmentation every time, and then separate again and commence the process of further cleavage. According to Quatrefages the same thing occurs in the annelid *Sabellaria*. From the midst of four cleavage-spheres so formed and lying in one plane arises now a clear vesicle, which quickly divides into four small nucleated spheres, and soon both the four large and four small spheres—always preceded by their nuclei—again divide, so that the egg now consists of sixteen nucleated cleavage-spheres (B). The large spheres overgrow now with their progeny the smaller, and we have at last a spherical mass, which consists externally of large, internally of small cleavage-spheres, accordingly exactly the reverse of what occurs with the cleavage-spheres of the Opisthobranchiata and Prosobranchiata (C). Finally, however, the segmented egg consists of large nucleated cells ·02 to ·025 mm. in diameter, which do not as yet present any cell-membrane.

"At the end of the second day modifications of this cell-mass are seen. On one side the cell-mass hollows itself out, then flattens itself, and at the same time the in-sinking narrows its area, so that the mass presents a cavity within and a narrow emarginated opening leading into it. These are the alimentary cavity and the mouth (D); the outer cells are still larger than the inner ones. Beneath the mouth the body now flattens itself out and forms a process—the foot, and the embryo begins now its well-known and—since the time of Leuwenhoeck—celebrated slow movements of rotation. This rotation must be ascribed to cilia; but they are so fine that they have not been seen in *Limnæus*, although one may suppose by analogy that they exist especially on the foot (E). The foot grows more and more prominent, and the body becomes partially embraced by an annular ridge, in which the later mantle-margin is soon recognised (F). From behind now—over against the mouth—a new in-sinking is formed, anus and rectum, which grows up against the primitive alimentary cavity, and finally unites with it (G). The alimentary tract now becomes hollowed out, and in its neighbourhood large yelk-spheres are formed, the first rudiments of the liver (H).

"As yet the alimentary tract traverses the body almost in a straight line (I); but, now as the body becomes more elongated and cylindrical, it begins to bend on itself, and the anus takes up a position forward on the right-hand side. At the same time the mantle-margin grows greatly, and the hinder part of the body rises up in a dome-like fashion. On it one can now observe the small cap-like shell (*g*), and in the body a to-and-fro circulation, such as is seen in a much more marked manner in the land Pulmonata.

"The foot forms now a prominent bilobed process, and above it near the mouth, which also begins to push forward in a snout-like fashion (K), the tentacles are seen, and at their bases the eyes. The mantle ridge arches now more and more widely forward and raises itself up, so that we can now clearly distinguish a lung-chamber, in which ciliary movement is observed; also the heart is recognised by its contractions in the middle line behind the mantle-ridge.

"In the neck region the first rudiment of the nervous system is now seen (L), whilst the foot grows considerably, as also the shell-bearing hind-body.

"In the pharynx the commencement of the odontophor is seen, and in the further developed lung-chamber the kidney. Upon the eye-pigment a lens is now clearly seen, and now, at last, according to Lereboullet, the otocysts make their appearance, which in most snails appear in a much earlier stage.

"At first the otocysts are empty, but gradually the otoliths are secreted, and cilia appear on the walls of the sacs.

"The embryo is now so large that it fills up the egg-shell, and soon breaks it and creeps out. The rate of development varies much, according to temperature, but lasts at least twenty days, and may take double that time."

In reference to the passages lettered in the preceding quotation, the observations recorded in this paper lead to the following corrections:

A. The velum is not wanting in the freshwater Pulmonata; in its earlier annular and in its later heart-shaped form it is well developed, and becomes the subtentacular lobes of the adult Lymnæus.

B. The origin of the four smaller cells from a single pellucid cell, coexisting with four larger cells, is not satisfactorily demonstrated, such a single pellucid cell being possibly only a Richtungsbläschen.

C. Nor is the enclosure of the smaller by the larger cleavage-spheres clearly made out, though possible enough.

D. The in-sinking and its orifice are not the alimentary cavity and mouth, but the gastrula-stomach and orifice of invagination; the latter closes up, and the pedicle so formed becomes the rectum, which terminates *blindly*.

