PHILOSOPHICAL TRANSACTIONS.

I. *Contributions to the Developmental History of the Mollusca.* *By* E. RAY LANKESTER, *M.A., Fellow of Exeter College, Oxford.* *Communicated by* GEORGE ROLLESTON, *F.R.S., Linacre Professor of Physiology.*

Received January 19,—Read March 12, 1874.

No. I. *The Early Development of* Pisidium pusillum.

IN the months of April and May 1871 I obtained a supply of the freshwater bivalve *Pisidium pusillum*, from a muddy little stream near Jena, in Saxe Weimar.

The fact that the development of the eggs of this mollusk takes place within a pair of brood-cavities formed at the root of the inner gill-lamella on each side, enables the observer very readily to obtain embryos in different stages of development.

LEYDIG and O. SCHMIDT had previously to this described the development of species of *Cyclas*, which genus really embraces *Pisidium*. LEYDIG studied *Cyclas cornea*, SCHMIDT studied *Cyclas calyculata*. At the period when their studies were made the questions of histogenesis were not quite in the same position as they are to-day; and accordingly in their papers little will be found relating to the topics now discussed. Moreover, on account of the greater transparency of the eggs of *Pisidium*, I have been able to work at them with an objective of as high magnifying-power as HARTNACK'S No. 10 *à immersion*.

I propose in the present communication to take up the figures in the accompanying Plates in the order in which they present themselves as developmental stages, and thus to combine an account of the changes and their significance with a description of the Plates.

Plate 1. fig. 1 represents an ovum from the oviduct of *Pisidium pusillum* at the breeding-season. The egg-cell is not yet fully grown, and is seen to lie in close apposition to a coiled highly refringent mass, which is a secretion of adjacent cells, and is assimilated by the egg-cell as "deutoplasm," in consequence of which its "body," which is now pellucid, becomes granular, as seen in fig. 3*.

Plate 1. fig. 2 represents a number of such ova with adjacent masses of deutoplasm and spermatozoa. The genus *Cyclas* is hermaphrodite, and so is *Pisidium*. Whether

* March 7th, 1875.—I should prefer to speak of such matter uniformly as "food-material" in all eggs where it occurs.

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self-impregnation occurs is not definitely ascertained, but it seems possible. LEYDIG was unable to give a satisfactory account of the arrangement of the ducts and generative glands from a study of the large *Cyclas cornea*, and I have not attempted to enter upon this question with the much smaller *Pisidium*.

Plate 1. fig. 3 is drawn from an egg removed from the brood-pouch. It is now granular in the body owing to the inception of deutoplasm, and has undergone impregnation. This is inferred from the fact that it is enclosed in a transparent envelope or egg-shell of membranous consistency. The nucleus and nucleolus seen now in the egg may or may not be the original germinal vesicle and spot of the egg-cell. Though these structures disappear in some eggs, it cannot be asserted that they may not be persistent in others. One point of interest in this and other eggs figured on the Plate is the presence of the membranous envelope to the egg, which was not found by either LEYDIG or SCHMIDT in their studies on *Cyclas*.

This fact has been especially insisted upon with regard to *Cyclas*, and it is therefore important to note the presence of the envelope in *Pisidium*. It is very delicate, and is ruptured and discarded after the first stages of development.

Plate 1. fig. 15 shows a similar egg in its envelope; in this egg two nucleoli are present in the nucleus (? germinal spots and vesicle).

Plate 1. fig. 16 gives a surface-view of the first pair of cleavage-grooves. They are seen to embrace the whole egg.

Plate 1. fig. 17. The cleavage-grooves are now four meridional, and the first circumferential is beginning to make its appearance. These two views are taken so as to exhibit the grooved surface of the yelk.

Plate 1. fig. 4 exhibits the four nuclei of the four first cleavage-segments.

Plate 1. figs. 5 & 6. The cleavage-products have increased largely in number, so that the egg is now a ball of embryonic cells or a polyplast.

Plate 1. figs. 7 & 8 exhibit a very important condition of the early development. A deep in-pushing of the surface of the polyplast is obvious, the result being the invagination of a part of the superficial cells, in the same way as a woven nightcap is tucked in to make it assume the form of a cap. The occurrence of this *primitive invagination* of the embryonal polyplast has been demonstrated by KOWALEVSKY in *Ascidia* and *Amphioxus*, and has now been recognized in some members of all the large groups of the animal kingdom. The process results in the production of a form which I proposed*

* Annals and Magazine of Natural History, May 1873.

The formation of a *Gastrula* by invagination is obviously indicated though not recognized by the author, in LOVÉN's admirable studies on the development of Mollusca, as also in KARL VOGT's memoir on the development of *Actæon*. In the Nudibranchs and in *Limax* I have observed and drawn the *Gastrula* in course of formation by invagination (see Contribution No. III.).

Dec. 1874.—Also in *Lymnæus* (see Quart. Journ. Mic. Sci., October 1874) and in *Paludina vivipara*.

March 7th, 1875.—Though the name *Gastrula* is expressive, I am at this moment inclined to prefer the original term *Planula*, on account of the ascribing of a *mouth* by Professor HAECKEL to his typical *Gastrula*. The orifice of invagination, when it occurs, is not known to be a mouth. I propose to call it the blastopore.

to call the *Planula*, but which Professor HAECKEL has better termed the *Gastrula*, reserving the former name for a condition of the *Gastrula* which sometimes presents itself in which there is no aperture of invagination. The *Gastrula* thus formed consists of an outer and an inner layer of cells, forming a wall which encloses a cavity (the primitive gastric cavity) which communicates with the exterior by the aperture of invagination. The two layers of cells are thus respectively the representatives of the ectoderm and endoderm of Cœlenterata, and further of the epiblast and the hypoblast of the developing Vertebrate.

Up to this point the membranous envelope of the egg is intact; but now it disappears, since the egg increases very largely in size (Plate 1. figs. 9, 10, 11). This increase in size is due to the rapid growth of the outer layer of cells, which expands and separates itself entirely from contact with the invaginated layer, excepting at the part corresponding to the lips of the orifice of invagination. The orifice entirely closes, and the primitive gastric cavity remains as a small shut sac formed by well-marked cellular elements, affixed to one part of the large expanding epiblast, ectoderm, or outer cell-layer (see fig. 10). The space between the two primitive layers is occupied by a colourless transparent liquid. A surface-view of an embryo in this stage is given in fig. 9, figs. 10 & 11 being deeper views of the same embryo.

The surface-cells are seen to lie closely packed, with a small quantity of granular matter surrounding each large clear nucleus. The granular matter represents the body of each cell, and is apparently in this condition not distinctly demarcated for each individual element; so that the epiblast is in the condition of a granular protoplasm with numerous closely packed imbedded nuclei. The clear pellucid nuclei present one, two, three, or four nucleoli, and are in process of multiplication by fission.

When the focus of the microscope is so adjusted as to bring an optical section of the embryo into view, we get the appearance given in fig. 10; the invaginated hypoblast is seen as a small oblong mass (*hy*) at one pole of the oval embryo, and the wall formed by the epiblast, which is only one cell thick, is seen in section.

But now closer examination shows here and there fusiform or branched cells (*me*) attached to the inner surface of the epiblastic wall. More careful focusing, so as to bring this surface precisely into view, gives the appearance represented in fig. 11, where a larger number of these subjacent branched cells are visible.

These branched cells are the commencement of the mesoblast. The great space between the invaginated hypoblast and the epiblastic wall is the mesoblastic cavity, that cavity which is the distinguishing characteristic of the higher groups of the animal kingdom, and which becomes ultimately blood-sinus, peritoneal cavity, or hæmolymph-system.

The minutest details as to the mode of origin of these first mesoblastic cells would be of the greatest interest in the present state of our knowledge as to the origin of the middle layer of the Vertebrate embryo, and I accordingly have paid especial attention to it.

Plate 1. figs. 12 & 13 give more highly magnified views of parts of the embryo

seen in figs. 9, 10, 11. There can, I think, be little doubt, after an examination of these figures and fig. 11, that *some* of these mesoblastic cells are proliferated from the epiblastic wall. In particular I may draw attention to fig. 13, where the continuity of some of the branching corpuscles of the mesoblast with the granular matter surrounding the large nuclei of the epiblast, two of which are seen (*ep*) in the figure, is obvious. It is perhaps necessary again to mention that these different views (figs. 10–13) are taken from the same embryo (without shifting its position) by altering the focus, a power of 1100 diameters being employed so as to obtain a series of optical sections.

It is a more doubtful matter as to whether any of the mesoblastic cells are derived from the invaginated block of hypoblastic corpuscles. In figs. 11 & 13 I would draw attention to the corpuscles marked *p*, which appear to be in the act of detaching themselves from the hypoblast, whilst the corpuscle (*pd*) has the appearance of a hypoblastic cell undergoing quadruple division.

It is not desirable here to summarize or discuss the various views now current as to the origin of the mesoblast. It is sufficient to say that the derivation of a portion of the mesoblast from the epiblast, and of another portion from the hypoblast is in accordance with the view most recently adopted, from various considerations, by Professor Ernst Haeckel*. At the same time we are by no means yet in a position to assert that the mesoblast has uniformly the same origin in the various classes of the animal kingdom, nor in all members of the same class, though this uniformity should be our working hypothesis.

Plate 2. fig. 18 represents in optical section an embryo somewhat more advanced than that of figs. 9–11, and with a consequently larger development of mesoblastic corpuscles in the cavity lying between epiblast and hypoblast.

Plate 2. fig. 19 exhibits this in optical section taken just below the epiblastic surface.

Plate 2. fig. 20 advances to a later stage. The hypoblast is now seen to be assuming a definite form. Seen thus in optical section, it appears as a bilobed mass supported by a peduncle, *rp*. This peduncle † develops subsequently into the rectum, and may therefore be designated the "rectal peduncle."

The cells or nucleated corpuscles of the mesoblast have greatly augmented in number, and in this particular view those especially are obvious which, accumulating at the pole opposite to the attachment of the rectal peduncle, lay the foundation of the *foot* (*f*).

Plate 2. fig. 21 shows epiblast and hypoblast in optical section, and is introduced to demonstrate the mobility of the walls of the vesicular embryo. Active movement does not occur; but slow changes of long and short diameter are noticeable at this period of development.

Plate 2. figs. 22 & 23 represent an embryo in two slightly differing depths of optical

* Die Gastræa-Theorie, die phylogenetische Classification des Thierreichs, und die Homologie der Keimblätter. Jena, September 1873.

† I have elsewhere applied the term "pedicle of invagination" to this same group of cells.

section. In fig. 22 the hypoblast is in section, showing clearly the character of its cells and their arrangement. In fig. 23 its somewhat irregular outgrowths (*hy*) are seen, and their relation to groups of the branched mesoblastic corpuscles.

The most important fact shown by these two drawings is the arrangement of certain of the mesoblastic branched corpuscles (*me*) in strings or groups, binding, as it were, others of the cells into groups. The large cells (*x*) of these figures are not distinguishable in form and character from the epiblastic cells in immediate contact with which they lie, and from which, with little doubt, they have been derived. They apparently furnish the primitive elements of the foot; but whether they are to be considered distinctly as mesoblastic elements or as epiblastic I cannot decide. Supposing that they give rise to muscular tissue, they establish a very close connexion between the "Hautfaserblatt" and the epiblast, which is paralleled in *Hydra* and in the higher Cœlenterata. On the other hand, it is possible that the strings of branched corpuscles (derived at an earlier period from the epiblast) which traverse these groups of large cells are the real foundations of the muscular tissue, and that the large cells serve only as so much material for their appropriation, or as the primitive elements of the nerve-ganglia.

Plate 2. fig. 24 is not so far advanced in development as figs. 22, 23. It presents two features of interest with regard to the mesoblast. First, several large fusiform corpuscles of the mesoblast are seen attached by one extremity to the mass of the hypoblast, and by the other connected with groups of mesoblastic cells. In connexion with a similar condition in the corresponding stage of development of *Aplysia*, to be described in a further communication, this has considerable interest; and so has the second feature, which also is presented by *Aplysia*, viz. the ciliation of the surface of some of these mesoblastic cells (*ci*). In this particular embryo a few cilia were seen also on the outer surface of the epiblast, as indicated in the figure.

The ciliation of the mesoblastic cavity is a common phenomenon in adult Vermes (*Gephyrea* and some Annelids), and has even been observed in a sporadic form in some Vertebrata exclusive of the ciliation of the Fallopian tube (Klein's observations on the peritoneum of the Frog).

Plate 2. figs. 25, 26 bring us to a later stage and more definite differentiation of parts than we have yet considered. They represent the same embryo, seen first in section and then from the surface. The rudimentary alimentary cavity (*al*) is seen hanging from its rectal peduncle as in fig. 20. It will hardly be right any further to speak of this mass as simply "hypoblast;" for it is by no means clear what changes have gone on, and there may be elements now present which represent the "Darmfaserblatt." The rudimentary alimentary sac is seen to have definite lobes now which will shortly develop into the two large juxtaposed chambers which constitute the bulk of the alimentary canal during the embryonic condition in *Pisidium*. The epiblast (*ep*) is seen not to be sharply marked off from a number of cells or corpuscles accumulated beneath its wall, both laterally (*me*) and at that pole which represents the foot (*f*).

Plate 2. fig. 26 is important, because it shows the way in which the mouth first makes its appearance, and its relation to the "rectal peduncle." Plate 2. figs. 25 & 26 represent the same embryo unmoved, but the focus slightly changed: hence it is obvious that the mouth (*o*) is about to eat its way into the epiblast's wall in order to reach the enlarging rudimentary alimentary cavity—quite *independently* of the original point of invagination; this is, indeed, as mentioned above, long since closed, and subsequently in its neighbourhood the rectum, at first cæcal, opens to the exterior.

Plate 2. figs. 27, 28 represent an embryo in the same stage of development, two views somewhat differently focused being given. They serve to confirm the disposition of parts ascertained from fig. 25. But in fig. 28 the focus is so arranged as to bring a larger number of mesoblastic corpuscles into view; in particular, above the mass of large cells at *f*, there is an indication of the strings of branched corpuscles which have already been seen in the phase drawn in fig. 23.

Plate 2. fig. 29 shows the commencement of the oral invagination and the development of cilia on the surface round this invagination. Cilia have, however, previously made their appearance.

Plate 3. fig. 30 takes a leap forward; but the gap is to some extent filled by figs. 32 & 33. The individual cells are no longer represented as in the optical sections of previous stages, but a general superficial view of the embryo is presented. The surface of the embryo has now become considerably differentiated. The ciliated region marked *f* is the foot, which is now contractile and takes on special growth. The plications in its side (*mn*) indicate the commencement of the mantle-flap, whilst the most important differentiation of the surface is the oblong or saddle-like patch (*sh*) formed of large elongate epidermal cells arranged along the sides of a groove. This remarkable saddle-like patch is the commencement of the secreting surface which gives rise to the shell, or rather pair of shells. I have traced its gradual extension from this commencement in later stages; but the constancy of its first appearance as a *groove* surrounded by peculiar elongate cells is the feature to which most importance must be attached. It will be seen from my observations on *Aplysia* that the first commencement of the shell of the larva or "*veliger* form" is there of precisely the same nature, viz. a groove surrounded by elongate secreting cells. In *Aplysia*, and also in *Neritina*, this groove is sufficiently deep to be entitled to the title of "gland" or "follicle." It is of the same order of structures precisely as the byssal gland, and gives rise to a chitinous plug in *Aplysia* and *Neritina*. In *Pisidium*, as will be seen from Plate 4. figs. 38 *a*, 39, the two calcareous valves do not make their earliest appearance in close contact one with the other. The central portion of the shell-gland is not concerned with them; and since it is precisely that point which in the Gasteropods cited gives rise to a chitinous plug, may we not see in the ligament of the bivalve, which occupies so precisely the required position, the homogen of that production?

At present I am not prepared to go further with this subject than to suggest that were the open groove of the shell-area to become closed in so as to form a sac, and

were it then to continue its chitinous secretion, we should have produced an internal chitinous rod like the pen of *Loligo*. A reference to what I have said on the development of the pen in another communication will show that I have not yet got the detailed demonstration of the mode of development of the "pen" of the Decapodous Cephalopods, which is required to substantiate the supposed relationship now suggested*.

Fig. 31 shows another embryo with the foot-surface turned to the right instead of the left. The focus is somewhat deeper, showing, instead of the ciliated surface and commencing mantle-flap, the rudimentary alimentary canal *al* and *rp*. The pharynx (*ph*) is seen lined with cilia; it now is about the stage of development at which it opens into the gastric chamber, *al*. The groove of the shell-gland is well seen (*sh*) in this figure.

Fig. 31 *a*. Mouth-region (*o*) of an embryo at a somewhat earlier period, more highly magnified. Surface-view.

Plate 3. figs. 32, 33, represent two views of an embryo less fully formed than that of fig. 30, but still showing the shell-gland remarkably well (*sh*). The embryo is also remarkable for the distinctness with which it exhibits the condition of the alimentary canal with its two central lobes or gastric chambers, and fore and aft the pharynx and the rectal peduncle.

Though the foot is developed to so slight an extent in this specimen and the body-walls generally were so thin and transparent as to suggest some abnormality of development, yet at the point marked *f* in the figure, slow movements of contraction and expansion were going on. From this phase onward, in fact, the foot exhibits muscular movements.

Plate 3. figs. 34, 35, 36 go together, giving different views of three embryos of very nearly the same stage of development—that is to say, a little in advance of the embryo of fig. 31. The foot has now grown out as a very prominent conical mass, and being covered with vibratile cilia and capable of considerable alteration of form, becomes the chief locomotive organ. The embryos in this condition move about freely in the brood-pouch, and feed on the material supplied to them from its walls. The pharynx (*ph*) now actively functions, expanding widely and bringing in material to its cavity by means of its ciliate lining, then contracting sharply, and passing on its contents to the left gastric chamber. Hence the food passes by a slow circular movement into the adjacent right gastric chamber, and thence to the rectum. As yet, however, there is

* Dec. 1874.—This evidence I subsequently obtained in the spring of 1874 at Naples. The pen-sac of *Loligo* does develop as an open pit, which becomes closed in, and it corresponds in position with the shell-gland, the existence of which I have now demonstrated in *Pisidium*, *Aplysia*, *Pleurobranchidium*, *Neritina*, *Limnæus*, and *Paludina*. M. Hermann Fol has, subsequently to the publication of my first observations on this matter (which were made in 1871 and 1872), observed the structure which I term the "shell-gland" in certain Pteropod embryos. Although there is a correspondence between the pen-sac of Cephalopods and the shell-gland of other mollusks, I have, in the Quart. Journ. Microsc. Science, Oct. 1874, adduced reasons (based on palæontological facts) for considering them not to be identical structures. See also the same Journal for January 1875.

no anal opening. The arrangement of these parts is seen best in the diagram, Plate 4. fig. 51.

The mantle (*mn*) originates simply as a continuation of the rim of the pharynx, carried along each side of the foot, as is well seen in fig. 35.

Plate 3. fig. 35 *a* gives in a diagrammatic way a view of the border of the pharynx surrounding the oral opening (*o*), and the similar border of the commencing mantle-flap surrounding the foot (*f*).

In Plate 3. fig. 36 an embryo of this period is seen in approximately complete optical section. The shell-gland, which belongs of course really to the surface, is introduced (*sh*), showing the double appearance which it has when focused thus, being in reality saddle-shaped, and extending on each side of the embryo a little way. In both this section and in Plate 3. figs. 30 & 35, certain large cells are conspicuous (*y*), which lie above the pharynx in what ought to be the cephalic region. I merely draw attention to them, but cannot offer any explanation of their late differentiation. They present the appearance of the earlier embryonic cells, and soon after this stage disappear.

It is perhaps well briefly to mention (what becomes obvious from the study of this development in full) that there is nothing which corresponds to the velum of the "*veliger* form" of Gasteropod development, though some marine Lamellibranchs, probably most, do exhibit a *veliger* stage. And it is even still more curious to note that not even at the earliest stage, when such a differentiation of parts might make itself apparent for a brief period, is there any thing which indicates or corresponds in the remotest degree morphologically to a head. There is a gap between the region marked *y* in fig. 35 and the pharynx, which might be filled by a head with paired eyes and tentacles. These have been as completely suppressed as though they had been cut away, and the sides of the wound so formed healed without leaving a trace.

In the section fig. 36 the differentiation of the cell-elements in the foot is to be observed, and the attachment of some of these fusiform muscular corpuscles to the stomach-wall. The lumen in the rectal peduncle is obvious, but it is also certain that the peduncle is as yet imperforate at its termination. A mass of tissue projecting inwards from the epiblast by the side of the rectal peduncle marked B is the rudiment of one of the paired "segmental organs," or organs of BOJANUS, of the mollusk. In Plate 4. figs. 44 & 45 much more highly magnified views of similar in-buddings from the epidermal layer, which occupied similar positions in other embryos, are given. The position occupied subsequently by what are clearly enough the rudimentary Bojanian organs, makes it highly probable that these buds are their first commencement. In fig. 37 the same bud-like process is marked B.

Plate 3. fig. 37 is of value as a step in this developmental history, for it helps to connect the phase just described with that which perhaps may be best understood by looking at figs. 39 & 43. Up to this point the embryo usually and readily presents a more or less accurate *profile* view of itself, lying on the glass slip with the foot to the right and the pharynx to the left, or *vice versâ*. But the result of the immediately

ensuing growth is that the embryo cannot be got to tilt over on its side as in the earlier state. It persistently presents a strictly dorsal, hæmal, or umbonal aspect, or an equally symmetrical, ventral, oral, or pedal aspect.

Fig. 37 represents an embryo which is nearing this change, but has yet to develop a great margin of mantle-flap, which is the efficient cause of this change of habitual attitude. In the later stage the observer is at first puzzled as to what has become of the shell-gland and its groove. In fig. 37 some indication is afforded as to what development it is undergoing (*sh*). It becomes very much less obvious than hitherto, owing to the relative development of other parts and to the flattening of the arched surface on which it formerly sat as a saddle. Its area is at the same time very greatly increasing—that is to say, the cells all round the original oval patch of columnar epidermal cells are acquiring the same character, and ultimately the cells of the general surface of the mantle will assume the same character. The very large growth of the gastric cavity at this stage is remarkable. The whole embryo is of course now continually increasing in size, which is not indicated in the figures; but the gastric chamber or pair of chambers have dilated into one great bilobed sac, to which the rectal peduncle forms but a small appendage. Up to this period the cellular elements of the walls of the gastric chamber have not presented any noticeable feature, ciliated on their inner surface, and apparently consisting of but a single series (though possibly a second series may be present but not obvious) of corpuscular elements. In the stage to which we are about to pass, they appear to take on the most extraordinary activity; and it becomes quite clear that what has up to this point functioned as an aproctous alimentary canal is a mere *larval* affair, and not even the rudiment of a part of the permanent digestive chamber. The cells or corpuscles of its walls proliferate and arrange themselves in new masses to form the permanent alimentary tract, and its glandular appendage the liver. The pharynx and the rectal peduncle are, however, unaffected by this process of re-formation.