E. With a good English quarter, or, better, with Hartnack's 10 immersion, and the use of osmic acid, the cilia which cause the rotation may be seen. They are disposed on an annular band, the commencing velum.

F. The annular ridge has nothing to do with the mantle's margin, but is the velum.

G. The new in-sinking has no connection with the anus or rectum, which latter already is taking shape in the pedicle of invagination. It is the "shell-gland," a structure common to many embryo mollusca, but hitherto unrecognised.

H. The so-called large yelk-spheres are not now first formed, but have been there all the time, forming the wall of the invaginated gastrula-stomach. They now undergo important segregative changes, and present the appearance of large clear globules, covered in by a fine granular reticulum.

I. The alimentary canal is from the first bent, the cæcal termination of the rectum lying a little forward, and not opposite the mouth.

J. The shell, as an exceedingly delicate membrane on the surface of the shell-patch (in the centre of which lies the shell-gland), is observable long before this.

K. The mouth never pushes forward, but rather becomes sunk and enclosed by the increasing development of the border of the velum, where it overhangs the mouth. This part of the velum forms the subtentacular lobes of the adult.

L. It can be seen at a very much earlier period.

A NOTE *on* ENDOTHELIUM. By JOHN CAVAFY, M.D., Assistant-Physician and Lecturer on Physiology at St. George's Hospital.

IN the last number of this Journal[1] there is a paper by Dr. M. Foster, "On the term Endothelium," in which he gives various reasons against the further use of this word in histological terminology. He objects to the word, both because its etymology is "of the most grotesque kind," and also on far more important anatomical grounds.

Much that is brought forward by Dr. Foster is, doubtless, true; but some portion of his statement must, I think, be

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[1] 'Quart. Journ. of Mic. Sci.,' 1874, p. 219.

EXPLANATION OF PLATE XVI,

Illustrating Mr. Ray Lankester's Memoir on the Development of the Pond-snail.

Fig. 1.—An egg after the formation of the first cleavage groove. Two Richtungsbläschen (*R.*) are seen. Nat. size of the egg $= \frac{1}{190}$ inch.

Fig. 2.—An egg after division into four cleavage-masses, three of which are seen, and the Richtungsbläschen (*R.*). Nat. size $\frac{1}{180}$ inch (long measurement).

Fig. 3.—The same quadripartite egg seen from below.

Fig. 4.—An egg of a later stage in which smaller cleavage-spheres have made their appearance at one pole. A Richtungsbläschen (*R.*) is seen attached between the four larger cleavage-spheres.

Fig. 5.—The same egg seen from above.

Fig. 6.—The same egg seen from below.

Fig. 7.—A later stage. At the pole *g m* the gastrula-invagination is now commencing. At *R* the Richtungsbläschen, entangled in the discarded vitelline (?) membrane, is seen.

Figs. 8—12.—Various views of the Gastrula of *Lymnæus.* Natural size $= \frac{1}{180}$ inch. The appearance varies according to the position which is assumed. Fig. 9 gives a surface view as seen by reflected light. Fig. 10. The same specimen seen by transmitted light. Fig. 11. Another specimen, two thirds profile view; *g m* is the gastrula-mouth or orifice of invagination.

Fig. 13.—The early phase of the Trochosphere with large lateral lobes (the figure is turned sideways). *m.* Commencing formation of the permanent mouth. Long measurement of this specimen $\frac{1}{130}$ inch.

Fig. 14.—Trochosphere with ciliated annular ridge and commencing mouth, *m.* The large cells of the Gastrula-endoderm are seen to be in connection with the body wall by means of delicate processes. Longest measurement of this specimen $= \frac{1}{140}$ inch.

Fig. 15.—*a, b, c, d.* Successive outlines presented by such a trochosphere as that in the preceding figure during rotation in the antero-posterior direction. The small prominence seen in *b*, and also in fig. 13, in a similar position, is probably the first indication of the foot.

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EXPLANATION OF PLATE XVII,

Illustrating Mr. Ray Lankester's Memoir on the Development of the Pond-snail.

Fig. 1.—An embryo between the Trochosphere and Veliger phases—somewhat compressed; longest diameter about $\frac{1}{120}$ inch. *m.* Mouth. *v.* Velum. *f.* Foot. *g e.* Gastrula-endoderm, now assuming a bilobed character—the sac enclosed by it having therefore a double cavity, a right and a left. *g.* Point of closure of the gastrula-mouth. *p i.* Pedicle of invagination—the future rectum. *s p.* The shell-patch—a thickened area of the body wall, on the surface of which the shell first forms, and by invagination of which the shell-gland is produced.

Fig. 2.—Young Veliger, surface view, showing—*m.* Mouth. *v.* Velum. *f.* Foot. Longest diameter about $\frac{1}{100}$ inch.

Fig. 3.—A similar specimen from the oral aspect.

Fig. 4.—A similar specimen somewhat compressed and seen in incomplete optical section. *m.* Mouth. *f.* Foot. *p i.* Pedicle of invagination. *s h.* Shell overlying the depression of the shell-gland, which is now visible.

Fig. 5.—Surface view of a more advanced Veliger, longest diameter about $\frac{1}{90}$ of an inch. *f.* The foot, showing bilobation. *v.* Velum now forming a heart-shaped area, with *m,* the mouth, at its base. *t.* The eye-tentacles.

Fig. 6.—Surface view of a more advanced embryo, in a position frequently assumed at this period of development. Length of the specimen, about $\frac{1}{70}$ inch. *fp.* A doubtful structure, lying between the two lobes of the foot, possibly a foot-pore. Other letters as above.

Fig. 7.—A much more advanced embryo, about $\frac{1}{40}$ of an inch long. *f.* Foot. *fp.* Foot-pore. *v.* Velum now assuming the character of "sub-tentacular lobes." *t.* Tentacles. *l.* Lung-chamber. *m f.* Mantle-flap, or free border of the mantle. *sh.* Shell.

Fig. 8.—An embryo, a little older than that of fig. 5. Length about $\frac{1}{80}$ of an inch, compressed, treated with osmic acid, and seen in partial optical section. *m.* Mouth. *ph.* Pharynx. *ods.* Odontophore-sac. *f.* Foot. *p i.* Pedicle of invagination (rectum) with cæcal termination. *m f.* Mantle-

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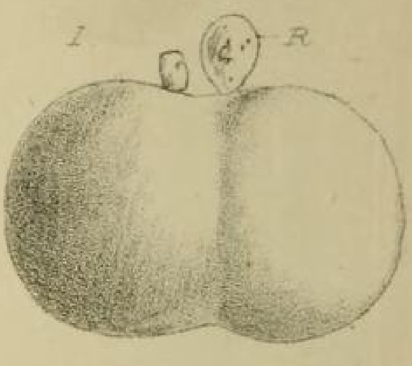

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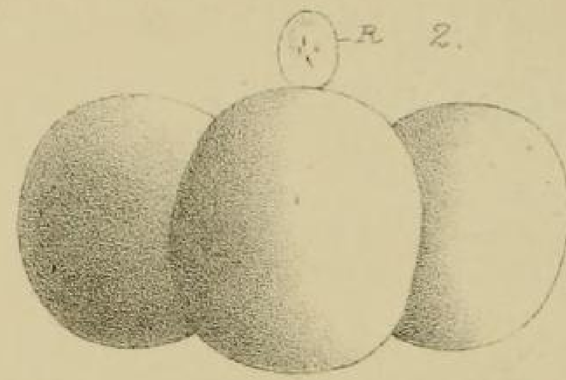