In Plate 3. fig. 37 the blind termination of the rectum is clearly seen.

In Plate 3. fig. 38 it is again obvious (*rc*); and in this figure the first rudiments of the shell-valves, which now become evident, are introduced. The lower of the two is seen lying in contact with a part of the shell-gland (*sh*), which is in optical section, and extends really across the whole area occupied by the two shells.

Plate 4. fig. 39 gives a dorsal or umbonal view of an embryo in the next stage of development—that in which the mantle has freely developed its large border. The length of the foot has now greatly increased, and the shell-valves are larger and more nearly approximating at their umbones than in figs. 38 & 38 *a*. Showing through the mantle-surface beneath the shells are the two lobes of the gastric chamber, now undergoing those curious developments of its cell-elements of which mention has just been made.

Plate 4. figs. 40, 41, 42 represent a series of the modifications which the cell-elements of the gastric chamber undergo. They are taken from different embryos of three successive ages. A number of large pellucid nuclei first make their appearance,

highly refringent, entirely devoid of structure, and very conspicuous. These are surrounded by a coarsely granular matter. What relation these nuclei bear to the original elements of the hypoblast is not known. Nucleoli commence to appear in these nuclei (Plate 4. fig. 41), and these enlarge very much, developing secondary and tertiary nucleoli, whilst more than one primary nucleolus makes its appearance in each of the original refringent bodies. The explanation of this sudden and striking cell-development requires more extended study, but it looks like a rapid process of endogenous proliferation.

Plate 4. fig. 43 is chiefly interesting as showing the position of the mouth (*o*) and the form of the mantle (*mn*). The great gastric chamber obscures the full view of the root of the foot, which is seen lying symmetrically between the flaps of the mantle behind the mouth.

Plate 4. fig. 38 *a* sufficiently explains itself. Fig. 43 *b* gives a view of detached cellular masses lying within the faintly indicated wall of the gastric chamber at a stage corresponding to that of fig. 37. Their significance is obscure.

Plate 4. figs. 44 & 45 have been already alluded to as giving highly enlarged views of processes from the epidermis budding inward, which appear to be the foundations of the organ of BOJANUS of one side. They are seen in their natural position close to the rectal peduncle in Plate 3. figs. 36 & 37, B.

Plate 4. fig. 46 again brings us a large step forward in the developmental history of *Pisidium*; and beyond the stage here presented I have not followed it. The shell-valves (*v*) have increased largely in size; the mantle-border (*mn*), hanging like a skirt all round the foot, covers it more and more. But the new feature which marks this stage of development is the appearance of the rudiments of the branchiæ (*br*). On each side they are seen as four blunt processes springing from a line which runs towards the mouth from the angle formed posteriorly by the junction of the foot with the mantle. They now appear confined to this region at the posterior root of the foot; but later, as appears from LEYDIG'S researches on *Cyclas cornea*, extend in the direction of their basal line towards the mouth—that is to say, new buds make their appearance along this line on each side of the foot, progressing from the posterior to the anterior pedal region.

The origin of the gill-lamellæ of the Lamellibranchiata as short stump-like tentacles which become ciliated has long since been worked out by LOVÉN. Its significance has been, I am inclined to think, overlooked. In relation to this matter I will now merely draw attention to the close general agreement of the disposition of these tentacular branchiæ, the foot, the mouth, and the anus in this embryo *Pisidium* (see Plate 4. fig. 52), with the disposition of tentacles, epistoma, mouth, and anus in a Hippocrepian Polyzoon, or more strikingly with the same parts in the exceedingly interesting form *Rhabdopleura*, as worked out by M. G. O. SARS *, where, if the so-called "buccal shield" be taken as the equivalent of the Lamellibranch's foot, the homology of the gill-tentacles in the two cases cannot appear doubtful.

* Quart. Journ. Micr. Sci., Jan. 1874.

The mass of the central portion of the alimentary canal and its glands has in the present stage of development become dark granular, and its details very obscure. Anteriorly to the umbones of the shell-valves in the middle line appears a vesicle (*v*) which lies below the surface, but is not imbedded in the tissue of the alimentary tract. One might take it for the commencing pericardium or cardiac ventricle, but that those structures certainly in later life lie posteriorly to the umbones.

Plate 4. fig. 47 presents the same specimen as that of fig. 46, seen from the pedal aspect instead of the umbonal aspect.

The drawing is not made so as to give a definite plane of optical section, but parts are allowed to show themselves in virtue of the partial translucency of the embryo.

Plate 4. fig. 48 gives a more highly magnified view of the problematical vesicle, *v*, of figs. 47, 46.

Plate 4. fig. 49. The same vesicle from another specimen, in which it is less strongly marked.

Plate 4. fig. 50 represents an embryo a very little younger than that of Plate 4. figs. 46 & 47 (less developed by one gill-process), drawn with the camera lucida. The arrangement of the dark and clear masses in the central mass of tissue belonging to the alimentary tract is of interest as indicating an approaching differentiation into the coils of the intestine and the glandular adjacent liver. The rectum (*rp*) is here obvious, its walls having become thin and translucent as compared with their former condition, when we spoke of them as "the rectal peduncle." The anus is now perforate. At *lr* the lumen of the rectum as it opens into the now much modified gastric chamber is seen. On either side the rectum two coiled tubes (B), the exact disposition of which it is impossible to make out on account of their delicacy and the not too great transparency of the body-wall, are to be observed. The position and character of these delicate structures renders it exceedingly probable that they are the future organs of BOJANUS, and are developed from the rudiments marked B in earlier figures.

In front of the shell-valves in this figure (50) a transverse striation lying below the surface *Ad* marks the commencing differentiation of the anterior adductor muscle.

Plate 4. figs. 51 & 52 represent, somewhat schematically, an earlier and the present phase of the development of *Pisidium*.

In figure 51 the arrows indicate the direction of ciliary currents, by which matters (chiefly or perhaps entirely liquid matter) are passed round the two lobes of the gastric chamber.

At this stage my observations on *Pisidium* cease. There are some structures the rudiments of which I was continually in search of, which seem to deserve mention on account of their absence. For instance, the byssal gland figured by LEYDIG in the foot of *Cyclas cornea* at an early period (quite within the period here gone over) was absent. No trace of any thickenings or invaginations to lay the foundation of the otocysts, nor of the cephalic, pedal, or branchial ganglia, was to be detected.

A study of the later phases of *Pisidium pusillum* would no doubt throw some light on the origin of these structures as well as on the origin of the labial tentacles, the nature of which, especially in relation to the branchiæ, requires investigation.

Explanation of the lettering of the figures in Plates 1, 2, 3, 4.

a. Anus.
al. Central portion of the alimentary tract.
Ad. Anterior adductor muscle.
B. Rudiments of BOJANUS'S organs.
br. Branchial buds.
ci. Cilia.
ci'. Cilia of the mesoblastic cavity.
chy. Lumen of the hypoblastic invagination.
ep. Epiblast.
f. Foot.
hy. Hypoblast formed by invagination.
lr. Lumen of the rectum.
me. Mesoblastic cells.
mn. Mantle-flap or border.
o. Mouth.
p. Cells apparently in the act of budding off from the hypoblast to form mesoblastic elements.
pd. One of these cells dividing into four.
ph. Pharynx.
rp. Rectal peduncle of the hypoblast.
rc. Cæcal termination of the alimentary canal.
sh. Shell-groove or shell-gland.
v. Problematic vesicle.
x. Large cells doubtful as to being epiblastic or mesoblastic.
y. Large cells persisting until late development in the epipharyngeal region.

No. II. *The Early Development of two Species of* Aplysia (Aplysia depilans *and* Pleurobranchidium, sp.).

At Naples, in the winter of 1871–72, I searched for the ova of some Gasteropodous mollusk which would by their transparency permit the same kind of study with high powers as to the early phenomena of development as those of *Pisidium* had previously enabled me to carry on. Generally the ova of Mollusca are so highly charged with finely granular matter, and the limits of the individual embryonic cells so little defined, that it is impossible to do much with them on account either of opacity or of indefiniteness. The eggs of some Nudibranchs afforded interesting results as to the mode of formation of the "*Gastrula*" by invagination, which form the subject of a further communication; but the particular ova which seemed most favourable for study, on account of transparency, clean definition of parts, and unlimited abundance, were those of *Aplysia*. I kept the eggs of two species of this genus (or rather species of *Aplysia* and of the subgenus *Pleurobranchidium*) under examination from time to time during several months. The eggs occur in masses, which resemble vermicelli, and are known by that name to the Neapolitan fishermen. The object of my work did not lead me to identify the precise species of *Aplysia* to which my observations refer. I am, however, able to identify the egg-coils; and it is sufficient for all questions of histological and embryological interest to distinguish these as the larger and the smaller species of *Aplysia* (*A. major* and *A. minor*). I am nearly certain that my *A. major* is the common big *A. depilans*. It is the largest *Aplysia* which is common in the Bay of Naples. On the other hand, all I can say of my *A. minor* is that it is a much smaller species than the former; and from comparison of eggs laid by a *Pleurobranchidium*, I take it to be a species of that subgenus. The egg-coils are distinguished by their size. Those of *A. major* are about one tenth of an inch in diameter, whilst those of *A. minor* are but two thirds of that width. The coils are, further, very completely distinguished by structure involving a numerical character. The substance of the coils is a crisp gelatinous material, in which are closely packed spherical capsules (Plate 5. fig. 1, *a*). These capsules are of nearly the same size in the two species—a very little larger in the larger species. But whereas in the larger species each capsule contains from thirty to forty ova, each one of which undergoes development up to a far-advanced stage, in the smaller species each capsule contains but from five to seven ova, each one of which develops and finally emerges from the capsule as a swimming embryo.

In the case of the smaller species, I kept the eggs from the earliest condition of cleavage to the liberation of the *veliger* embryos; but when once free I could no longer retain them in my tank, since they were carried away by the stream of sea-water which it was necessary to use to ensure aëration. The constant injection of a fine jet of air into a small vessel of sea-water might obviate the difficulty which the water-stream always presents in the treatment of minute swimming embryos.

In the case of the larger species, I never actually hatched any of the embryos, though the condition of Plate 6. fig. 37 cannot be far from that in which the embryo escapes.

The ova and embryos were removed from the capsules for examination by cutting across the egg-rope. Numbers were always thus extruded on to the glass slip used, and a certain amount of liquid with them. A small piece of paper being placed at one corner to protect them from pressure, the thin cover-glass was placed over them.

Abortive Embryos of larger Aplysia.—This is perhaps the place to mention a curious feature in the history of the larger *Aplysia*. The egg-capsules in this form contain as many as thirty or forty ova. They all advance in development to the condition presented in Plate 6. fig. 24, with well-developed rudimentary shell, velum, &c. But at this stage numbers of loose shells are to be found in the capsules, and the embryos are fewer in number. I at first thought that this was a case of casting a larval shell, as observed by KROHN in some Pteropods; but it soon became apparent that the embryos to which these shells belonged had disappeared. In some cases the embryos in a capsule were reduced to ten only. It is remarkable that just after this period the digestive canal of the embryos is fit to function—the mouth opens, and the primitive stomach-sac is ready to receive food.

It seems most probable that we have here, then, a parallel to the case of certain Gasteropods (*Purpura*, *Buccinum*, *Neritina*), in which out of many true ova included in an egg-capsule only one develops, feeding on the others when it has attained digestive capacities. In this large *Aplysia* the destruction and appropriation of the weaker embryos is not consummated until they have all considerably advanced in development, and then a desperate struggle and subsequent cannibalism takes place.

It is possible to suggest as an explanation of what occurred in the egg-cords of *A. major* kept by me, that abnormal conditions brought on an unhealthy condition leading to the death of a number of the embryos; but this does not seem to be likely, though it should be borne in mind as possible.

Nothing of the kind occurred in *A. minor*, though kept under precisely the same conditions in the same tank with a constant stream of sea-water. This is contrary to the hypothesis of a diseased condition. One of the chief features of interest in the observations which follow is the comparison which they afford of the development of two very closely similar species, which, notwithstanding their marked identity in adult form, yet exhibit very curious divergences in the details of their early development.

Development of Aplysia major.—Plate 5. fig. 1 represents an ovum from an egg-rope or egg-coil, in which all were at this very early phase of development. The upper part of the egg is seen to be coarsely granular and of a yellow tint; the lower pole is paler and more transparent. The lower pole corresponds, as will be seen, to the cleavage-patch of *Loligo*, the yellow part to the residual yelk *—though here, as in most Mollusca Gasteropoda, there is not a complete segregation of cleavage-yelk from food-

* March 5th, 1875.—The term "residual yelk" I made use of in a portion of this memoir relating to the development of the Cephalopod *Loligo*. I have withdrawn the greater part of that section in order to incorporate observations made in the spring of 1874. In reference to the use of terms descriptive of parts of the yelk I may refer to my paper in Quart. Journ. Micr. Sci., April 1875.

yelk, and consequently the yellow mass or residual yelk shares in the first cleavage. In both species of *Aplysia* it is only this one cleavage which the coloured or residual yelk undergoes. In other Gasteropods, e. g. *Neritina*, it cleaves a second time, so as to form four masses; whilst in other cases, as also in the Batrachia among Vertebrata, we know that yelk which corresponds to what is here called "residual" (that is, yelk which does not itself build up structure) may exhibit a very extensive cleavage, and the corpuscular or cell-elements therefrom resulting be nevertheless gradually broken down and absorbed.

At the lower pole of the egg (Plate 5. fig. 1) a shrunken vesicle, marked R, is seen escaping from the colourless yelk. It appears to be the remains of the germinal vesicle, and has been frequently observed by others in a variety of mollusks, being sometimes spoken of as the "Richtungsbläschen." Plate 5. figs. 2, 3 represent the results of the first two cleavage-furrows. The yellow yelk is in the condition of two larger balls, the white yelk in the condition of two smaller balls.

Plate 5. fig. 4. The yellow yelk divides no further; but the white yelk now presents four masses instead of two.

Plate 5. figs. 5, 6, 7. These continue to multiply and spread over the two balls of yellow yelk, which they finally enclose. Clear pellucid nuclei of large size occur in the yellow spheres of *A. minor* at this period (compare the figures, Plate 7), but, curiously enough, are altogether absent here.

Plate 5. fig. 8 shows some of the klastoplasts or cleavage-products of the white yelk after their complete investment of the two spheres of residual yelk. These cleavage-products not only invest the yellow masses, but are piled up at one pole, the original cleavage-pole. I sought here for some indication of the *Gastrula*-invagination; but obtained no evidence of it. In a recent paper, Dr. Emil Selenka has contrasted the process of invagination as "embolé," with that of overgrowth (such as occurs here and in *Loligo*) as "epibolé." It is not yet clear how far they are equivalent processes or reciprocally exclusive *. The presence of a large mass of "deutoplasm" or food-yelk is what, more than any thing else, seems to necessitate epibolé; and we require much more numerous and detailed accounts than we at present possess of the origin of the hypoblast in various animals before asserting that the enclosure of the mass of residual yelk (containing often or invariably *some* formative as well as nutritive material) by the marginal increase of the cap of small cleavage-products is essentially the same thing as the enclosure of the hypoblast by invagination. If it were so we should certainly have, in cases of epibolé, to look for the exact equivalents of the invaginated hypoblastic corpuscles in corpuscles arising from or making themselves apparent in the mass of residual or coloured yelk. In cases where this enclosed residual yelk does *not* give rise to the hypoblast (the chick, osseous fish, *Loligo*?), but in which the latter is derived by a process of "lamination" from the enclosing mass of cleavage-cells, there can be no

* March 7th, 1875.—At the present moment I incline altogether to the view sustained by Kowalevsky in his invaluable researches on *Euaxes* and *Lumbricus*, to the effect that these two processes are one and the same.

morphological identity between the enclosed portion of the embryo resulting from epibolé and the enclosed portion resulting from embolé. But, on the other hand, in those cases of epibolé where, as in *Aplysia*, and more strikingly in *Neritina*, there is clearly formative material mixed with the enclosed nutritive mass as indicated by its cleavage, we may look for a segregation of that formative material to form hypoblastic elements; and if such takes place, the enclosed mass of this case of epibolé becomes a true equivalent of the enclosed mass of embolé. Nevertheless it must be remembered that it has not been demonstrated in any one case that the hypoblast has such an origin, and that in the frog we have corpuscular elements resulting from segmentation, which serve no other purpose than that of nutritive evanescent yelk.

The ascertainment, then, of the further arrangements and dispositions of the embryonic cells of *Aplysia* has great general interest. The difficulties of observation, however, entirely prevent any one set of observations from being at all conclusive as to these questions.

Plate 5. fig. 9 shows an embryo in which the surface-layer of cells has condensed so as to form a firm "epiblast," consisting of but one row of cell-elements (*ep*). The yellow yelk (*ry*) has commenced to break up, no longer retaining its definite spherical form, and between the two masses of yellow granular material a mass of colourless closely aggregated cells has forced itself (*x*). This strongly contrasts with the corresponding phase in *Aplysia minor*, where the yelk-spheres retain their form unchanged (Plate 7. fig. 3). The yelk-spheres may be said in *A. major* to have now *fused* with the cells (*x*), for there is no demarcation or limit to the two masses; the individual yellow angular granules of the yellow yelk retain their sharp outlines, but the matrix in which they were imbedded seems either to have segregated and become indistinguishable from cells formed at the original cleavage-pole, or to have been assimilated by those cells, which have now worked their way between and right into the two yellow spheres.

Plate 5. fig. 9 is a median optical section.

Plate 5. fig. 10 gives the same embryo focused more superficially.

Plate 5. fig. 11. There is now some differentiation in the mass of cells (*x*), which, as already explained, *may* contain corpuscles derived from the yellow spheres, or may be solely the remnant of the colourless cleavage-yelk after the separation of the epiblast (*ep*). We notice now first of all the formation of a distinct cavity (*c*), which must be identified with the mesoblastic cavity of *Pisidium*, and more generally of all the embryos of higher animals. But in addition to this the outer cells of the mass (*x*) have taken on definite character, and form a dense layer, with fine processes passing from them to the epiblastic wall. The comparison of this with the similar stage in *Pisidium* is instructive.

In this and the preceding figure a pair of cells (*mn*) projecting from the epiblast are obvious. These two cells constantly appear in this stage of development in various Nudibranchs. They are seen when followed out to be the first commencement of the mantle-flap, and indicate approximately a point at which the anus subsequently is

placed in the fully formed *veliger* larva. Plate 5. fig. 9 is in median section, whilst fig. 11 is somewhat more superficial.

Plate 5. fig. 12 gives a surface-view of the same embryo, indicating the condition of the surface-cells at this period, as seen in the living condition.

Plate 5. fig. 13 exhibits another embryo in the same plane of optical section (approximately) as that given in fig. 9. The differentiation of the outer lot of the original cell-mass (*x*) to form a markedly denser layer (*me*) is shown. In this specimen minute actively vibrating cilia were detected among the cells (*ci*). They may correspond to the mesoblastic cilia described in the preceding contribution in *Pisidium*, or may be only the forerunners of the general ciliation of the gastric cavity. This latter view is the more probable, since it is undoubtedly from cells occupying the position *ci* that the epithelium of the chief alimentary cavity must be formed in this species of *Aplysia*.

At the point marked *shp* a thickening of the epiblast is indicated, which is the commencement of the secreting-area of the shell or shell-patch, as it is convenient to call it. In the *Aplysia minor* it will be seen how strongly developed this patch becomes, so that it readily is detached from the embryo with its delicate circular secretion—the rudimentary shell. It corresponds with the *shell-groove* of *Pisidium*.

Plate 5. fig. 14. The same plane of optical section of a more advanced embryo. The ring of cilia (*vv*) which now appears, indicating the velum, is seen at the points where it is traversed by the plane of section. At *ot* the first indication of the otocysts, that of the right side, is seen. In Plate 5. figs. 17 & 18 the earliest commencement of this organ is more fully exhibited. It originates as a vacuolation of a spot in the epiblast near to the commencing oral invagination. It never communicates with the exterior; and by the unequal development of surrounding parts it is gradually transferred from this primitive position to that which it subsequently occupies in the foot. I shall speak of this again in describing the same stage in *A. minor*.

In Plate 5. fig. 14 the epiblast is also seen to be considerably thickened at the uppermost point, *v*. It is here that the inward growth to form mouth and pharynx rapidly takes place. The history of mesoblast and hypoblast is to some extent affected by what is shown in the lower part of the figure. Between the darker wall-marked *ime*, which seems to correspond with *me* of fig. 13, and the shell-patch there now appears a mass of cells (*pme*), the origin of which is quite uncertain. A similar mass appears at a corresponding period in *Ap. minor*, and they must have one of two origins; either they have been "delaminated" (proliferated) from the epiblastic mass of the shell-patch, or they are segregated from *me* of fig. 13. It is really of considerable importance to determine which view is correct; for this mass (*pme*) appears to be concerned, most certainly in the case of *A. minor*, in building up the intestinal portion of the alimentary canal, perhaps only furnishing its outer walls. In *A. major* the position of this mass of cells does not permit one so readily to follow out its connexion with the alimentary canal as in *A. minor*. These two tracts of cell-aggregates I distinguish as inner mesoblast (*ime*) and parietal mesoblast (*pme*), without attributing definitely a particular

origin to them, or a particular further development, exceping so far as that it is obvious that *ime* forms the chief bulk of the wall of the primitive gastric sac of *A. major*, though probably *not* its lining epithelium.

Plate 5. fig. 15 is another and very similar embryo, in which the same arrangement of parts is observed.

Plate 5. fig. 16 is an embryo a very little further advanced and a little turned on its axis. The "clearing up" or "hollowing out" of the primitive gastric cavity is now advancing, though not yet is there any thing like a well-defined space there, but merely a looseness and fluidity of material, such as accompanies the formation of a cavity by absorption.

Plate 5. figs. 17, 18 have been already referred to. They exhibit on a larger scale the earliest indication of the otocysts; fig. 17 that of the right-hand side, fig. 18 that of the left-hand side. This first rudiment of the otocyst developing in the epiblast may be termed the "otocystic vacuole."