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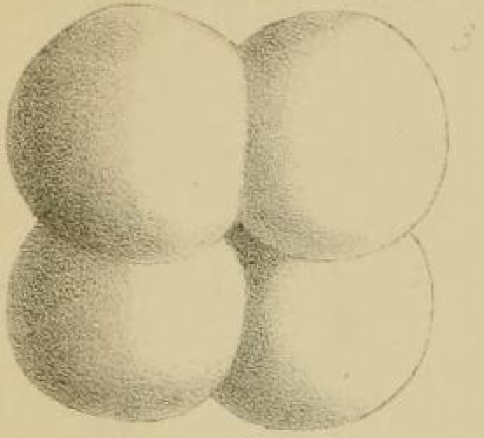

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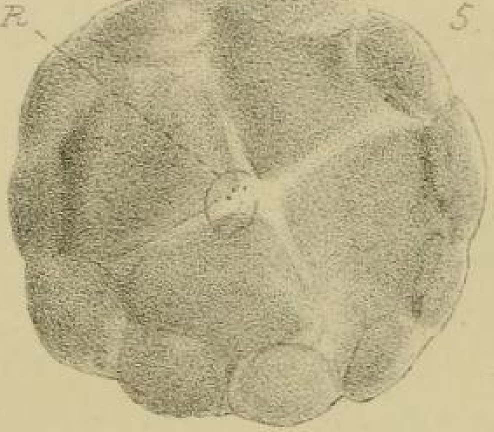

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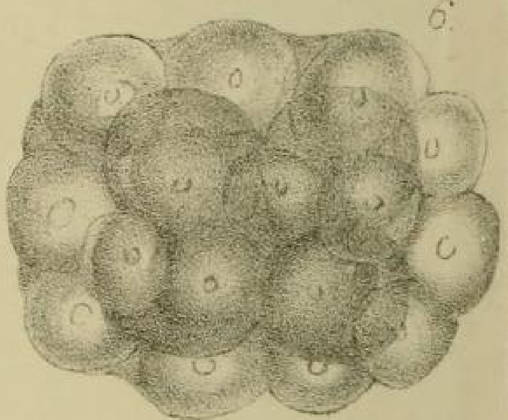

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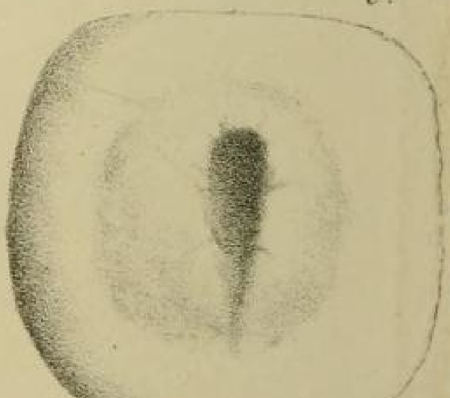

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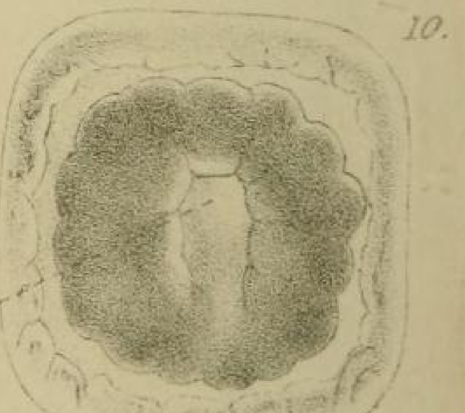

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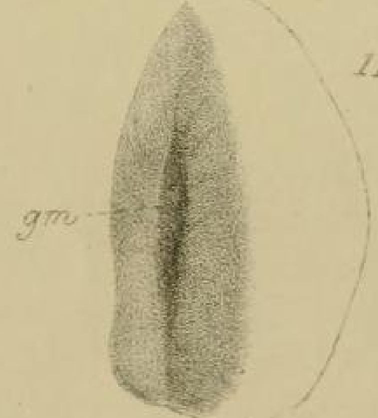