Plate 5. fig. 19 takes the development a step beyond fig. 16. The alimentary cavity (*al*) is much more distinctly marked, and the mass of tissue which has grown inward from the epiblast to form the pharynx (*ph*) is in conjunction with it. The foot (*f*) is beginning to push itself forward, and the velum (*v*) is becoming elevated into a kind of cap.

A main point of interest in this stage of development, as compared with *A. minor*, is that the yellow yelk-granules are constituents of the mass which forms the wall of the primitive alimentary cavity. In *A. minor* they remain outside it entirely, persisting as the original nucleated yellow yelk-spheres, absolutely unchanged morphologically until the embryo is of large size and freely swimming with its alimentary canal highly developed; they dwindle by absorption of their material and become relatively minute bodies as the embryo increases in size, but they do *not*, as in *A. major*, enter into the actual substance of the wall of the alimentary canal.

A close parallel to this is seen in the development of two allied Oligochætous Annelids described by KOWALEVSKY, *Euaxes* and *Lumbricus*. In the former there is a large quantity of nutritive matter in the form of angular granules mixed with the egg as laid. This granular matter, by the process of segregation and invagination (by epibolé), becomes confined to the central part of the embryo. The large cells of which this mass is formed differentiate to form the glandular lining of the alimentary canal, enclosing a number of the large cells as "contents" to the alimentary cavity, which are gradually absorbed. The primitive hypoblastic wall of the alimentary cavity is thus formed by protoplasmic elements, each of which is distended with coarse angular granules, which are only gradually absorbed. This is parallel to the case of *Aplysia major*. In *Lumbricus* the egg is much smaller and comparatively free from an admixture of coarse deutoplasmic particles. The hypoblastic wall of the alimentary canal, when developed, is also free from them, and consists of pellucid columnar cells. This agrees with *A. minor*, excepting (and this is an important distinction, for which it is not easy to

find a parallel outside the class Mollusca) that in *A. minor* there *is* a quantity of granular nutritive yelk, which, though not forming part of the substance of the hypoblastic corpuscles, nor yet enclosed within the alimentary cavity, remains in contact with the developing alimentary canal lying *outside* its cavity *, as is seen on a very much larger scale in *Loligo*.

Plate 5. fig. 21 displays the shell-patch when seen from above. It has now grown to some thickness, as may also be remarked in fig. 20. The patch is in the fresh condition, and its constituent cell-elements are not discernible; but the important feature which it exhibits is the groove or slight invagination. It thus presents the most striking correspondence with the grooved shell-patch of the Lamellibranch *Pisidium* described in the preceding contribution.

Plate 5. fig. 22 is a portion of the foot of such an embryo as fig. 20, on which a little fresh water has been allowed to act. This separates and brings into view the constituent cell-elements of the epiblast.

Plate 6. figs. 23, 24. We now pass to a much more advanced embryo. The shell is well marked and shovel-shaped. It is in this phase that I found so many of the shells loose in the egg-capsules and packed one within the other, the embryos to which they belonged having become broken up, either by a normal process or owing to some injurious conditions.

The embryos now become very difficult to examine. The slightest pressure is apt to cause them to fall out of the shell, and endosmotic action swells out the body-wall in the way seen in fig. 23. At the same time the velum being now well grown, they swim about with incessant activity. A slight pressure is sufficient to rupture the embryo and separate the foot and velum from the rest, as seen in fig. 35. Such fragments show well, however, the true form of the velum at this period. In figs. 23, 24 the focus is so arranged as to give a surface-view of the mass of the alimentary cavity. The strongly marked sulcus results from the original separation of the yellow yelk-masses.

Plate 6. fig. 25, 26, 27, 28 are different views of the shells at this stage of growth. The narrower end has the brownish-yellow colour belonging to chitinous substance.

Plate 6. fig. 29 is a somewhat more advanced embryo, the focus taking a plane below the surface of the wall of the alimentary cavity. The tract of the pharynx is now very sharply marked out, though at present it is only a plug of ingrown epiblast, and not a tubular body. In the velum-area a thickening of the epiblast is seen forming a distinct boss or lobe, which appears to be the commencement of the cephalic nerve-ganglion. The shell is not represented in fig. 29.

Plate 6. fig. 30 represents the alimentary cavity of the same embryo, more superficially focused, so as to display the sulcus and the disposition of the yelk-granules.

* March 7th, 1875.—Therefore in the mesoblastic cavity. Such a position being occupied by a part of the endoderm or hypoblast, suggests a comparison with the development of *Sagitta*, where the mesoblastic cavity has been shown by KOWALEVSKY to be simply an outgrowth of the primitive endoderm, as in Echinoderms according to MECZNIKOW.

Plate 6. fig. 31. The operculum appears on the lower surface of the whole length of the foot (*op*), and the mouth (*o*) is commencing to break through the pharyngeal plug. The otocyst (*ot*) is now seen to have become quite detached from the epiblast in which it originated. The original vacuolar cavity is surrounded by regularly disposed columnar cell-elements. It is still free from any solid contents.

Plate 6. fig. 32 is a portion of the body-wall more highly magnified, to show (*fu*) fusiform cells lying just below its surface, which appear to be the muscular elements of the parietes.

Plate 6. fig. 33 represents the left face of such an embryo as that of fig. 31. It is focused high, so that the surface of the alimentary mass is in view, and also the surface of the cephalopedal region. This brings into view the fold *dv* (descending border of the velum), by which the edge of the velum is continued on each side on to the foot. The embryo is now becoming markedly unilateral in its external features, as may be seen by comparing the next figure with the present.

Plate 6. fig. 34 represents a similar view to that given in fig. 33, but now it is of the right side of the embryo. It is on this (the right side), as in other Nudibranchs, that the two cells already so early distinguished (*mn*) develop into a prominent mass, at which point subsequently the anal termination of the alimentary canal develops, and from which there grows also a fold which partially overlaps the shell in this region, and increases in extent so as to form the rudiment of a mantle-flap.

Plate 6. fig. 35 is a detached cephalopedal mass, or velum and foot, of the phase represented in fig. 29. The horseshoe-shape of the velum with the mouth (*o*) lying in its hollow is well exhibited.

Plate 6. fig. 36 represents an embryo further advanced. The shell is not here seen of its proper proportionate size, on account of the position into which it has slipped. The marked advance in this embryo consists in the clear definition of the cavity of the double gastric sac (*al*), and its attachment to the body-wall by transverse muscular fibre-cells.

Plate 6. fig. 37 is not quite so far advanced; but greater detail is given of the cephalic regions. In particular, fibres are seen passing backwards from the neighbourhood of the cephalic ganglion (*ng*), which is now large. They may be muscular attachments to the pharynx or nerves.

In Plate 6. figs. 36, 37, the furthest stage to which I have traced *A. major* is given. The history so far furnishes interesting data for comparison with *A. minor* and with other Mollusca, though I have fully stated the doubts and guesses connected with the interpretation of much which is figured. In this, as in other cases, the figures must at any rate serve as a basis of fact, interpret them how we may. In a subject so vague and tentative as the embryology of the lower animal classes must for some time remain, the best contribution which one can expect as yet to offer towards unravelling the complicated phenomena, is the observation and record of fact—a contribution which can best be effected by few words and copious drawings.

The condition of the alimentary tract in the embryo of *Aplysia major* as we now leave it is exceedingly interesting, and is never presented by the embryo of *Aplysia minor*, nor by other Nudibranchs studied by me. It is in the condition of a pair of freely communicating gastric chambers, or a double chamber which is connected by a pharynx with the exterior, but is *entirely devoid of rectum or anus.* It would be important to ascertain how these latter organs make their appearance. At the same time, if the figures of the development of *Pisidium pusillum* are referred to, it will be seen that at one time *Pisidium* is in a closely similar condition, having a perforate pharynx leading into a double gastric chamber, which is suspended in a large body-cavity, and though possessed of a so-named "rectal peduncle" due to the very earliest feature of the development, yet this peduncle is relatively very small, and does not open to the exterior.

Development of Aplysia minor=*Pleurobranchidium*, sp.—We must now go back to the earliest stages of development, to compare them with those of the smaller species of *Aplysia* figured in Plates 7 & 8 of this memoir.

Plate 7. fig. 1 represents a single ovum of *A. minor* in the condition exactly corresponding to fig. 5 of Plate 5 of *A. major*.

Fig. 2 represents a condition further advanced, in that the colourless cleavage-products have extended round the two yellow spheres. It corresponds exactly to fig. 7 of Plate 1; but we observe this difference between the two. In *A. minor* the yellow yelk-spheres are, each of them, beginning to show evidence of a central pellucid nucleus.

Plate 7. fig. 3 brings us on to the stage corresponding with Plate 5. fig. 9; and now the differences are more obvious between the two species. In the present species the outermost cleavage-cells have "condensed," if that expression is allowable, to form a very clearly marked epiblast (*ep*). Already this is thickened at the aboral pole, to form the basis of the shell-patch (*shp*). The two pioneer-cells of the mantle (*mn*) are prominent; and within we have, as in *A. major*, the yellow residual yelk-spheres (*ry*), and a mass of undifferentiated cleavage-products (*x*). But the condition of the yellow masses is very different to that of those in the same stage of *A. major*: their outline is strongly marked; they retain their circular contour, and possess each a large brilliant and colourless nucleus. There is no question in this case of any breaking up of the yellow masses, or of their possibly furnishing formative elements by segregation to take the sole or a part of the work of building the hypoblast. They remain sharply defined, and keep their granular angular particles compacted together throughout the subsequent stages of development, although they become distorted and flattened by the pressure upon them of other growing elements, and probably dwindle and thin out in consequence of the absorption of some of their material.

Plate 7. fig. 3 is very carefully rendered in every detail, as seen under a HARTNACK'S 10 *à immersion.* The figure represents an optical section in the median plane, and the region which will give rise to the foot is turned to the right.

Plate 7. fig. 4 represents a similar view of an embryo a little further advanced, in

which the potential foot is to the left. In this figure a darker mass of cells (*x*) is distinguished from a paler group (*pme*). There can be no doubt that the cleavage-corpuscles enclosed by the epiblast are now in process of arranging themselves, to lay the foundations of particular groups of organs; but whether *x* in this case is to be regarded merely as a mass of primitive cells from which *pme* have become detached, or as a group destined to give rise to the hypoblast, subsequent phases of development do not enable me to decide. I am inclined to take the latter view, especially on looking at the position occupied by the mass *x* in fig. 5.

Plate 7. fig. 5 is a little further advanced than fig. 4. Already the circle of cilia belonging to the velum are present, and the first invagination of the epiblast for the pharynx (*ph*). The mass *x* is now clearly separate from *pme*; and it is now time to point out that the subsequent development of the embryo most fully agrees with the view that this mass (*x*) coming into close relation with the yellow spheres, gives rise to the hypoblast of the alimentary canal, whilst the mass *pme*, which is still in part actually continuous with the epiblastic wall (see fig. 11), forms the muscular wall of the alimentary canal, and especially develops the whole of its terminal part, being gradually eaten into by the cavity of the alimentary canal by the growth of the hypoblast: that is to say, in other words, the cavity of the main chamber or stomach is first formed by the development of the mass *x*, whilst *pme* forms the outer wall of the intestine, into which an outgrowth from the stomach gradually extends. I do not wish to attach any importance to these statements beyond that of suggestions; for the investigation is a very difficult one on account of the smallness of the embryos and their want of clearness in detail of structure, though in this respect they are better than most molluscan embryos.

Plate 7. fig. 8 shows the pharynx further advanced (*ph*); the shell already exists as a delicate pellicle (*sh*), and the foot (*f*) is beginning to push. Now is the earliest period at which I have seen the otocyst (*ot*) in this species. On account of the position in which the embryo is lying on the glass slip, the otocyst is not brought to the edge of the section, but is seen lying in the foot. It is, however, still near the surface, and is in the condition of a vacuole excavated in the thick epiblast of this part.

Plate 7. fig. 6 gives a much more superficial view of an embryo of the same stage in a reversed and oblique position. The otocyst (*ot*) is seen near the surface in the foot-region. But the most important feature in this drawing is the shell-patch and shell-groove (*shgr*), which are seen here quite superficially. The close similarity of this structure to the shell-groove of *Pisidium* cannot be overlooked. This is the earliest stage also at which the pigment-spots (one on each side) (*pg*) are visible. They are small superficial vesicles, at first circular in outline, containing four finely coloured pink granules. They enlarge and become oval, whilst the number of granules which they contain increases. I shall only speak of them as pigment-spots, for their function is altogether obscure.

Plate 7. figs. 7, 9, 11 represent embryos of one and the same age, not quite so far advanced as that of fig. 8. Their positions (accidentally assumed as they lay on the

glass slip) are a little different, and the plane of focus differs a little in each case, being, however, nearly median, but more superficial in fig. 9 than in figs. 7 & 11. Plate 7. figs. 7 & 9 are so disposed by focus and attitude as to catch strongly the shell-groove and the thickened mass of tissue at the aboral pole. In fig. 11 the indentation or groove itself is out of focus, but the thick epiblast (*ep*) is well shown, and the mass of adherent cells (*pme*), which, as stated above, undoubtedly take a chief part in forming the intestinal portion of the alimentary canal.

Plate 7. figs. 12, 13, 14, 15 show a great advance in the development of the foot and of the pharynx. They are, however, chiefly of interest in relation to the groove of the shell-patch, which they show with remarkable clearness. Figs. 12 & 15 present the same embryo, with the least possible change of focus, fig. 12 being a very minute bit higher than fig. 15. The result of this little change of plane on the appearance of both pharynx and of shell-groove enables one to make out the direction and character of these structures.

The shell-groove is perhaps the most important structure to which I have to draw attention in this paper, and I may therefore now say a few more words about it. Is this groove connected with the secretion of the shell? or is it perhaps an invagination to give rise to a block of tissue connected subsequently with the rectum and anus? That question occurred to me; and if the former supposition could not be supported, the apparent analogy with the shell-groove of *Pisidium* would be a false one; also the possibility that this primitive groove in Mollusca generally may represent the closed epidermal sac, in which the pen of *Loligo* is developed, would have no basis. I am able definitely and conclusively to show that the "shell-groove" in *Aplysia* does really belong to the shell, and in fact sometimes contains a *plug* of chitinous secretion, an imbedded shell in fact, the possible homogen of the internal pen of Cephalopoda. The specimens which gave this interesting result, and which also throw light on the connexion of the rectal portion of the alimentary canal with the early aboral thickening of the epiblast and the cell marked *pme*, are *artificially produced deformities*.

I was in the habit of keeping egg-coils of *Aplysia minor* in a basin, through which there ran a constant current of sea-water. From the same egg-coil I cut from day to day a small piece of the coil, in order to examine the embryos contained in its capsules. I noticed that in some cases which had been left for several days untouched, the bit of the coil near the cut edge had assumed an opaque and curiously pink appearance. The capsules at this part on examination proved to contain most strange and irregular-looking embryos, which were, however, in a high state of activity, moving about by means of their cilia, as though their distorted conformation made little difference to their vitality. Before proceeding further, I may, however, say that I did not succeed in bringing such embryos on to an advanced stage of development. Two of these embryos are represented in Plate 6. figs. A, B, C. Most were similar in condition to that represented in figs. B, C; but some were as abortive and shapeless as that of fig. A. Of that embryo I have nothing special to say beyond drawing attention to its

rudimentary condition. All the deformed embryos agreed in this—that the yellow yelk-spheres were gone; whether they had been extruded (as I think most probable), or whether they had been absorbed, I could not determine. In that drawn in figs. B, C, and in others a simple yellow oily-looking body (*ry*) appeared to be the only remnant of the yellow spheres; and from its position it suggests that the rest had escaped through a rent in the epiblast. The mouth in these deformities was open, the alimentary cavity complete and lined with cilia, its walls nevertheless quite free from any of the yellow granules of the residual yelk. A peduncle of apparently solid tissue (R) passed from the lower part of the gastric sac to the side of the large thickened "shell-patch." The condition of the shell-patch, as exhibited in the specimen figured and in others, was most important; for it had produced a thickened and brown-coloured (chitinous?) shell of small area, but relatively great solidity. A button or knob (*pl*) continuous with this thick disk-like shell occupied the groove or indentation of the shell-gland, forming thus an *enclosed plug*. Thus the real significance of the shell-groove of the embryo is demonstrated by a pathological condition artificially induced.

In a subsequent part of this memoir will be found the description and figure of a similar chitinous plug in connexion with the earliest rudiment of the shell in *Neritina fluviatilis*, which I studied at Oxford in May 1873.

The development of the alimentary tract in these deformities, in the absence of the two yellow yelk-spheres, seems to show that it is independent of them in origin, its ciliated lining being derived elsewhere than from material furnished by them. And, again, the separate position and solid condition of the intestinal piece marked R agrees well with what has been put forward above as to the origin of the two parts of the alimentary canal. The gradual pushing of the ciliated lining of the gastric cavity (*al*) along the solid piece R would give an intestine lined by "hypoblast" and built up exteriorly by mesoblastic muscular elements.

Plate 7. figs. 10 & 16 show two planes of one embryo, the pigment-spot (*pg*) being introduced into each as a fixed point of comparison. The foot and velum are now taking definite shape, the former already provided with a very delicate operculum. From the anterior horizontal border of the velum a fold (*dv*) descends on each side of the foot as in *A. major*. In the deeper view (fig. 10) the letters *int* mark a part of the cell-mass (*pme*) of fig. 11, now assuming development as part of the alimentary tract.

The figures on Plate 8 chiefly illustrate what can be ascertained of the development of the alimentary canal.

Plate 8. fig. 18 is the most rudimentary shell, discoid in form, with an irregular surface, hyaline and exceedingly delicate in texture.

Plate 8. fig. 19 is the shell-patch as detached by pressure sufficient to break the embryo. The same structure was figured from *A. major* in Plate 5. fig. 21.

Plate 8. fig. 20 represents an embryo (of the same lot as that drawn in fig. 17) seen from behind in such a position that the posterior border of the velum forms its upper boundary. Seen through is the pharynx (*ph*), and on each side (also seen through) are the pigment-spots (*pg*).

Plate 8. fig. 21 represents a similar embryo seen from before, in such a position that only the ciliated border of the velum is in view. The anterior margin of the foot here forms the upper boundary of the figure. The want of bilateral symmetry due to the development of the region in connexion with the early-appearing mantle-cells (*mn*) is now apparent. The mass of tissue (*int*) is assuming form as alimentary canal, and is overlaid by the flattened out, but not disintegrated yellow yelk-spheres. In other specimens of this age the connexion of the intestinal rudiment with the region *mn* was obvious. The continuity was so complete as to suggest the notion of an ingrowth or invagination of the tissue at the point *mn* to form the mass *int*. We have, however, seen that it is derived from the mass *pme* of Plate 7. figs. 8 & 11. In *Aplysia major* no such structure as this *int* could be made out. The alimentary tract developed as a double gastric chamber with the yellow yelk imbedded in its walls; no trace of intestine or rectal termination could be ascertained, the mass *pme* apparently giving rise only to traversing muscular bands (if to any thing). The contrast with the present case is very strong, and though possibly not rightly understood in the light of my present observations, must furnish an interesting problem affecting general principles in embryology.

The series of figures in Plate 8 now must be looked at in connexion with the alimentary canal, and we can then pass through them again in connexion with other details of velum, foot, nerve-ganglion, &c.

In figs. 17 & 22 certain of the cells which are to take part in the formation of the alimentary canal, and which have hitherto been obscured by the relatively larger development of other parts, are seen to enlarge very greatly. The mass which they form is marked *int*. In fig. 22, at the point A, the cells are so arranged as to enclose a space as seen in the enlarged drawing (fig. 23); in fig. 24 a quite superficial view of the same group of cells is given, and fig. 25 an intermediate view. It is seen from these drawings that we have here large pellucid cells devoid of nucleus.

Plate 8. fig. 26 shows that these cells have not, in the stage represented in Plate 8. fig. 22, attained their full growth. They are now individually of very large size, and occupy a great part of the embryo. This has grown considerably in size, whilst the relative bulk of the colourless elements of the alimentary tract and of the persisting yellow yelk-masses is greatly changed. In fig. 26 attention must be drawn to what is the most definite phenomenon to which one can point in this part of the development of *Aplysia minor*—namely, the growth of some of the colourless cells into the substance of the yellow yelk at the point marked in this figure *int*, resulting in the cutting off of a piece of this material from the rest of the yellow residuary yelk. This detached piece is marked *dry*. The detached piece does not retain its coarsely granular character, but speedily becomes broken down in substance and changed in colour to a dirty brown. This detached piece is rapidly invested by the colourless cells, and becomes, in the fully formed *veliger*-larva, a sac-like mass lying by the side of the anus—almost certainly the renal organ, the homogen of the Lamellibranch's organ of BOJANUS, and of the cuttle-

fish's ink-bag. It does not follow because its foundations are thus laid that its lining cell-layer is not derived from ingrowth of the epiblast, which is what one would look for.

In Plate 8. fig. 27 the large cells have given rise to smaller cells more closely packed, and giving indications of the outlines of the coils of the alimentary canal (*int*). The wall of the detached piece of yellow yelk has become clearly defined.

The steps of the passage to the condition of fig. 28, and from this to the phases represented in figs. 32 & 33, are so much obscured by difficulties of observation, that I doubt whether it can be useful to attempt a *rationale* of them.

It is sufficient to point out that in Plate 8. fig. 28 the cavities are becoming more clearly defined; and whilst the embryo has increased in size, they continue to preponderate more and more over the yellow yelk-masses.

Plate 8. fig. 29 represents the alimentary tract and surroundings of the same embryo, focused at a somewhat higher level.

Plate 8. figs. 30 & 31 represent respectively the right lateral and the left lateral aspects of a more advanced embryo. The part marked *int* is now clearly enough to be identified as the chief gastric cavity, and its inner surface is covered with vibrating cilia. The part marked *int'* is the rectum, which turns suddenly upon the gastric chamber. It is this which was first sketched out by those cells which intruded themselves between *dry* and *ry*. The rectum is not as yet perforate.

Plate 8. figs. 33 & 34 give a right and left lateral aspect respectively of an embryo of *Aplysia minor* at the time of quitting the egg-capsule. The whole region of the alimentary tract is now fully formed, though possibly there is no anal aperture at A as yet. The residual yelk (*ry*) still remains, each original yellow sphere still retaining its large clear nucleus, though now no longer a sphere, but rather a disk-like body. From what appears to take place in other Nudibranchs, and indeed in the Cephalopoda also, it is pretty certain that duct-forming outgrowths from the wall of the gastric cavity penetrate these masses, and assimilating and absorbing their substance, establish in the place occupied by them the molluscan liver.