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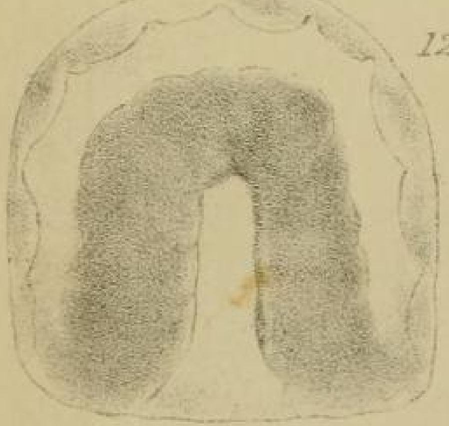

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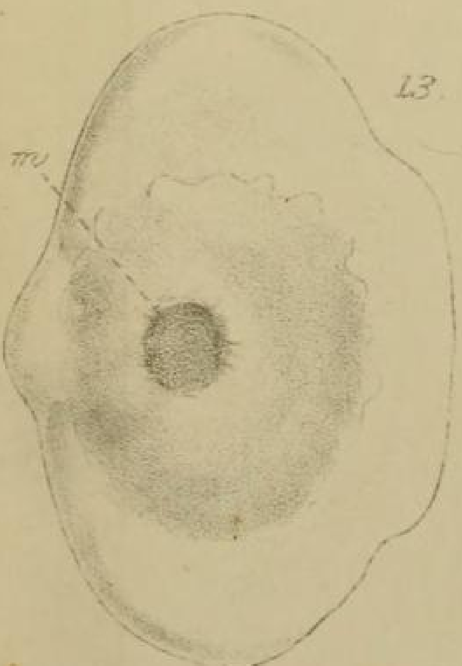

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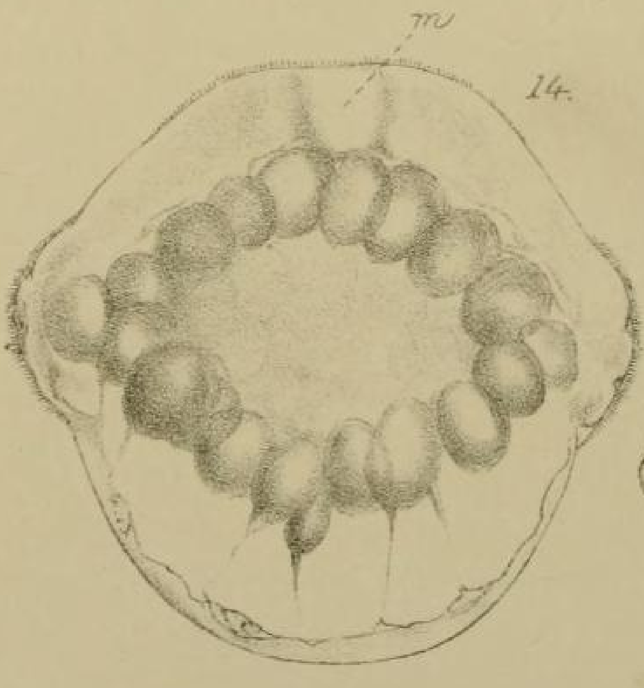

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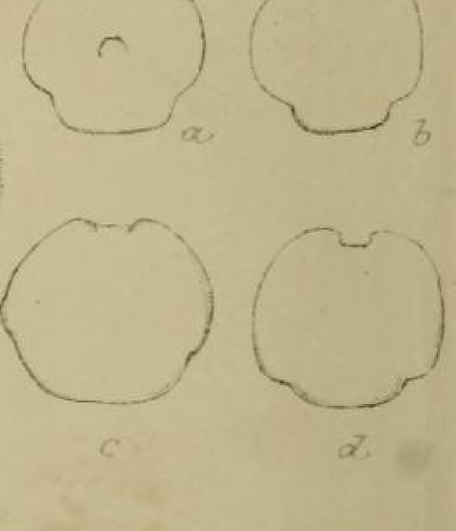

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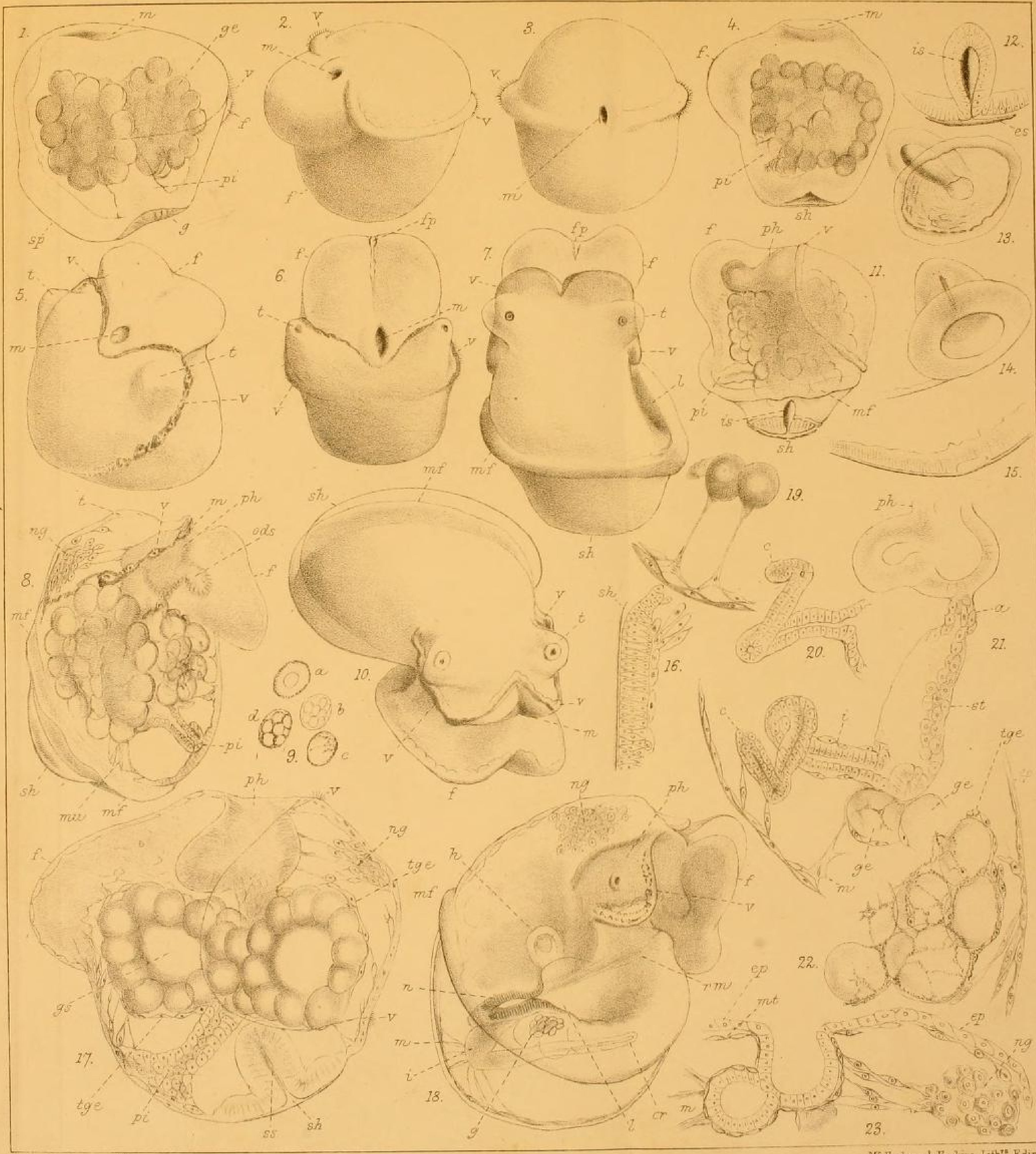

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