Plate 8. fig. 32. In all the views given of the later growth of the *Aplysia* embryo the œsophagus is obscured by the yellow yelk-masses which lie in the way of a lateral view; but when looked at from above, as in fig. 32, and rightly focused, the whole of the first part of the alimentary canal may be very clearly made out as a ciliated tract running from the mouth to the gastric cavity marked *int* in the figure, and passing between the two yellow yelk-spheres.

In fig. 32 the embryo is closely drawn into its shell, and the plane of focus is near the surface, so that the outline of the shell and the superficial extent of the yellow yelk-masses is given to advantage. The figure represents the embryo after its escape from the capsule.

We may now pass back for a moment to note the development of the nerve-ganglion. As in *A. major*, this is seen, in Plate 8. fig. 22, making its appearance as a thickening of the epiblast in the velar region. In Plate 8. fig. 26 it is large and

sharply defined. In Plate 8. fig. 28 it has become fully differentiated from the overlying tissue, and consists of a separate pair of rounded bodies (of which one only is seen in this side view). In close connexion with it are other smaller rounded masses of the same appearance (*ng'* and *ng''*). It seems very probable that these are outgrowths from the primary nervous mass to form the pedal ganglia. The otocyst is seen in close relation with these supposed nervous masses. Of the otocyst it is merely necessary to point out that the cells surrounding it gradually form for it a definite wall, and that then in its centre appears a small otolith which gradually increases in size. It is not uncommon for the otolith to make its appearance in one of the two otocysts before it does in the other, as in Plate 10. fig. 5.

The muscle of the velum marked *mv* in Plate 8. fig. 22 is worth mention, since it appears at an early period. It passes from the border of the velum to the foot. By the contraction of this muscle the velum becomes doubled to some extent on itself, as seen in figs. 30, 31, and the movement of the cilia stops.

The sudden stoppage of the cilia of the velum during life, and the erect sheaf-like appearance which they assume, is quite different to the stoppage and disordered entanglement which they exhibit when the embryo is killed by acid. The rigid character of the position of rest of these large cilia is exactly repeated in the case of the perianal circlet of large cilia in such Annelidan embryos as that of *Terebella*.

The first trace of the great posteriorly placed retractor muscle may be made out in embryos which are looked at from behind, when of about the same age as that of fig. 28. The further differentiation of this finely fibrillar muscular band is seen in figs. 31 & 34, *M, M'*. I was unable to observe the mode of development of this structure, though in some Nudibranchs its differentiation from corpuscular elements lying beneath the epiblast, and derived originally from it as a part of the parietal layer of the mesoblast, is clear enough.

The matters of interest to which it has been the object of this part of the present communication to draw attention are as follows:—

1. The primitive arrangement of the results of the cleavage-process.
2. The mode of development of the otocysts, by vacuolation of the epiblast.
3. The development of the cephalic-nerve ganglion-pair as a thickening of the epiblast.
4. The "shell-patch," "shell-groove," and its plug.
5. Artificially produced monstrosities of the embryo.
6. Points of wide divergence in the development of the alimentary tract, and its relation to the yellow residual yelk-masses, between the two closely allied species here spoken of as *Aplysia major* and *Aplysia minor*.

No. III. *The Early Development of* Tergipes, Polycera, Tethys, Neritina, Limax, *and* Limnæus.

Tergipes.—The early history of the development of some of the Nudibranchs is of considerable interest, since it clearly exhibits a *Gastrula* phase similar to that described in my contribution on *Pisidium*, but which I could not discover in *Aplysia*. Carl Vogt, in his memoir on the development of *Actæon*, has described and figured the "sillon" which results from the invagination of the wall of the primitive blastosphere; but he did not distinctly recognize it as an invagination, nor are his figures sufficiently large to give much information on the subject.

In Plate 9 the early development of a small *Tergipes*, the species of which I did not identify, but which was common at Naples, is given. The invagination is very well marked in this case, since there is relatively but a small amount of "deutoplasm" present in the egg, that constant disturber of typical modes of development and of satisfactory observation of the eggs by transmitted light.

Plate 9. fig. 1. The cleavage-cells do not present great disproportion in size.

Plate 9. fig. 2. Already in the centre there is a pit due to the tucking in of the cleavage-products.

Plate 9. fig. 3 gives a later embryo in optical section. The invaginated group of cells (*hy*) are seen lying within the wall-forming cells (*ep*). The cavity of the invaginated group (C) still communicates with the exterior.

Plate 9. fig. 4 is an optical section at right angles to the preceding, so that the aperture of invagination is not brought into view.

Plate 9. fig. 5. A surface-view of an embryo at the same stage, showing the long groove formed by the aperture of invagination. This is the groove detected by Vogt in *Actæon*. It closes up shortly, and the layers of the embryo proceed on their special lines of development.

Plate 9. fig. 6 shows the embryo with the aperture of invagination or *Gastrula*-mouth* now closed. The velar circlet of cilia has developed, and the two layers of the embryo are breaking up into smaller and specially differentiated cells or corpuscles.

Plate 9. figs. 7, 8 show the separation of a middle layer (*me*) between the inner and outer. It appears to be derived from the epiblast, to judge from the appearances seen in Plate 9. fig. 7; but the hypoblast may also contribute to its formation.

Plate 9. fig. 9. Surface-view of the aboral pole of an embryo of the same stage as the preceding, showing a fold or scar which is the remnant of the primitive invagination aperture.

Plate 9. fig. 10 represents an embryo in which velum (*v*), foot (*f*), and shell (*sh*) are already taking form. The pharyngeal invagination (*o*) is also indicated.

In this and preceding figures two small cells are marked R, which appear to be "Richtungsbläschen;" they are well known in the development of Mollusca.

Plate 9. fig. 11 represents the embryo at a much more advanced stage; the shell is

* March 7th, 1875.—Better called "blastopore," since it is not known to represent a mouth.

of a very peculiar boat-like form, and the velum is placed near the middle of it like a pair of paddle-wheels. In fig. 11 such an embryo is seen from above. In fig. 12 the outline of the same is drawn, in order to show the two muscular bands (*m*) which come into view with a deeper focus. One of these is seen at fig. 12, *a* as displayed by a HARTNACK'S 10 *à immersion*.

Polycera and *Tethys*.—In Plate 10 figures are given of the embryos of *Polycera quadrilineata* and of *Tethys* at a time when they give evidence of a primitive invagination.

In Plate 10. figs. 1, 2, 3, three views are given of the embryo of *Polycera*, showing the long groove of invagination, similar to the condition of Plate 9. fig. 5. The outer cells are more transparent than the inner.

In Plate 10. figs. 10, 11, an early condition of the yelk-division of *Tethys* is presented. I am not able to figure the steps of invagination in this molluscan embryo; but the stage illustrated in figures 12 to 16 gives some evidence of the remains of an aperture of invagination (*i*).

Plate 10. figs. 12 & 16 are left lateral views; fig. 13 is a right lateral view; fig. 14 an aboral view; fig. 15 an oral view of the same embryo.

These embryos are interesting to compare with the early stages of *Aplysia* described in the preceding section of this communication. Especially the two mantle-rudiments (*mn*) are to be noted as making here an early appearance as in *Aplysia**.

The remaining figures of *Polycera* embryos, viz. Plate 10. figs. 4–9, are chiefly of interest for the sake of comparison with the corresponding "*veliger*" of *Aplysia*.

Plate 10. figs. 4 & 5 represent two views of a young stage in which the shell is just beginning to appear. The curiously dark-coloured mass (*q*) I am not able to explain. In Plate 10. fig. 5 it is seen that one otolith has formed before the other.

Plate 10. figs. 6–9 represent fully formed embryos nearly ready to escape from their capsules. Fig. 6 is a right lateral view; fig. 7 a back view; fig. 8 a front view; fig. 9 a three-quarters profile view. A comparison of these figures with those of the *veliger* of *Aplysia minor* will show the close correspondence even to the fusiform muscle-cells which pass from the perianal mass (*dry*) to the body-wall.

Neritina fluviatilis.—Plate 9. figs. 1–8 represent early stages in the development of this mollusk. It is abundant in the river Thames at Godstow, near Oxford. After searching in various spots I at last succeeded in obtaining the egg-capsules in quantity from stones at the bottom of the river in front of the little inn near Godstow Priory. The stones in this part of the river are covered with the broken remains of the capsules deposited and hatched-out in former years. The fresh ones in the month of May stud these stones in great numbers, each capsule being about the size of a large pin's head. The specimens obtained thence in 1873 were transferred to the histological laboratory of

* March 7th, 1875.—From observations made in December 1874 and communicated to me by my friend Mr. F. M. BALFOUR, of Trinity College, Cambridge, it seems that the cells *mn* have *not*, as I supposed, the same significance as in *Aplysia*, and that the part marked *f* in Plate 10. figs. 13 & 16 is not the foot but the velum.

Exeter College, and kept there under a slow-running stream of water. Only one out of the many ova contained in a capsule undergoes cleavage and further development. The others break up and furnish nutritive material to the developing individual. This phenomenon, which has been established in other Gasteropods, as by CLAPARÈDE in *Neritina*, connects itself at once with a view which has been with much justice put forward by GEGENBAUR—namely, that the glands in Mollusca and Vermes which secrete "deutoplasmic" material which is appropriated by the growing ovarian egg, or is enclosed with it in a capsule, are to be regarded as abortive portions of the ovary. Thus the material which feeds the favoured egg-cell, whether it be presented in the capsule or in the ovarian tubes, is one and the same by origin—namely, potential ova.

The easiest way of examining the contents of the capsules of *Neritina* I found to be to open them under a dilute solution of osmic acid (·1 per cent.). This prevented the breaking up of the various ova and the young embryo, which is likely to be caused by other media, even by iodized serum.

In Plate 9. figs. 13, 14, 15, three stages of cleavage are represented. In fig. 13 the first division into two masses is commencing. The separation of formative and of food-yelk is already quite obvious. The constitution of the clear straw-tinted food-yelk, consisting as it does of spherical non-nucleated corpuscles, is a point of interest. When cleavage has advanced to a further point, they assume a more homogeneous character.

Plate 9. figs. 16, 17 represent a polar and a lateral view of two embryos further advanced. They are already actually of twice the diameter of the embryos 13–15. The cleavage-cap of cells is gradually embracing the four spheres of residual colourless (not coloured as is usual) yelk.

Plate 9. fig. 18. The enclosure is complete, and internal arrangements are in progress which the opacity of this species does not permit the observer to follow. The four yelk-spheres are still intact.

Plate 9. fig. 19 represents the phase which has most importance for the present occasion. The embryo has greatly enlarged, and is assuming the well-known *veliger* form. When caught at the right angle, the shell in a rudimentary state, as a delicate disk, is seen to cover the thickened aboral surface. CLAPARÈDE saw the shell at an early period, but he did not detect what is of so much interest in connexion with what I have described in *Pisidium* and in the deformed *Aplysia minor*—namely, the deep indentation in this shell-patch or shell-secreting surface occupied by the plug of chitinous material (*pl*), which in *Aplysia* I spoke of as the shell-plug.

Plate 9. fig. 20 gives a more highly magnified and cleanly focused view of the same shell-plug and shell-patch.

Limax agrestis.—Plate 9. figs. 21 & 22 give two views of two different embryos of *Limax agrestis*. I kept a large number of ova of *Limax* and of *Arion* at Jena in April 1871, and followed out the development to a certain extent. I submit on this occasion only the two drawings (figs. 21 & 22), because they establish the occurrence of the *Gastrula* form developed by invagination in these Pulmonate Gasteropods.

Fig. 21 is a day younger than fig. 22; the former gives a profile view, the latter is seen from the surface with the aperture of invagination uppermost. The aperture (*i*) closes entirely a day later, and the development of the true mouth proceeds at another spot still later. The sharp distinction between the invaginated cells (*hy*) and the thick layer of smaller epiblastic cells (*ep*) makes this *Gastrula* form one of the most typical among Mollusca.

*Limnæus stagnalis**.—Although I am unable to present at this time any drawings of the development of this common Pulmonate, I must yet point out that it is one of the most interesting and important in relation to the two new features of molluscan development pointed out in these contributions, viz. the invaginated *Gastrula*-phase and the rudimentary shell-sac and plug.

In *Limnæus stagnalis* a *Gastrula* is developed by invagination, which is one of the best marked in all the animal kingdom. Its aperture of invagination has been mistaken by LEREBOULLET (who has well figured it without, as may be supposed, appreciating its significance) for the mouth.

Similarly in the same mollusk, at a later stage, a thickened "shell-patch" develops, which exhibits a very deeply marked groove or pit, the shell-groove. This has also been seen and figured by LEREBOULLET, who has mistaken it for the commencing invagination of the anus.

Thus *Limnæus* presents these two important developmental features in a strongly marked condition.

* January 7, 1875.—The above was written in January 1874, and the facts to which it refers were observed in the summer of 1871. In the summer of 1874 I took an opportunity of studying *Limnæus* in greater detail, and published an account of its embryology in the Quart. Journ. Microsc. Sci., October 1874, with two plates.

General considerations relative to the observations contained in the preceding Contributions (Nos. I., II., III.).

Before leaving the preceding records of observations to the consideration of the reader, I may point out briefly their bearing on two matters of theoretical importance, viz. (1) the origin and significance of what has been called the *Gastrula* phase of development, and (2) the homologies or homogenies (as I should prefer to say) of the shells, ligaments, and internal pens of the Mollusca. More facts have to be sought out and brought to bear on these questions; but whilst occupied in that further search, let me indicate the anticipations which must guide and stimulate it. Before doing so I must mention that there are a variety of other matters of interest in the facts recorded in the preceding pages which cannot yet be brought into any theoretical structure, but which I have not on that account kept back, as they will probably be of some service in their isolated condition.

(1) KOWALEVSKY was the first to describe, in a precise manner, the formation of the foundations of the alimentary tract in a developing embryo by invagination of the wall of a simple primitive blastosphere, or hollow ball of embryonic cleavage-corpuscles. He detected this mode of development in *Amphioxus*, and subsequently in *Ascidia*. By later researches he was able to indicate the same mode of development in certain Vermes (*Sagitta*, *Lumbricus*); and he mentioned incidentally that he had observed a similar development in the Heteropodous mollusk *Atalanta*. I was at this time studying the development of *Pisidium* and *Limax*, and obtained evidence of the invagination of the primitive blastosphere in those two widely separated mollusks. Subsequently at Naples I found the same process occurring in Nudibranchs. The probable identity of this process of invagination with that so well known in the Batrachians, especially through STRICKER'S admirable work on the subject, became clear, to those occupied with embryological studies, from the facts established by KOWALEVSKY; and the "anus of RUSCONI" could now be recognized in the "orifice of invagination" present in members of the three large groups of Vermes, Mollusca, and Vertebrata.

The embryonic form produced by this invagination-process is a simple sac, composed of an ectoderm and endoderm, with an orifice connecting the exterior with the cavity lined by the endoderm. It, in short, presents the typical structure of the simplest Cœlenterata, and corresponds exactly with the so-called *Planula* of the polyps and corals. Hence we are tempted to see in this primitive invagination-form the representative of the Cœlenterate phase of development of the whole animal kingdom. In a paper published in May 1873*, containing the substance of lectures delivered in the preceding October, I have discussed this notion at some length, and other points connected with the attempt to work out the correspondences of the embryonal cell-layers of the various groups of the animal kingdom. At the end of the year 1872, Professor HAECKEL'S splendid Monograph of the Calcareous Sponges appeared, in which the same questions are methodically discussed. The name *Gastrula* is given by

* Annals & Mag. Nat. History.

Professor HAECKEL to the embryonic form which I had proposed to designate by the old name *Planula*; and the multicellular blastosphere, from which the *Gastrula* is developed, which I had proposed to speak of as a *polyplast*, he well christens the *Morula*. Professor HAECKEL was able to show in his monograph that the Calcareous Sponges exhibit a beautifully definite *Gastrula*-larva, which swims freely by means of cilia. LIEBERKUHN, MIKLUCHO-MACLAY, and OSCAR SCHMIDT had previously shown that certain sponges exhibit such an embryonic form; but Prof. HAECKEL described it in many cases, and showed fully its mode of development and structure.

This brings us to an important point in what HAECKEL calls the "*Gastræa* theory"*. The *Gastrula* form of the Calcareous Sponges is *not* formed by invagination. Without any opening in the blastosphere making its appearance, the cells constituting its walls divide into an endoderm and an ectoderm; then, and not until then, an orifice is formed from the central cavity to the exterior by a breaking through at one pole. Careful accounts of the development of Cœlenterata, with a view to determine the mode of development of the *Planula* or *Gastrula* form in regard to the question of invagination, are not to hand in a large number of cases. But, on the one hand, we have KOWALEVSKY'S account of the development of *Pelagia* and *Actinia*, in which the formation of a *Gastrula* by invagination is described, as in the cases already cited among Vermes, Mollusca, and Vertebrata; on the other hand, we have ALLMAN'S observations on the Hydroids, SCHULTZE'S on *Cordylophora*, KLEINENBERG'S on *Hydra*, HAECKEL'S on the Siphonophora, and HERMANN FOL'S on the Geryonidæ, in which the ectoderm and endoderm of the embryo (which is at first a *Planula* without mouth, then a *Gastrula* with a mouth) are stated to arise from the splitting or "delamination" of a single original series of cells forming the wall of the blastosphere. HERMANN FOL'S observations are of especial value, since he shows most carefully how, from the earliest period, even when the egg is unicellular, its central part has the character of the endodermal cells, its peripheral part that of the ectodermal cells.

The question now arises, can the *Gastrulæ* which arise by invagination be regarded as equivalent to those which arise by internal segregation of an endoderm from an ectoderm? and if so, which is the typical or ancestral mode of development? and what relation has the orifice of invagination in the one case to the mouth which, later, breaks its way through in the other?

It is not within the scope of the present memoir to discuss these questions at length; but I may say that I am of opinion that we must regard the *Gastrula*-sac, with its endoderm and ectoderm, as strictly equivalent (homogeneous, to use another expression) in the two sets of cases. One of the two methods is the typical or ancestral method of development, and the departure from it in the other cases is due to some disturbing condition. I believe that we shall be able to make out that disturbing element in the condition of the egg itself as laid, in the presence in that egg of a greater or less amount of the adventitious nutritive material which EDOUARD VAN BENEDEN calls "deutoplasm."

* His most recent views on this matter are contained in a pamphlet dated June 1873, 'Die Gastræa-Theorie.'

This and certain relations of bulk in the early-developed organs of the various embryos considered, determine the development either by invagination or by delamination. The relation of bulk to the process of invagination I may illustrate from a fact established in the preceding contributions. In *Loligo* * the large otocysts each develop by a well-marked invagination of the epiblast forming a deep pit, which becomes the cavity of the cyst. In *Aplysia* the smaller otocysts each develop by a simple vacuolation of the epiblast without invagination. Again, in Vertebrata the nerve-cord develops by a long invagination of the epiblast; in *Euaxes* and *Lumbricus* the corresponding nerve-cord develops by a thickening of the epiblast without any groove and canal of invagination.

The bulkier structures in these cases are seen to develop by invagination, the smaller by direct segregation. Invagination therefore acts as an economy of material, a hollow mass being produced instead of a solid mass of the same extent.

A. Gastrulæ *developed by invagination, or invaginate* Gastrulæ, *with either* (1) *embolé or* (2) *epibolé*.—That the presence of a quantity of deutoplasmic matter, or of a partially assimilated mass of such matter, in the original egg is not accompanied by well-marked invagination of the blastosphere, whilst the absence of much deutoplasm is the invariable characteristic of eggs which develop a *Gastrula* by invagination, is shown by a comparison of *Aplysia* and *Loligo* with *Pisidium* and *Limax*, and of the Bird with the Batrachian. In some cases, such as SELENKA has characterized by the term "epibolé," it seems that the enclosure of the large yelk-mass by the overgrowth of cleavage-cells may be held as an equivalent to the invagination of the large yelk-cells by "embolé;" and the intermediate character which the development of *Euaxes* and of *Lumbricus* presents in this respect, as described by KOWALEVSKY, tends very strongly to establish a transition.

B. Gastrulæ *developed by segregation, or segregate* Gastrulæ.—But the mode of development of the *Gastrula* of Geryonidæ, described with so much minuteness by FOL, which is obviously the same as that of the *Gastrulæ* of Spongiadæ and most Hydroids, is clearly no masked case of invagination. There is no question of "epibolé" here, but a direct and simple splitting of one cell into two; so that what was a sac formed by a layer of cells one deep, becomes a sac formed by a layer of cells two deep, or of two layers each one deep. It is yet a question for much further inquiry as to how this mode of forming a double-walled *Gastrula* can be derived from, or harmonized with, the formation of *Gastrulæ* by the embolic or epibolic forms of invagination.

It would certainly seem, at present, that the orifice of invagination of the invaginate *Gastrula* must *not* be regarded as the equivalent of the later erupting *mouth* of the segregate *Gastrula*†, which is the true permanent mouth of the Sponge or Cœlenterate.

* See Annals & Mag. Nat. History, Feb. 1873; also Proc. Roy. Soc. no. 151, 1874, and Quart. Journal of Microsc. Sci. January 1875.

† In my paper in the 'Annals' for May 1873, I have inclined to the view that it *may* be so regarded.

In a paper written a year after the date of the present memoir, and published in the Quart. Journ. Micr. Science, April 1875, I have proposed to retain the original term *Planula* instead of *Gastrula*, and to speak of the orifice of invagination as the "blastopore."

In no case is the orifice of invagination of the invaginate *Gastrula* known to persist under any form. It appears solely to effect the invagination, and when that is effected vanishes.

Enough has been said to show the importance of observations relating to the *Gastrula* phase of development. In the preceding parts of this paper well-marked invaginate *Gastrulæ* are described from:—

1. *Pisidium* (Lamellibranch).
2. *Tergipes* (Nudibranch).
3. *Polycera* (Nudibranch).
4. *Limax* (Pulmonate).
5. *Limnæus* (Pulmonate).

In addition to these cases of the development of invaginate *Gastrulæ* among Mollusca, the examination of the very beautiful figures in the papers of LOVÉN on molluscan development leaves no doubt that he has observed invaginate *Gastrulæ* in the following cases, but has not understood their structure:—

6. *Cardium* (Lamellibranch).
7. *Crenella* (Lamellibranch).

Similarly, KARL VOGT'S observations on *Actæon* indicate the same state of things as I have pointed out in *Polycera*; and hence we may add

8. *Actæon* (Nudibranch),

and, finally, from KOWALEVSKY'S statement, though not accompanied by figure or description,

9. *Atalanta* (Heteropod).

(2) The second matter of theoretical interest (namely, the early features in the development of the shell) has not been previously discussed, since the structures described in the paper as shell-patch, shell-groove, and shell-plug were unknown.

If, as seems justifiable, the Cephalopoda are to be regarded as more nearly representing the molluscan type than do the other classes, or, in other words, more closely resemble the ancestral forms than they do, we might look in the course of the development of the less typical Mollusca for some indication of a representative of the internal pen of the higher Cephalopoda. We might expect to find some indication of the connexion between this and the calcareous shell of other forms; in fact the original shell of all Mollusca should be an internal one, or bear indications of a possible development into that condition.

In *Pisidium*, in *Aplysia*, and in *Neritina* I have submitted evidence of the existence of a specially differentiated patch of epidermic cells at the aboral pole, which develops a deep furrow, groove, or pit in its centre, almost amounting to a sac-like cavity opening to the exterior. The first (chitinous) rudiment of the shell appears as a disk on the surface of this gland, but also in some cases the cavity or groove is filled by a chitinous plug.

Let the walls of the sac close and the activity of its living cells continue, and we

have the necessary conditions for the growth of such a "pen" as that of the Decapodous "Cephalopods."

At present the details of the development of the "pen" in the Cephalopoda are not fully known *. I have evidence that it is formed in an enclosed sac-like diverticulum of the epidermis, but have not yet ascertained the earliest condition of this sac. The history of its development becomes surrounded with additional interest in relation to the shell-gland of the other Mollusca.

The position of the groove of the shell-gland in *Pisidium* suggests a possible connexion of its chitinous plug with the ligament, which it will be worth inquiring into in other developmental histories of Lamellibranchs.

In *Dentalium* and *Fissurella* it appears to be exactly that region of the shell which would correspond with the first-produced chitinous shell-disk and its plug, which is altogether absent, leaving an open hole.

The internal shells of other Mollusca besides the cuttlefish are certainly not in some cases (e. g. *Aplysia*) primitively internal, but become enclosed by overspreading folds of the mantle. But in the case of *Limax* and its allies, it is possible (though requiring renewed investigation) that the shell is a primitively internal one, representing the shell-plug.

There is yet one more possible connexion of this shell-gland and plug: this is the chitinous secretion by which *Terebratula* and its allies fix themselves to rocks &c. The position of the peduncle exactly corresponds to that of the shell-gland; and an examination of Professor MORSE'S recently published account of the development of *Terebratulina*, leaves little doubt that at the pole of attachment, which very early develops its function and fixes the embryo, an in-pushing occurs, and a kind of shallow gland is formed, which gives rise to the horny cement. My own observations on the development of *Terebratula vitrea* do not extend to so early a period as this.

It is perhaps scarcely necessary, in conclusion, to point out the close resemblance of shell-gland and plug to the byssal gland and its secretion. They are closely similar structures; but there does not appear to be any reason for regarding them as "serial homologues," or as more closely related than are, say, the hairs on the head of a man with the hairs on his chest.

Explanation of the lettering of Plates 5, 6, 7, 8, 9, 10. (For explanation of the lettering of Plates 1, 2, 3, 4 see page 12.)

al. Alimentary canal.
C. primitive gastric cavity.
c. Body-cavity or cœlon.
ci. Cilia.

* March 7th, 1875.—I may be permitted to refer to two papers published since the above was written, in which my subsequent observations are related establishing the mode of origin of the Cephalopod's pen-sac as an open pit. They are contained in the Quart. Journal of Microsc. Science, October 1874 and January 1875.

dry. Detached portion of the residual yelk concerned in the formation of the renal organ.
v. Descending border of the velum.
ep. Epiblast or ectoderm.
f. Foot.
hy. Hypoblast or endoderm.
ime. Darmfaserblatt, or alimentary layer of mesoblast.
int. Intestine.
int'. Terminal portion of the intestine.
m, *m'*. Retractor muscles.
me. Mesoblast.
mn. Mantle rudiment.
ng. Nerve-ganglion.
ng', *ng''*. Secondary ganglionic masses (? pedal ganglion).
o. Mouth.
o'. Thickening which precedes the mouth.
œ. Œsophagus.
oi. Orifice of invagination (blastopore).
op. Operculum.
ot. Otocyst.
pg. Pigment-vesicles of unknown function.
ph. Pharynx.
pl. Plug of the shell-gland or groove.
pme. Hautfaserblatt, or tegumentary (parietal) layer of the mesoblast.
q. Dark-coloured cell-mass of unknown significance.
R. Richtungsbläschen, or particles extruded from the cleaving egg-cell, frequently recognizable as the remains of the germinal vesicle.
ry. Residual yelk.
sh. Shell.
shgr. Shell-groove, or follicle of the shell-gland.
shp. Shell-patch, or primitive shell-secreting area.
x. Undifferentiated cells of the colourless (or segregate) yelk, enclosed by the epiblast. In Plate 7. figs. 4, 5, 8, 11, the letter *x* is applied to a deep-lying dark-looking mass of cells which lies between the two coloured residual yelk-spheres.

No. IV. *The growth of the Ovarian Egg of* Loligo *and* Sepia.

The following observations were made during the months of February, March, and April, at Naples, in 1872*. The eggs of *Loligo* were obtained in abundance from the fishermen, as the spring advanced becoming more common. They were preserved in a basin into which a jet of sea-water was allowed to run continually; others were sunk in a basket in the fishermen's harbour at Santa Lucia. I chose the eggs of *Loligo* rather than of *Sepia* for the purpose of commencing the study of the development of the Cephalopoda, because the egg-envelopes are colourless, and the egg itself sufficiently small to be transparent and easy to examine in the living state. The eggs of *Sepia*, on the other hand, require very careful treatment in order to remove the dark-coloured envelopes, and are even then unwieldy objects for examination with high powers in the fresh state. The first part of the observations recorded below relate actually to the ovarian egg of *Sepia*, on which I found it more convenient (from the size of the eggs and from the fact that I possessed well-preserved ovaries of that genus) to carry out inquiries as to the mode of building-up of the egg previous to fertilization, and as to the significance of its basket-worked tunic. At the same time I have made many parallel observations on the ovarian eggs of *Loligo* itself; and I believe that it may be asserted with full confidence, that the ovarian egg of *Loligo* differs from that of *Sepia* only in the size to which it attains.

In examining the progressive development of the deposited eggs of *Loligo*, I adopted the following method of manipulation. One of the finger-like colourless strings of the eggs being taken, I removed the outer coating of gelatinous matter, so as to expose the deeper gelatinous material which forms a separate capsule to each egg, the capsules being grouped longitudinally in four series around a central gelatinous string or axis; then with the scissors one, two, or three eggs were easily detached in their capsules and placed on the compressorium, which was allowed to press but very slightly on them. In this way (the egg being an elongated ovoid) a lateral view was of course always obtained. To obtain what I may call "a polar view" (that is, a view of the egg as seen from above when it is made to stand on end) is by no means so easy. I found the best way to be to cut a small diamond-shaped hole in a piece of cardboard, and, after having removed as much of the gelatinous investment of the egg-capsule as possible, by the aid of delicate forceps, to place the egg on end in the hole, with the pole to be observed uppermost. Then, keeping it well moistened with sea-water, the little piece of cardboard with the egg was placed in the compressorium, and the upper glass of that

* Jan. 1875.—The portion of this memoir now published relates only to the ovarian ovum. It stands as it was read in March 1874. The rest of the memoir relating to *Loligo* has been withdrawn for the purpose of incorporating new observations. An abstract of my observations (both those of 1872 and 1874) relating to the later development of *Loligo*, illustrated by two plates, is published in the Quart. Journ. Microsc. Science, Jan. 1875. In 1874, owing to the arrangements of Dr. Dohrn's zoological station, I was enabled to obtain abundant supplies of *Loligo* embryos in all stages of development.

most useful instrument brought gently down so as to touch the upper pole of the egg. The adhesion of the delicate egg to the glass was now sufficient to maintain it in the erect position. The eggs were examined thus in the living condition, and, in some cases, after the addition of dilute acetic acid. The method of hardening and cutting sections was not applied by me to the study of the deposited eggs of *Loligo*, which, on account of their great transparency, offer every facility for study in the fresh state with even the highest powers*; but the growth of the ovarian egg and its envelopes or præseminary development† has been followed by means of sections stained with carmine, cut from eggs hardened in absolute alcohol, and some in chromic acid, in the usual way.

The Ovarian Ovum.

The ovary of *Sepia* and of *Loligo* at the breeding-time is an arborescent organ, formed by a series of branches and twigs, on the ends of which the eggs are seen like so many grapes on a bunch, but differing from a grape-bunch in the fact that the eggs are of very various sizes (Plate 11. fig. 13). I do not propose here to go into the larger anatomical features of the ovary, but to confine myself to the history of the growth of the individual eggs as exhibited in the variously sized specimens which occur in one and the same adult ovary. This, accordingly, excludes all question of the earlier development of the ovary and the ultimate origin of its constituent cells, a matter which must be treated of in due course in connexion with the later embryonic history of the developing Cephalopod.

Limits of size of the Ovarian Egg in Sepia.—The observations which follow, unless the contrary is stated, must be understood as relating to *Sepia*. The preparations to which they refer, some of which are represented in Plates 11, 12, were made in the histological laboratory of Exeter College during the present year (1873). The ovarian eggs of both *Loligo* and *Sepia* were also made the subject of study by me at Naples in the spring of 1872, when they were in the fresh condition.

The smallest eggs in the mature ovary of *Sepia* or of *Loligo* are to be found sessile among the long peduncles or stalks which support riper eggs. The smallest observed in *Sepia* were about $\frac{1}{500}$ of an inch in diameter. Before quitting the ovary the egg attains to nearly a quarter of an inch in long diameter, and has more than a hundred thousand times the bulk of these smallest egg-cells. The acquisition of new material by the egg-corpuscle, in passing from this smaller to that larger condition, is accompanied by structural arrangements, which are illustrated in Plates 11, 12.

First Stage of Ovarian Growth.—In Plate 11. fig. 14, the egg-corpuscle, with its nucleus and nucleolus, surrounded by a moderately developed "body" (the best, since the most indifferent, term which can be applied to that part of a nucleated plastid which is some-

* In the spring of 1874 I studied the development by means of hardening and cutting sections.

† Præseminary=before the junction of the semen with the ovum. Postseminary=after the junction of the semen with the ovum. Insemination=the junction of semen with ovum.

times called the protoplasm), is seen as stained by carmine imbibition. The egg is now a little over $\frac{1}{500}$ of an inch in diameter. It is surrounded by branched connective-tissue corpuscles, some three or four of which are closely applied to it. By simple plasmic nutrition (that is, by assimilation of matters which reach it by osmotic action from the blood) the egg-corpuscle now increases in size, especially that part of it which we called the body, and which now begins to assume the characteristics of an egg-yelk, viz. in the fact that it is taking on a special and excessive growth. With this increase of size, it is to be observed that the egg has acquired a more definite envelope (fig. 15, *oc.*). The egg continues to increase in bulk, and the "body" relatively more so than does the nucleus, the nucleolus of which has now become broken down. The capsule becomes now definitely pinched off from the surrounding tissue, and a peduncle forms to it which henceforward increases in length with the growth of the egg itself. Whilst the peduncle is forming, the connective-tissue corpuscles forming the capsule have proliferated in such a way as to form a double layer surrounding the egg, which henceforth we can distinguish as "inner" and "outer" capsular membranes (Plate 11. fig. 16). The corpuscles of the outer capsular tissue do not become materially changed; they increase in number, and form a firm connective-tissue tunic to the egg continuous with the peduncle. But the corpuscles of the inner capsular membrane, lying in direct contact with the naked surface of the growing egg-cell, take on a very different character; they form a secreting epithelium of columnar corpuscles, which have, up to a certain stage of the egg's growth, the characters of "goblet cells" (see Plate 12. figs. 27 & 28). Whilst the corpuscles of the inner capsular membrane are assuming this definite character, blood-vessels are pushing their way along the peduncle, and ultimately form a network lying between the inner and the outer membranes of the capsule, with an artery and a vein carrying the blood to and from the egg along the axis of the peduncle. The development of this vascular system is a gradual affair; but in an egg of the size seen in Plate 11. fig 5 it is already in operation. The development of marked longitudinal ridges on the inner capsular membrane is one of the first results of the penetration of the vascular system to the egg-capsule.

Second Stage of Ovarian Growth.—From this time forward the whole nutrition of the egg-corpuscle is fundamentally changed. Whereas it could previously be spoken of as a plasmic nutrition, it now becomes entirely dependent on the cells of the inner capsular membrane and their nutrition by the elaborate network of blood-vessels. The corpuscles of the inner capsule are continually growing afresh, undergoing a peculiar metamorphosis of their protoplasm, and pouring out the metamorphosed matter into the substance of the growing egg-cell, just as the goblet cells of a mucous membrane produce their glairy secretion (see Plate 12. fig. 28). The nutrition thus becomes one characterized by the assumption of visible semifluid material by the body nourished—inceptive nutrition. At a later period, it appears that it again somewhat changes its character. Whether the term "nutrition" is or is not applicable to such segregation of matter as here goes on may be a matter for discussion; but I am inclined to think

that we have no reason to suppose that the matter (deutoplasm of VAN BENEDEN) thus thrown into the original egg-protoplasm, together with the subsequently introduced male contribution of spermatozoa, is not assimilated so as to form with it an organic whole; rather it seems probable that the original protoplasm of the egg-corpuscle feeds on the matter brought to it, as does an *Amœba* or other unicellular organism, and that it is not until the final segregation of formative from food yelk on the completion of the blastoderm, that we can say what has not been digested, *i. e.* what stands over for the nutrition of the new generation of blastodermic cells.

With the development of vascularity in the peduncle and egg-capsule, longitudinal ridges make their appearance, and are plainly seen as a definite pattern through the outer egg-envelope. They increase very much in complexity as the egg increases in size; and finally the surface of the egg presents a complete basketwork tracery, which is shown in an incomplete condition in the *Loligo*'s egg (drawn in fig. 22), and has been figured and described by KÖLLIKER in his classical 'Entwickelungsgeschichte der Cephalopoden,' published at Zurich in 1844. It is at this point that my observations first come in contact with KÖLLIKER'S, who starts from this condition of the egg. KÖLLIKER'S is the only memoir on the development of any Cephalopoda to which I shall have to refer in the present paper, since there has been but one short notice on the subject of Cephalopod embryology during the last thirty years. That notice is due to Prof. METSCHNIKOFF, but is only known to me by a French abstract—like the Russian original, exceedingly short and devoid of illustration. I shall not have to refer again to METSCHNIKOFF'S paper, and there are but few points in KÖLLIKER'S work which come into contact with mine. At the time when Prof. KÖLLIKER made his admirable observations, many questions were in a very different condition to that which they hold at present; and microscopes were not of their present efficiency. Moreover, Prof. KÖLLIKER has described the early stages of postseminary development from the exclusive study of the eggs of *Sepia* and *Argonauta*, and mainly studied them by means of surface-views obtained with a low power of amplification.

The structure of the basketworked capsule in the ovarian egg of *Sepia* was figured and investigated by KÖLLIKER. He attributes the surface-pattern to the folding of the vitelline membrane of the egg itself, and points out that the egg-capsule does not take any part in it. He shows by a section of the egg, which is figured, that (what he mistakes for) the vitelline membrane is thrown into folds, which are pushed inward towards the centre of the egg, forming in section a series of incomplete septa traversing the egg. These disappear, KÖLLIKER shows, as the egg advances to maturity, and finally the egg escapes from its capsule with a perfectly smooth surface. If in the year 1842 our present methods of cutting and clarifying tissues for study with the microscope had been known, it would have been quite a simple matter for KÖLLIKER to have ascertained that he was mistaken in supposing that the membrane which is thrown into folds is the vitelline membrane.

The eggs of *Sepia* and of *Loligo* do not present any thing comparable to a vitelline

membrane. They lie perfectly naked within the egg-capsule. What Prof. KÖLLIKER identified with the then metaphysically important vitelline membrane, is certainly our inner membrane of the capsule.

It is the inner membrane of the capsule which, on the extension of long vascular trunks between it and the outer membrane, becomes longitudinally folded, in correspondence with those vascular trunks; and now, as the growth of the egg rapidly advances, the growth of these inwardly projecting folds or double ridges goes on to an immense extent. The whole cavity of the egg-capsule becomes parcelled out by them (see Plate 11. figs. 7, 8, 9); they push into it from every side, and drive the germinal vesicle to an extreme polar position (fig. 8, *gv*). Each fold is thoroughly supplied with blood-vessels, on which the rapid development of this great bulk of tissue, the increase in the total size of the egg, and the active secretion from the goblet cells of the whole of its inner surface depends. This folded inner capsular membrane, with its extensive system of vessels penetrating among its folds or follicles, may be regarded as a shut gland, constantly increasing in size and accumulating its secretion within its cavity.

The blood-vessels which lie between the inner and outer capsular membranes have their own walls well marked, and in sections are not necessarily adherent either to one or the other. The main trunks are seen at their point of entrance from the peduncle in fig. 19, Plate 12, and the surface-network which connects the venous and arterial trunks at this pole. But besides vessels which may be seen thus on the surface, there are those which branch from them and penetrate between the pushed-in folds of the inner capsular membrane; some of these (*bv*) are well seen in Plate 11. fig. 10, also fig. 9, and more minutely in Plate 12. fig. 23, in which the definite wall of the vessel, with its corpuscular elements, is distinguishable; and it becomes obvious that there is nothing like a lacunar blood-space between the two membranes of the egg-capsule. The completeness of this vascular supply, and the luxuriant growth of the inner capsular membrane, indicate great activity in this portion of the egg. The egg and its capsule attain nearly (Plate 11. fig. 8) if not quite full size, and still the septal ridges are everywhere occupying its cavity. It is true that into the channels or follicles between the ridges the active pavement of muciparous cells has poured out a certain amount of material, and the egg has thus enormously increased in bulk. But there is so much space at present occupied by the ridges, that the egg itself cannot be said to have attained any thing like half its volume.

Third Stage of Ovarian Growth.—This is effected by the gradual absorption of the entire inner capsular membrane, accompanied by the most active proliferation of its cells, which are thrown off in immense numbers to swell the yelk as the processes or ridges on all sides dwindle away and finally disappear. In figs. 10 and 11 sections of eggs are represented in this condition; the folds of the inner capsular membrane, seen in section as processes formed by two rows of cells, with frequently a blood-vessel between them, are in course of degeneration; and already a great mass has been added

to the yelk from their proliferous surfaces. In fig. 23, Plate 12, a portion of the same section, more highly magnified, is accurately represented, showing the cells in various stages of incorporation with the yelk, as they pass from the proliferous surface of the inner capsular membrane.

There does not appear to be any room at all for doubting that cells keep on passing off from the surface of these folds of the inner capsular membrane into the yelk, just as cells keep on passing away as scurf from the surface of the human epidermis. It is a very different question as to whether they retain their vitality and individuality after passing into the yelk. This question is now one of the very greatest importance in embryology generally; and without discussing the views of Professor His or his opponents, who have made the egg of the hen and of osseous fishes their study, I desire to draw attention to the facts observed in the case of the Cephalopods *Sepia* and *Loligo*. Of the cells which pass off or are proliferated into the yelk, so to speak, by far the majority are undoubtedly metamorphosed and broken down into a condition chemically lower than that of living protoplasm before they have long been there. Hence there is not such a wide distinction between this third mode of the egg's nutrition, which I shall call "corpuscular," and the earlier form of inceptive nutrition, which may be distinguished as secretional. In the latter a portion of the goblet cell or corpuscle was metamorphosed and thrown into the egg-mass; in the former it is a whole cell which is thrown in and subsequently metamorphosed.

The stages of the egg's nutrition may be thus grouped:—

1st stage	Plasmic	Osmotic.
2nd stage	Secretional	Inceptive.
3rd stage	Corpuscular	

But the question arises whether all the cells which migrate thus in such immense numbers into the egg-yelk are equally metamorphosed, and to be regarded as having lost their independent vitality. It is, of course, open to any one to maintain that the cells which lose all trace of their nucleus and become irregular, highly refracting masses of indefinite outline are yet capable of resuming their original properties as protoplasmic corpuscles, and that they are not really degenerated, but only temporarily modified. Cells or corpuscles which subsequently appear and take part in the formation of the tissues may then be ascribed to the retention of individuality and protoplasmic properties by the cells proliferated from the inner capsular membrane. I believe, however, that corpuscles which have undergone the changes above described and indicated in the Plates (Plate 12. figs. 23 & 24) will be considered by most persons, as by myself, to have passed irretrievably from the living condition to that of a metamorphic product. Strangely enough, however, as though to prevent our feeling any assurance that the survival of such cells in an egg-mixture is rendered quite improbable by the facts observed in *Sepia* and *Loligo*, we find, both in the fully formed and the immature ovarian eggs of *Sepia*, here and there scattered in the yelk, nucleated cells,

which are undoubtedly exceptional individuals of the migrated capsular cells which have not become fully metamorphosed. I have never observed more than fifteen of these in one egg, and those widely scattered, and all of those did not possess nuclei (Plate 12. fig. 25, also 24 & 26). They were observed only in *Sepia*, not in *Loligo*, and lying at a depth in the yelk, apparently in a zone of less dense yelk than that of the surface. Concerning these zones of yelk, or more strictly "stratified shells" (see Plate 11. fig. 12), there will be a few words to say below.

Corpuscles like these nucleated corpuscles, but devoid of nucleus, and rounder or hexagonal in shape, were often observed by me in the eggs of *Sepia* during its post-seminary development, widely separate and quite accidental in mode of occurrence. It may be possible to attribute great significance to these enduring cells; but the most satisfactory explanation of their occurrence seems to me that they are individuals which, owing to very slight individual differences of constitution (the existence of which may be assumed from the generality of the principle of variation), have delayed their vitelline metamorphosis, to which, however, they gradually (as evidenced by those without nuclei in older eggs) succumb.

The process of proliferation from the surface of the ridges of the inner capsular membrane goes on *pari passu* with the dwindling of the ridges themselves, until at last there is no trace of the ridges left. The capsule then bursts at the pole opposite to that at which the peduncle is attached. The egg, with its surface free from all trace of the ridges, escapes, perfectly naked and devoid of any thing in the form of capsule, vitelline membrane, shell, or other envelope *. It falls into the wide membranous end of the oviduct, where, during the breeding-season, a number of free, naked eggs of this kind may be found. The mode of dehiscence I do not know in detail; but, as in Plate 11. fig. 1, it is not unusual to observe ovaries with many empty shrunken capsules (*c*, *c*).

Condition of the Capsule after escape of the Egg.—The capsule, as thus left by the escape of the egg, consists of the outer capsular membrane, supported on its peduncle, of the main trunks of the blood-vessels which ramified between the inner and outer capsule, and of degenerating remains of some parts of the inner capsular membrane. These remains of the inner capsular membrane undergo a yellow degeneration, so as to form a true *corpus luteum* (Plate 11. fig. 21). The blood-vessels are easily traced on the inner surface of the empty capsules, and at intervals there are scattered shrunken yellow-coloured masses. Probably the whole capsule disappears before another breeding-season, but on this point I have no evidence.

Condition of the Egg after escape from its Capsule.—The egg is now no longer "ovarian," but is still for a brief space of time præseminary—that is, unimpregnated by the male element.

* March 13th, 1875.—Evidence of a very delicate structureless chorion, adherent to the surface of the yelk, is obtained at a later period, when the superficial organs of the embryo are making their first appearance. It separates then in shreds.

In this phase it is, as far as the eye assisted by the microscope can ascertain, in the *fresh* state, a homogeneous transparent viscid body, devoid of any special membrane to protect its surface, but retaining its ovoid shape, owing to the greater density of its superficial layer of substance. In this phase no marking of the surface to indicate the former sites of the capsular ridges *, no trace of a germinal vesicle, can be seen. I have not represented the egg at this period in the Plates; for it would be purely negative as seen by transmitted light, a simple ovoid outline and nothing more. I have traced the germinal vesicle up to the condition of eggs, such as Plate 11. fig. 8, but not beyond. I agree with KÖLLIKER that it disappears; but I have not traced the mode of its disappearance. It is not unlikely that it is absorbed at the same time as are the capsular ridges.

The homogeneous unfertilized egg which now lies in the upper portion of the oviduct is not, however, devoid of all differentiation of structure.

In the first place, when hardened in absolute alcohol, cut in sections and stained with carmine, a stratified arrangement of the substance of the egg becomes obvious (Plate 11. fig. 12), as many as four bands of differing intensity of staining being demonstrable. These apparently indicate differing density of the successive layers of yelk-substance, and are possibly connected with the successive modes of yelk-nutrition which we have distinguished. But, in addition to this, on breaking up a fresh specimen of an egg belonging to this phase, and allowing the yelk to spread out on a glass slip, covering and examining with a power of 600 diameters, it becomes obvious that the yelk is not in its nature homogeneous. In this case (Plate 12. fig. 24), and at later stages, a perfectly definite structure uniformly spread through the mass can be observed. It is possible to distinguish highly refringent, irregular, somewhat botryoidal masses and interspaces occupied by a less dense material, probably a liquid, the denser masses being viscous solids. The liquid must be relatively very small in amount; for it is only when carefully spread out that the yelk-particles become obvious, and with the highest powers they are seen as of a greenish tint, whilst the interspaces are pink†. The botryoidal denser matter must without doubt be directly traced to the metamorphosed cells thrown in from the inner capsular membrane. The forms and sizes of the masses assumed by this material when spread out are too indefinite to admit of measurements, but may be best judged of by the figures. It is necessary again to observe that, in the undisturbed egg, the particles are so densely packed that the mass has the appearance of being quite homogeneous. It is not until the particles are allowed to move on one another a little that the granular or botryoidal structure of the yelk becomes obvious.

* Such markings *are* sometimes to be seen.

† These colours are of course only due to the optical defects of high-power objectives.

Explanation of Plates 11 & 12 (illustrating *Loligo*).

Figs. 1 to 11 are drawn to the same scale.

Fig. 1. One of the smallest eggs from the ovary of *Sepia officinalis* at the breeding-season (April), $\frac{1}{500}$ inch diameter.

Fig. 2. A somewhat larger egg.

gv. Germinal vesicle and spot.

oc. First appearance of the egg-capsule.

Fig. 3. An egg further advanced.

oc. Egg-capsule.

bv. Blood-vessel.

Fig. 4. An egg still further advanced (same stage as fig. 18). The yelk has now received considerable addition to its substance, and there can be distinguished:—

oc. The outer egg-capsule.

ic. The inner egg-capsule, consisting of columnar cells.

gv. Germinal vesicle.

Fig. 5. The egg now shows traces of the development of folds or plicæ in its capsule.

Fig. 6. The folds are more clearly developed, and are seen here as focused in a surface-view of the egg. Their connexion with the blood-vessel (*bv*) is obvious.

Fig. 7. An egg, further advanced, in transverse section, to show the disposition of the now greatly enlarged folds of the inner capsular membrane (*ic*). The outer capsular membrane (*oc*) is seen to take no part in the formation of the penetrating ridges. The stained nuclei of the capsular cells have not been presented in this figure, but the carmine-stained matter occupying the cavity between the ridges of the capsule is indicated by shading. This matter is the yelk of the egg, which is being increased by the addition of new material from the capsular cells. Actual section.

Fig. 8. A much larger egg (in longitudinal section), showing the disposition of the ridges of the inner capsular membrane and the condition of the yelk-cavity. It is to be noticed that though the whole egg has increased greatly in bulk, the yelk-space has not as yet gained any thing as compared with the capsular folds or ridges.

gv. Germinal vesicle.

bv. Blood-vessels in section, lying between the outer and inner capsular membranes.

oc. Outer capsular membrane.

ic. Inner capsular membrane.

c. Yelk-cavity. Actual section.

Fig. 9. Transverse section of an egg not quite so far advanced. The nuclei of the cells of the inner capsular membrane are given in the upper part of the figure. Letters as in fig. 8. Actual section.

Fig. 10. Longitudinal section of a full-sized ovarian egg of *Sepia*. The process of absorption of the inner capsular membrane and its ridges has advanced to some extent. The germinal vesicle has also disappeared.

x. Dwindled inner capsular membrane, forming the periphery of the inner capsule. Other letters as in fig. 8. Actual section.

Fig. 11. Portion of a transverse section of an egg in the same stage of growth. Letters as in fig. 10. Actual section.

Fig. 12. Transverse section of a completely formed egg of *Sepia*, magnified only four diameters, to show the existence in the yelk of three concentric zones of differing density. Actual section.

Fig. 13. Portion of a ripe ovary of *Sepia*, showing ova of various sizes and some empty capsules, *c*, *c*.

Fig. 14. One of the smallest egg-cells observed in the ovary of *Sepia* at breeding-time. Cells like connective-tissue corpuscles are seen to be grouped so as to form the capsule of the egg. Optical section.

Fig. 15. An egg somewhat further advanced—the capsule now definitely formed. Optical section.

Fig. 16. The capsule has become pedunculate; but as yet there is no blood-vessel traversing it.

ic. Inner, and

oc. Outer capsular membranes. Optical section.

Fig. 17. A more advanced egg, drawn in the fresh state. By its side is a very small egg-cell. Letters as before. Optical section.

Fig. 18. The separation between inner and outer capsules and the characters of their respective corpuscles have become definite. The blood-vessels (*bv*) in the stalk of the egg-capsule have developed. Other letters as before. Optical section.

Fig. 19. Actual arrangement of blood-vessels between the inner and outer capsular membranes of a nearly fully-grown egg, as seen from the peduncular pole. The artery and vein are seen applying themselves at the point of attachment of the egg-stalk to the capsular surface, and spreading out in large longitudinal trunks connected by a network of smaller vessels transversely.

Fig. 20. The peduncle of the egg drawn in fig. 6, in optical section, so as to show the wall and contents of the blood-vessel (*bv*), the outer capsule (*oc*), and the cells of the inner capsule—*i. e.* not in section, but focused so as to show them lying in one plane.

Fig. 21. Portion of an empty capsule in the fresh state from the ovary of *Sepia*, showing blood-vessel and yellow degeneration of capsular cells.

Fig. 22. Ovarian egg of *Loligo*, showing peduncle, capsular plications, and germinal vesicle. Drawn from a specimen examined in the fresh state.

Fig. 23. Portion of a similar section to that drawn in fig. 10, Plate 11, but more highly magnified (HARTNACK'S No. 10 à immersion) in order to show the relation of blood-vessels to the folds of the inner capsular membrane, and the passage of cells *bodily* from the proliferous ridges into the yelk of the growing egg.

Fig. 24. Portion of the surface of a fresh egg of *Sepia*, after escape from the ovarian capsule (*i. e.* uterine), showing modified cellular elements.

Fig. 25. Modified cells (derived from the inner capsular epithelium) observed beneath the denser cortical substance of a fully formed or uterine egg of *Sepia*.

Fig. 26. Modified cells from a not fully formed ovarian egg of *Sepia*.

Fig. 27. Portion of the egg and capsule drawn in fig. 9, Plate 11, to show more fully the condition of the inner capsular epithelium.

The egg is not fully *grown*, and the process of proliferation from and absorption of the inner capsular ridges is not established as in the egg of fig. 23; but the cells have the character of those found on thickly secreting mucous surfaces, and some appear as goblet cells.

bv. Blood-vessel.

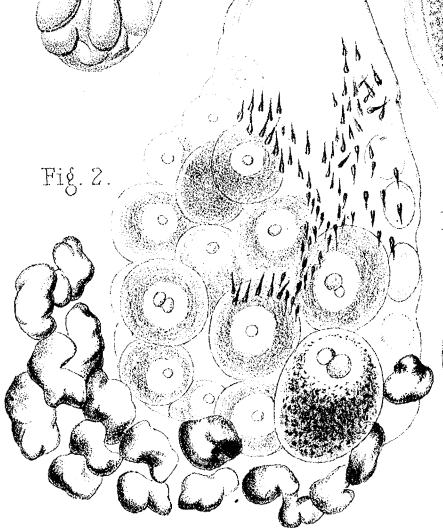
oc. Outer capsular membrane.

ic. Inner capsular membrane.

Fig. 28. More highly magnified view of goblet cells (*cc*) and simple connective-tissue corpuscles (*bb*) from a portion of the same section.

Fig. 1.

Fig. 2.



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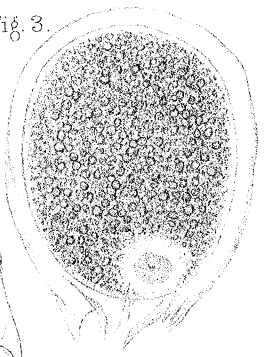

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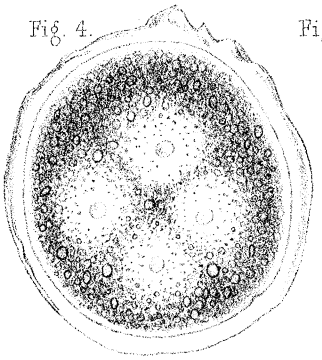

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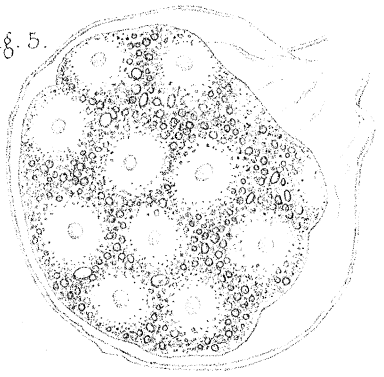

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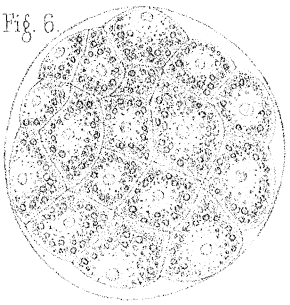

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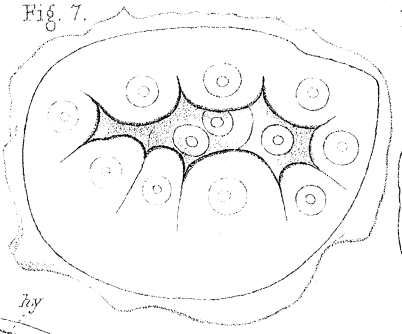
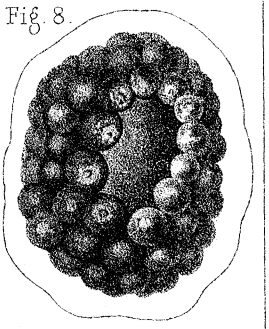


Fig. 8.



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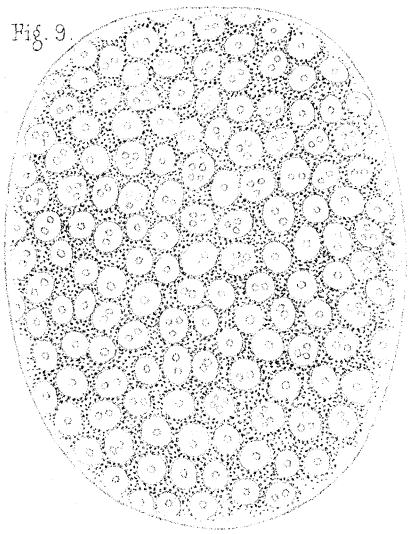

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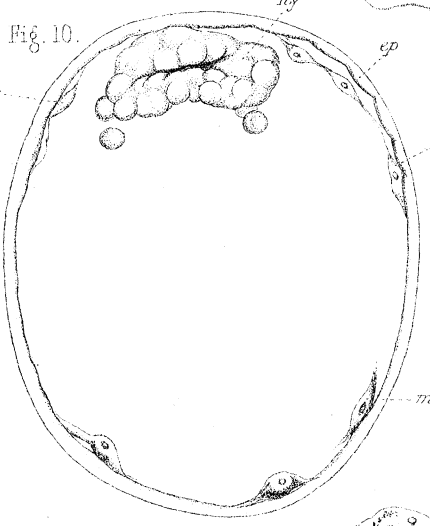
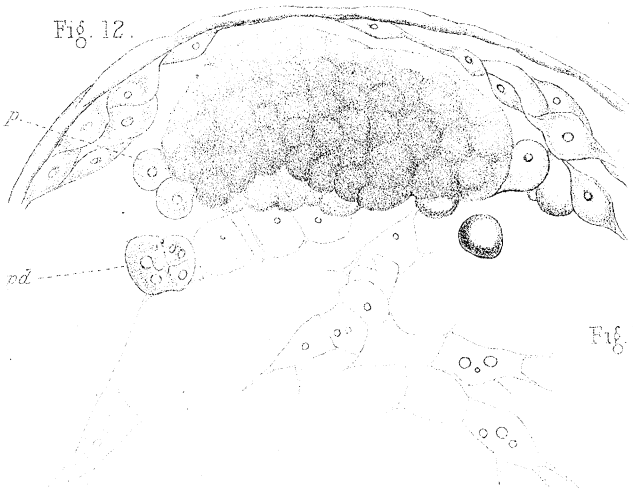


Fig. 11.

Fig. 12.



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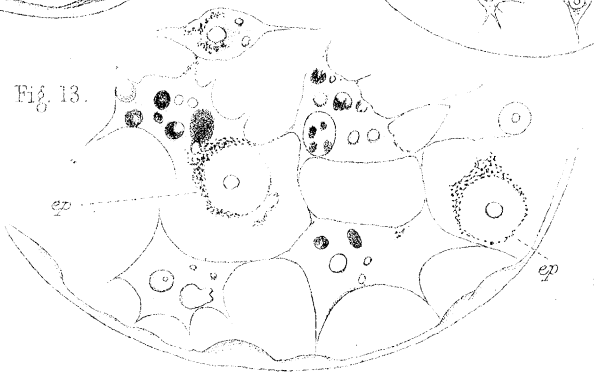
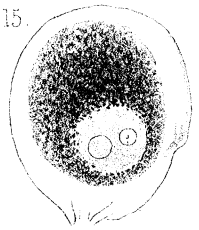


Fig. 14.

Fig. 15.



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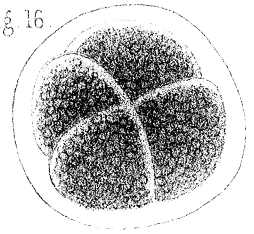

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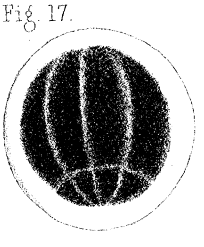

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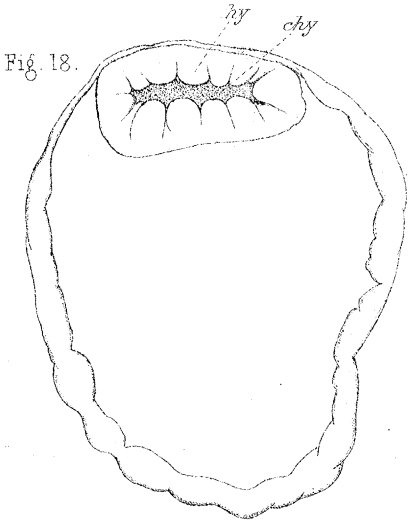
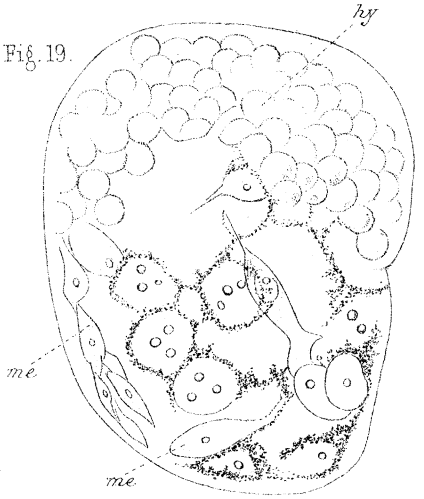
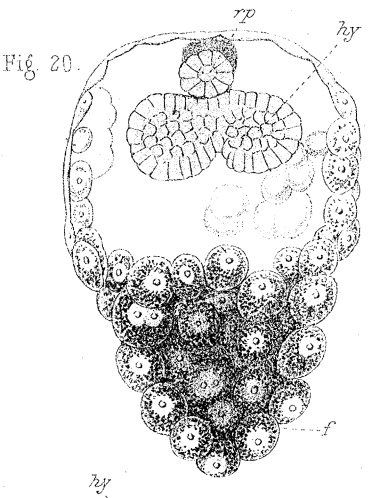
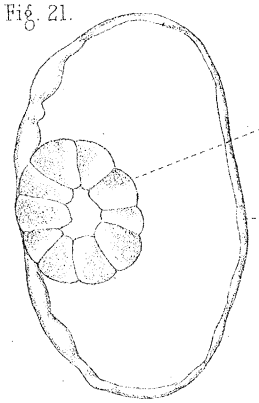
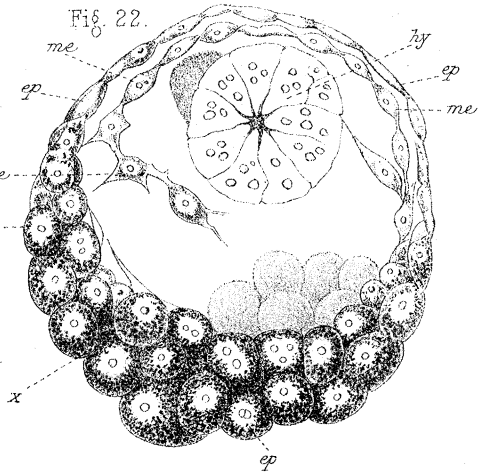
DEVELOPMENT OF PISIDIUM PUSILLUM.

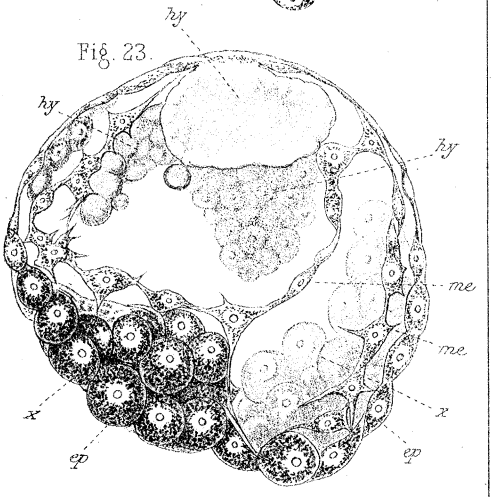


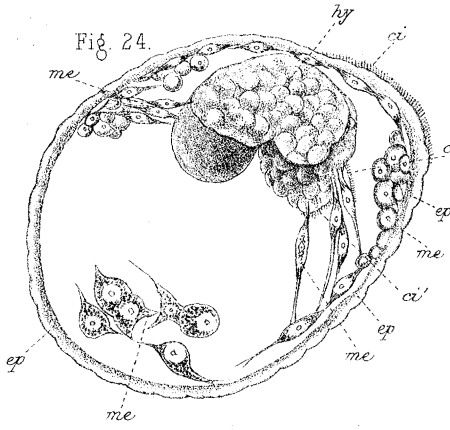


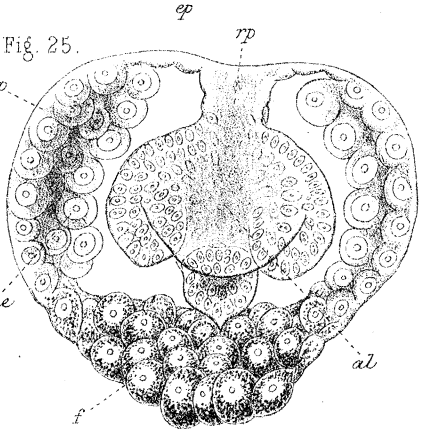


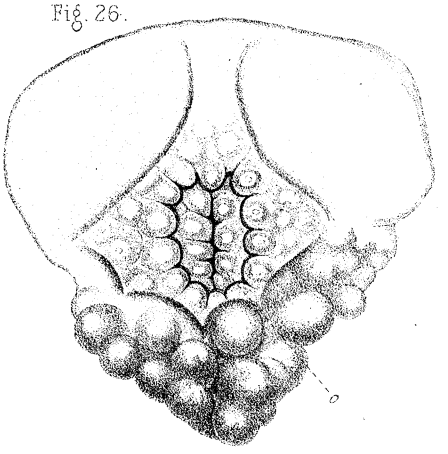


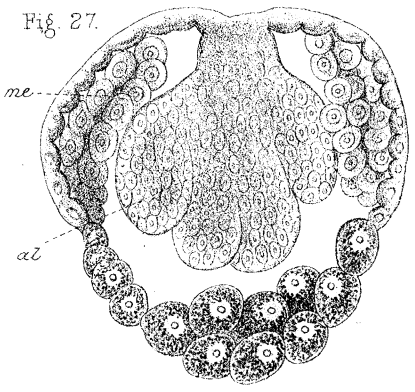


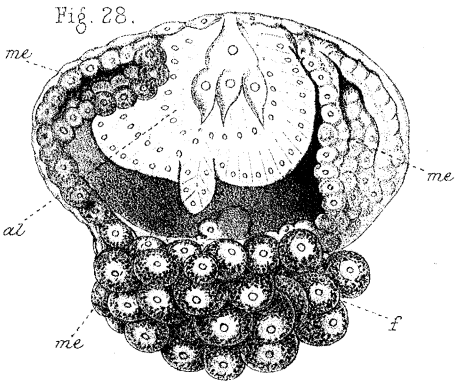












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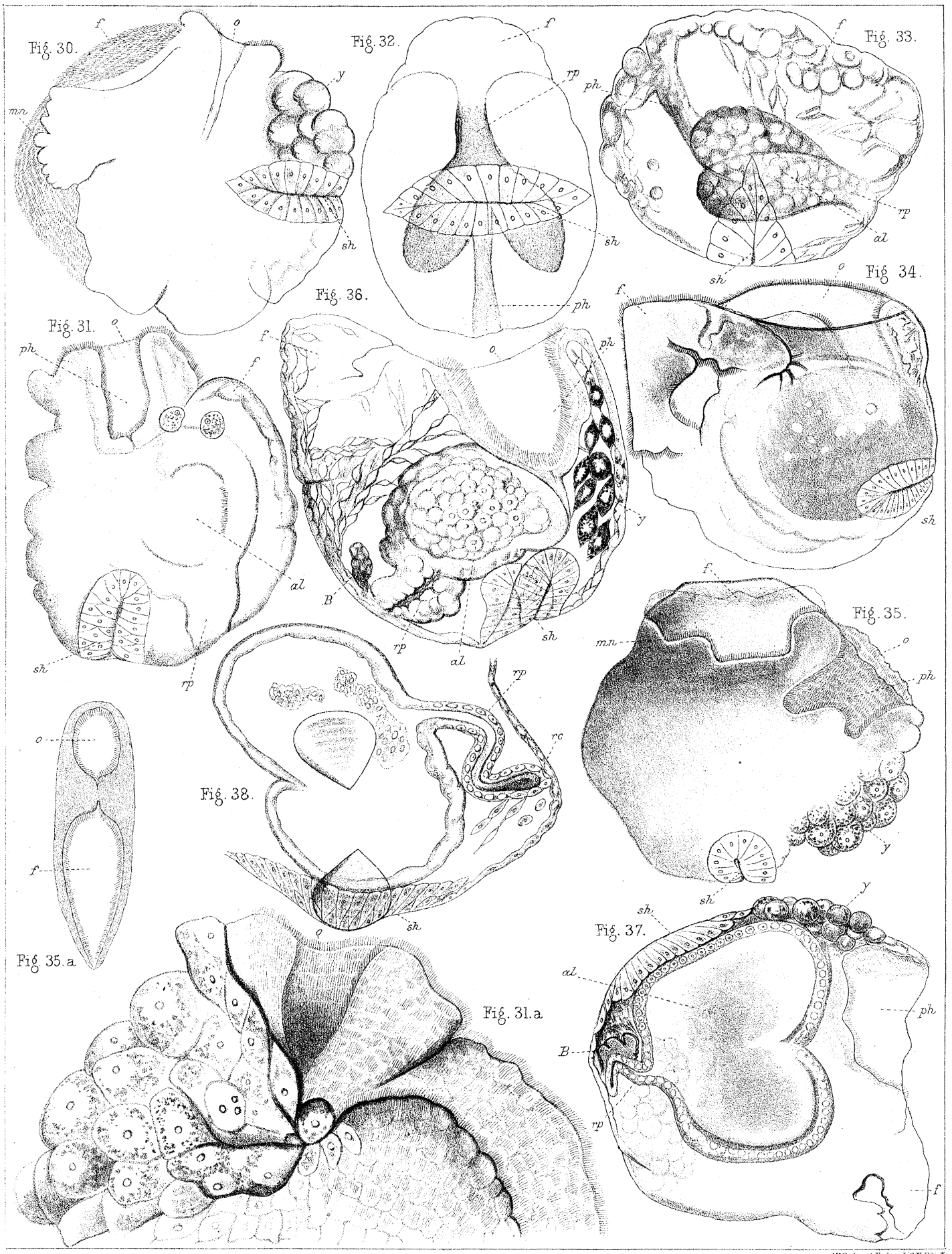
DEVELOPMENT OF PISIDIUM PUSILLUM.



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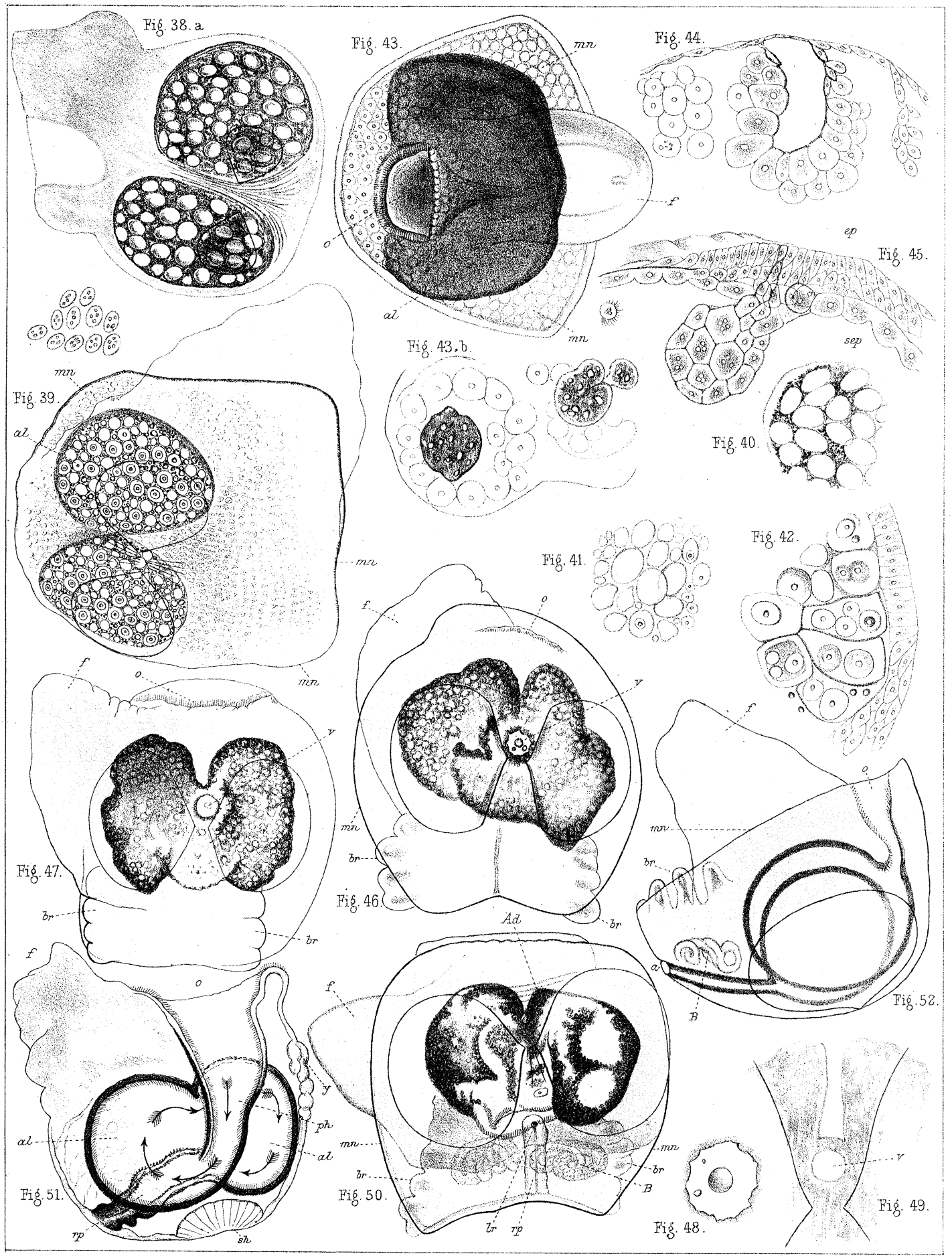

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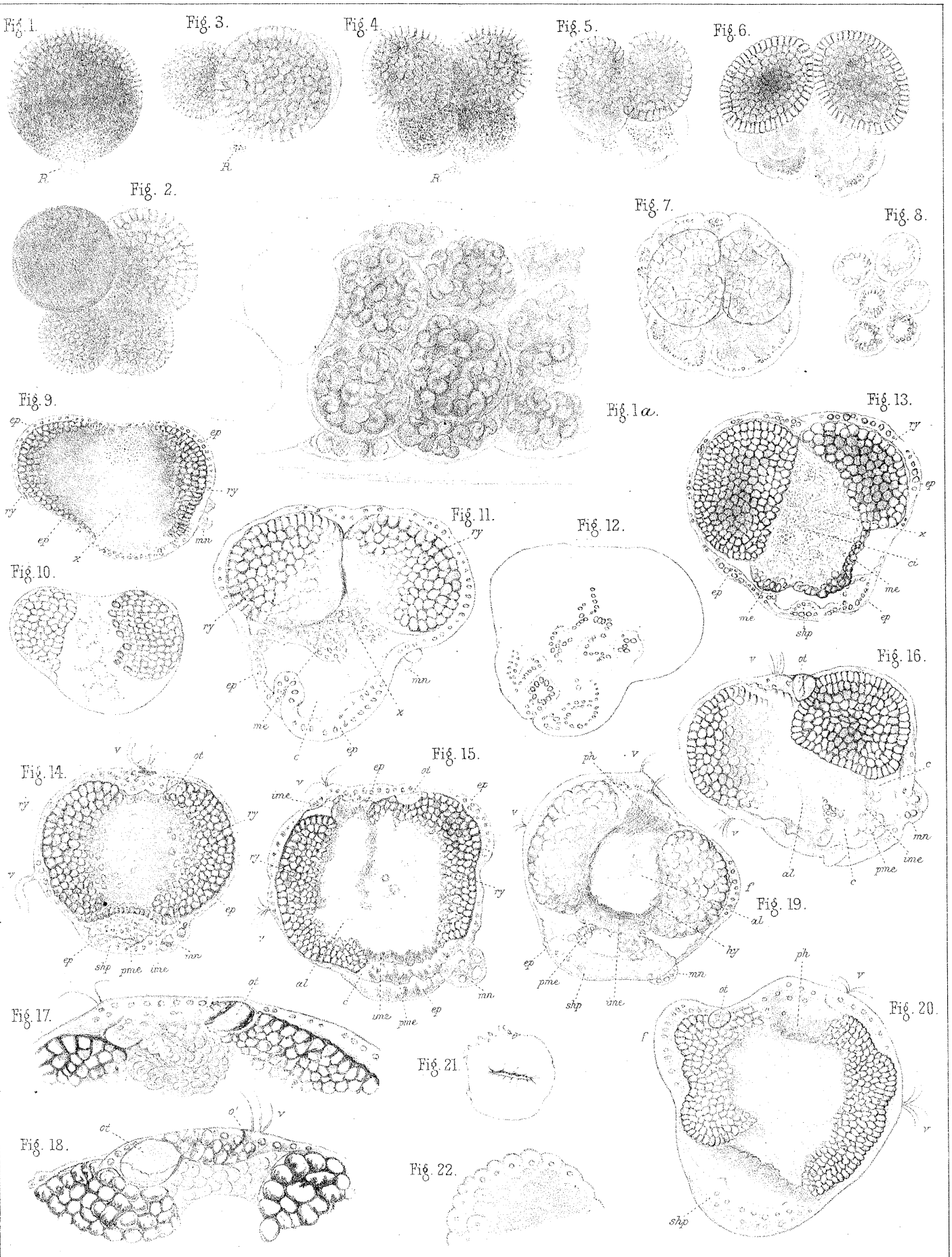

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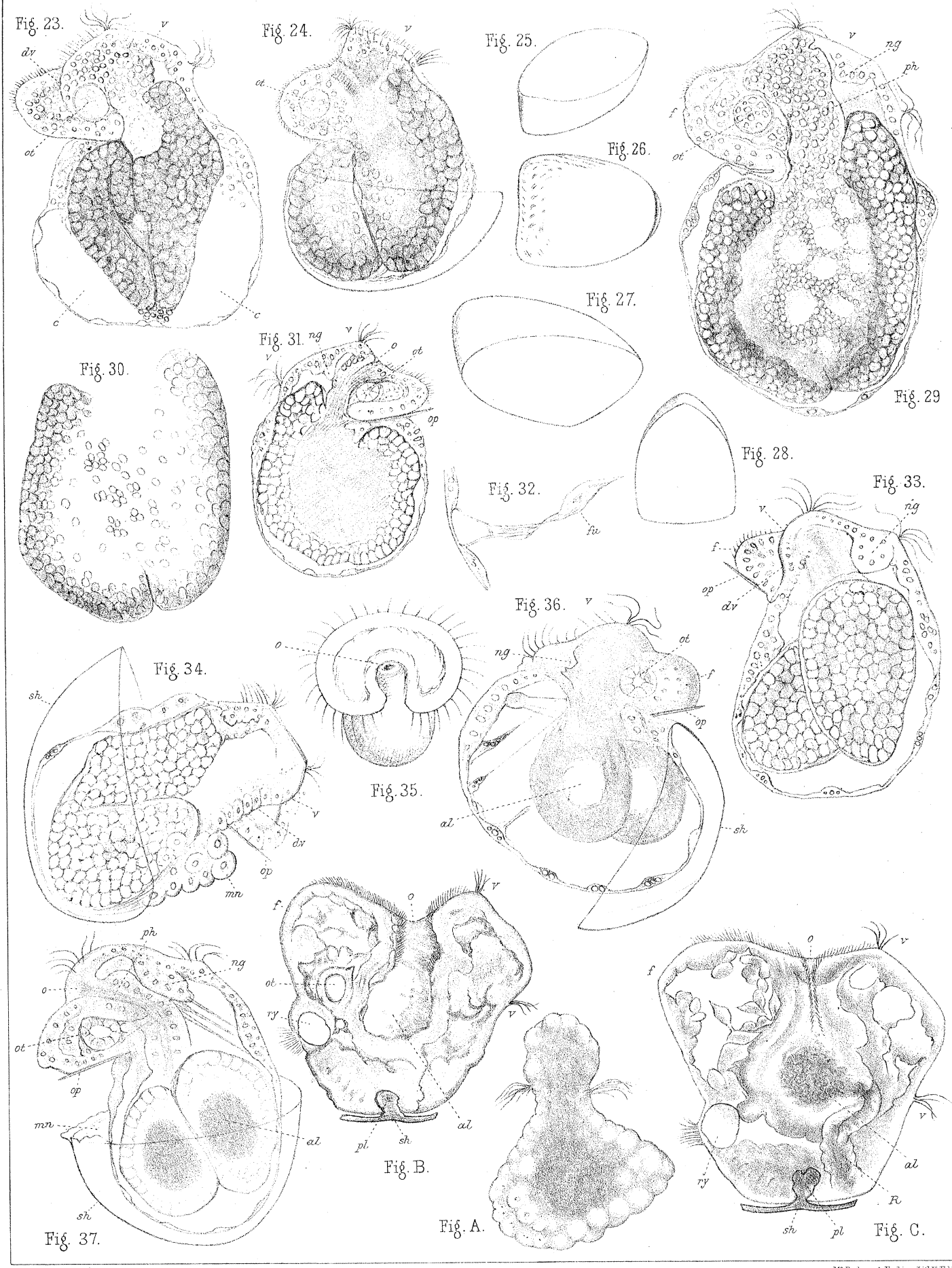
DEVELOPMENT OF APLYSIA DEPILANS.



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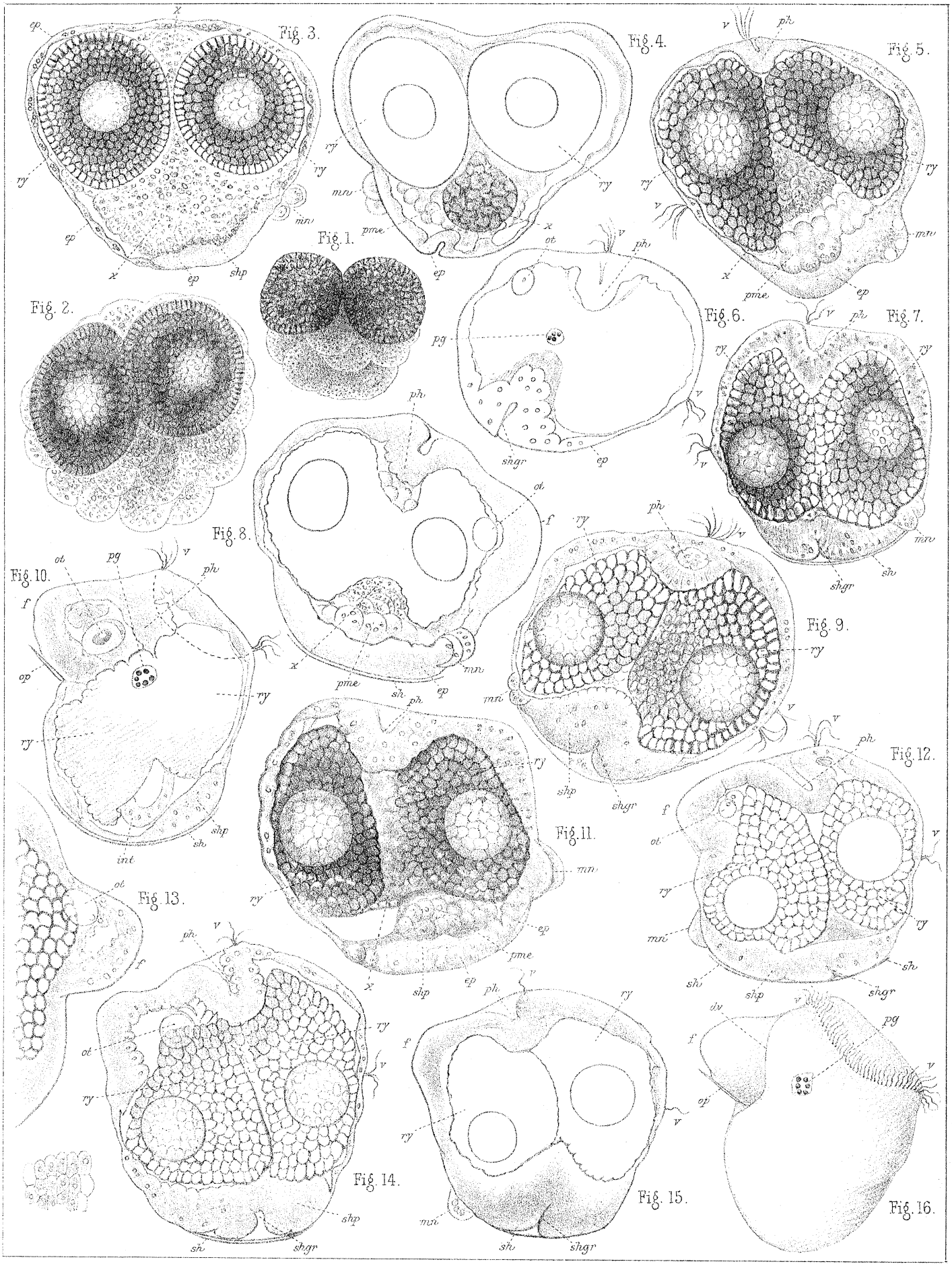
23 - 37 APLYSIA. Figs A, B, C, PLEUROBRANCHIDIUM.



DEVELOPMENT OF PLEUROBRANCHIDIUM.

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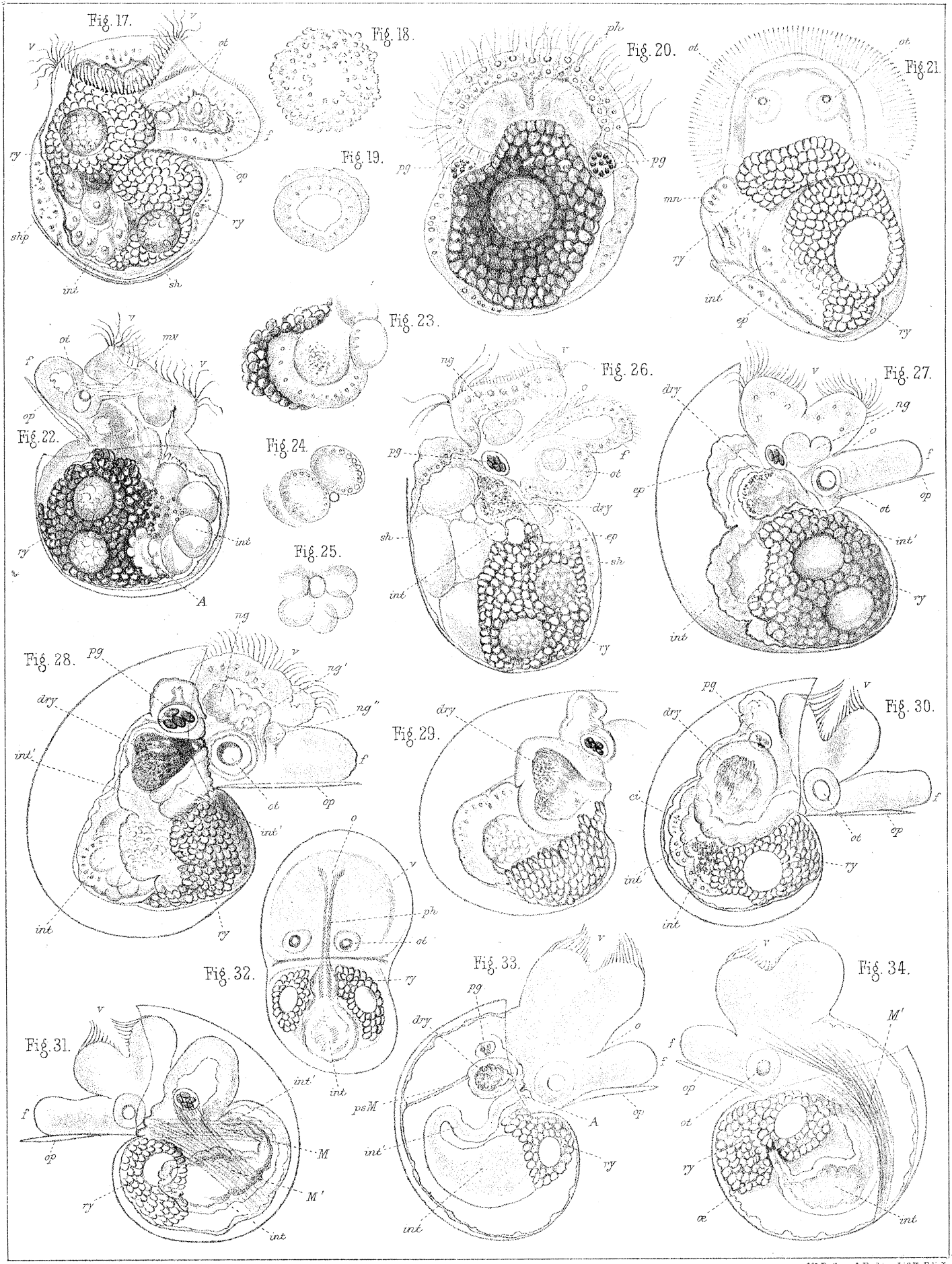

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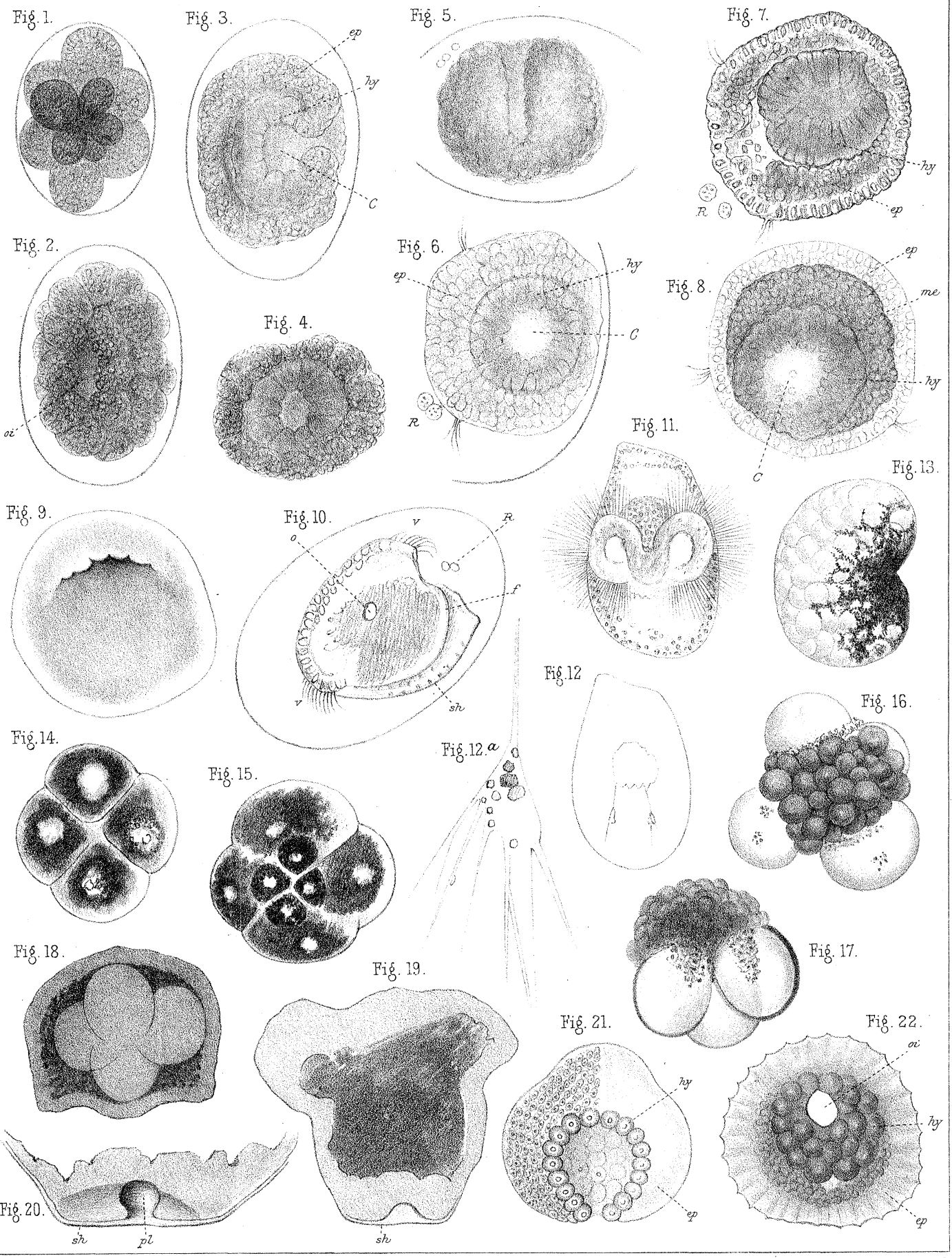
DEVELOPMENT OF PLEUROBRANCHIDIUM.



Mc Farlane & Erskine, Lith.rs Edin.r

1-12 TERGIPES. 13-20 NERITINA. 21-22 LIMAX.

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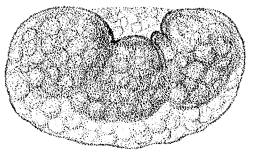

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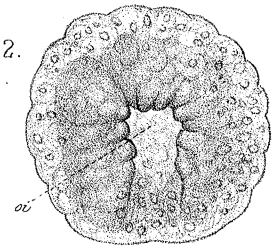

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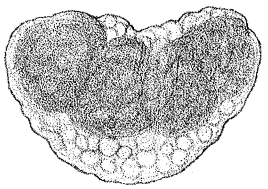

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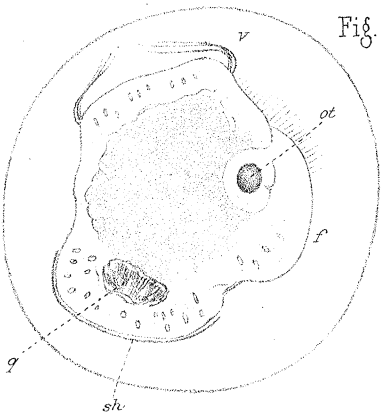

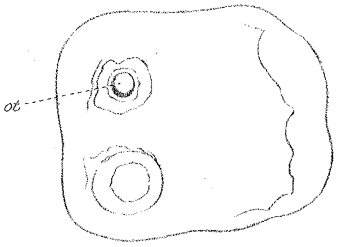

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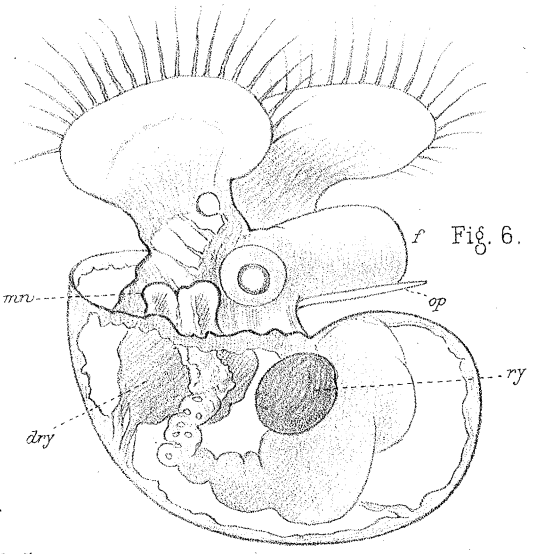

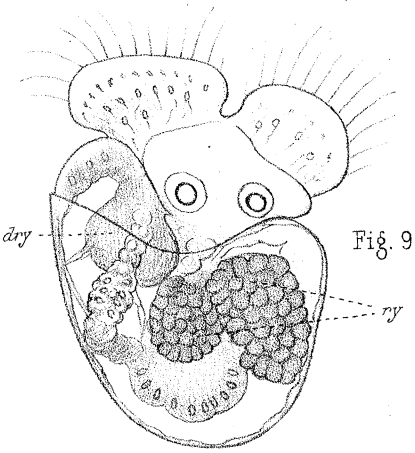

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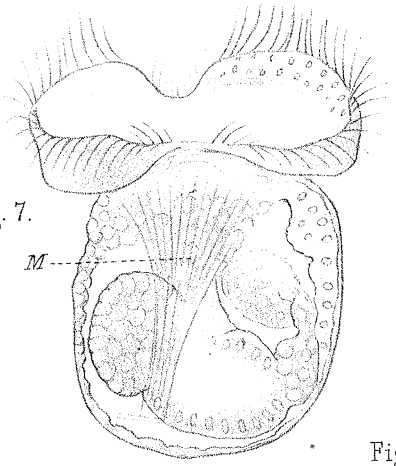

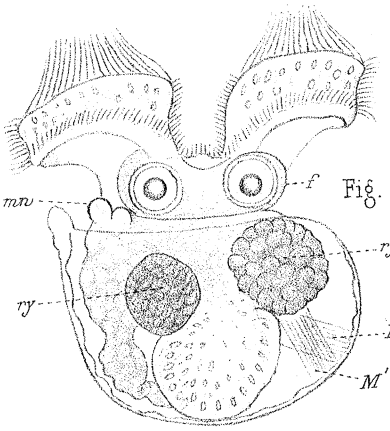

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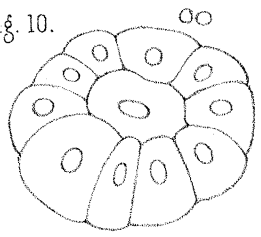
Fig. 10.



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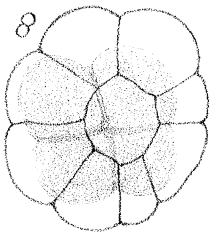

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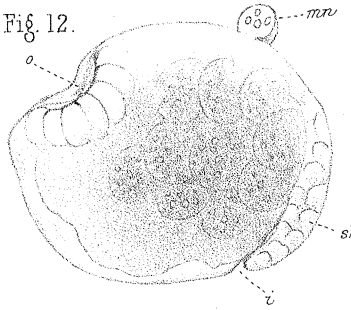

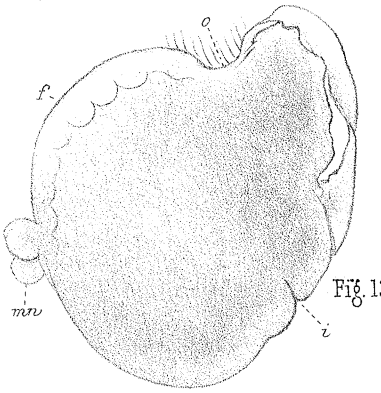

Fig. 13.

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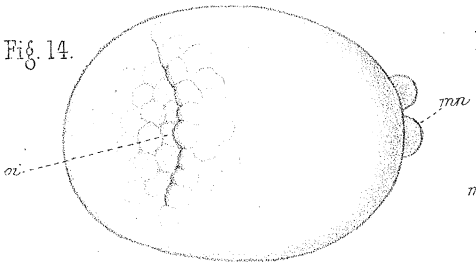

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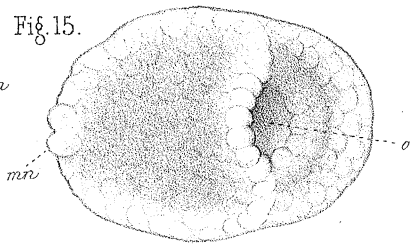

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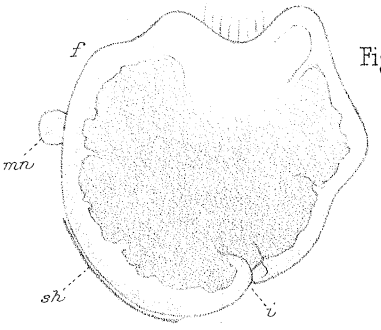
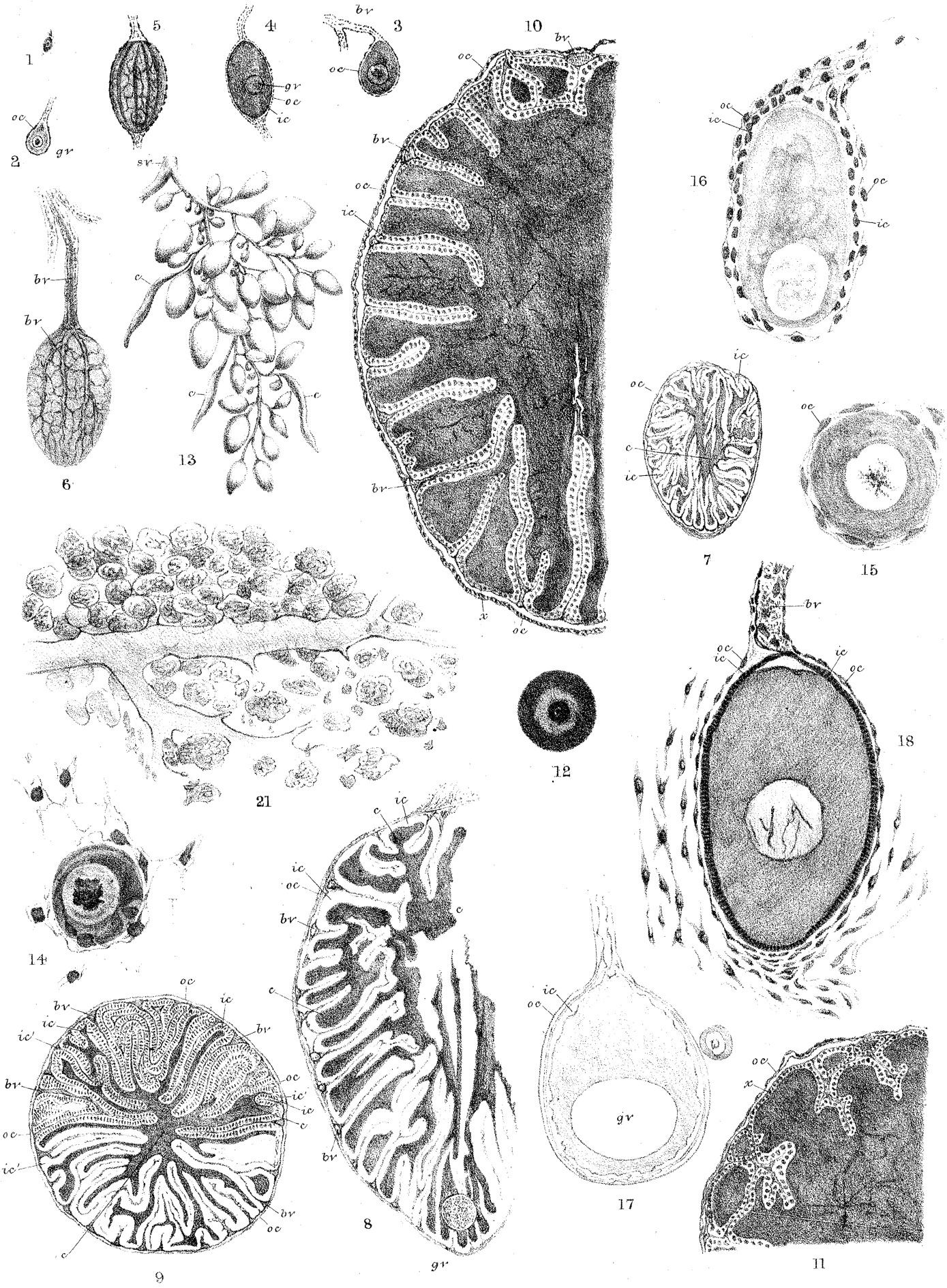


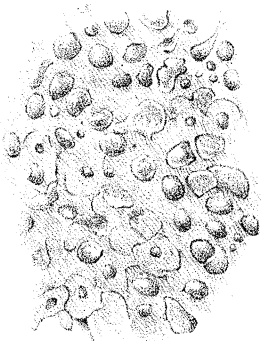
Mc Farlane & Erskine, Lith.rs Edin.r

1 - 9 POLYCERA. 10 - 16 TETHYS.



E.M.Williams F.L.S. lith.

W.West & Co. imp.



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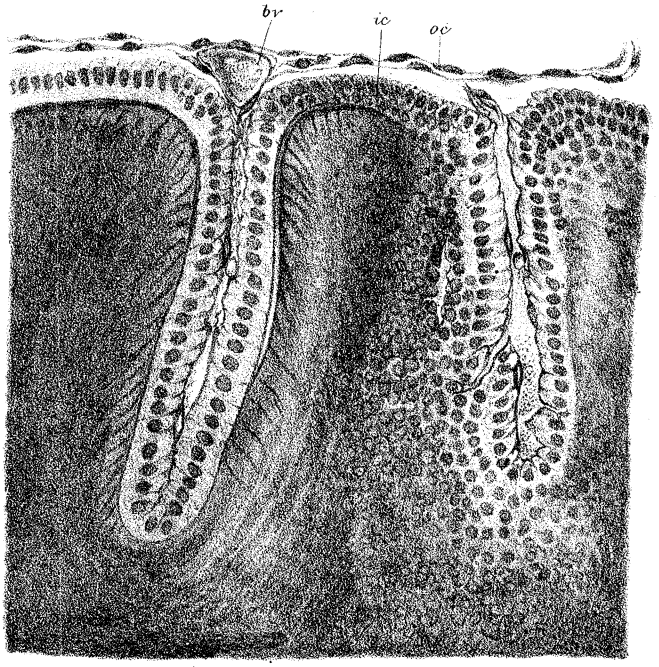

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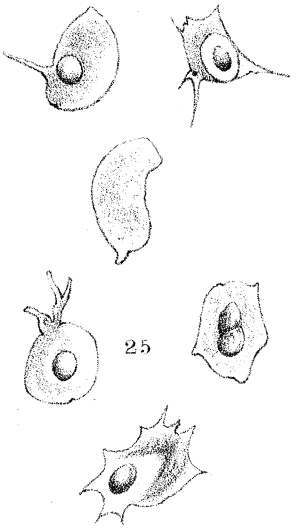

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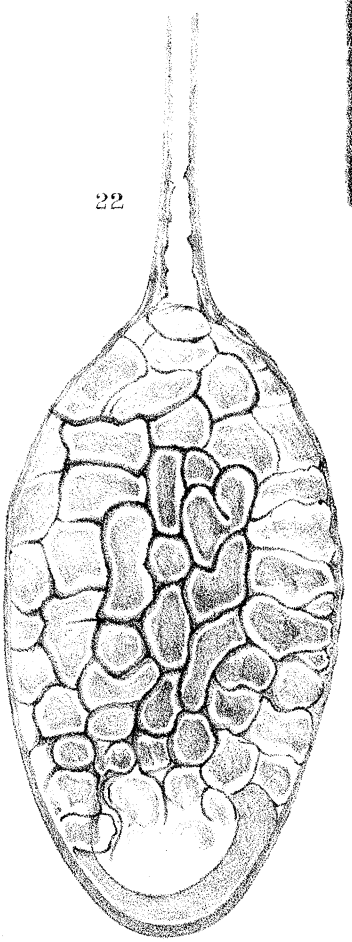

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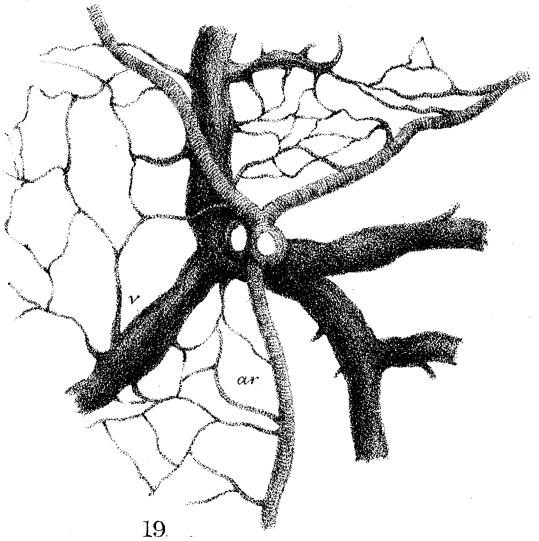

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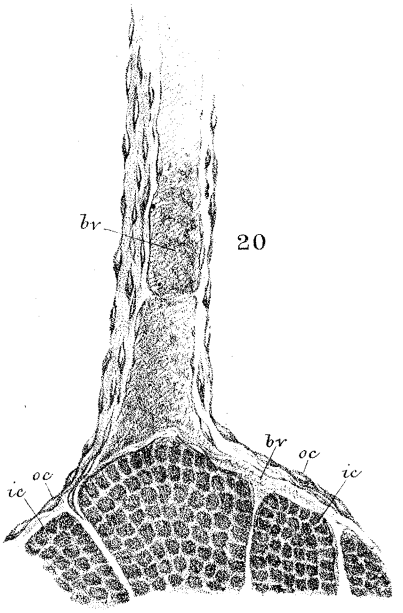

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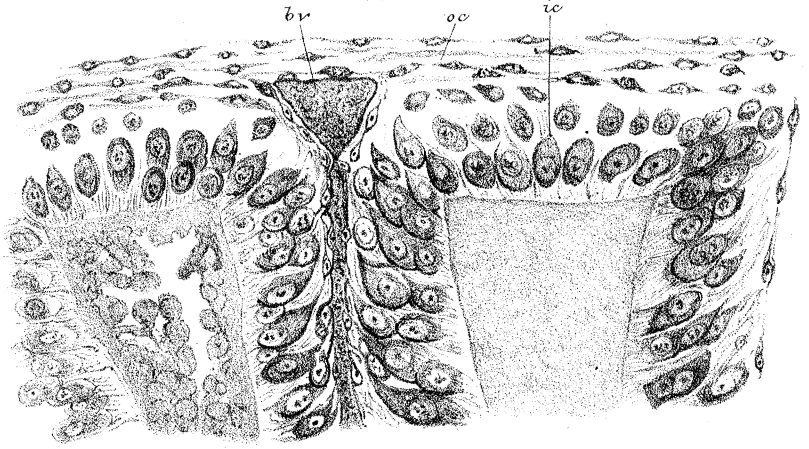

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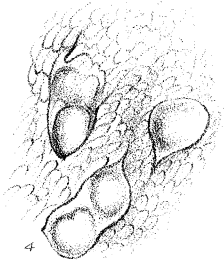

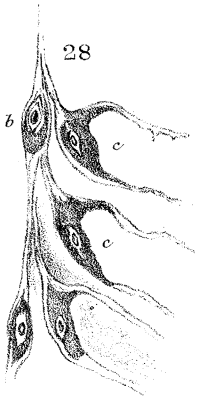

E.M.Williams,F.L.S.lith.

W.West & Co.imp.

Fig. 1.

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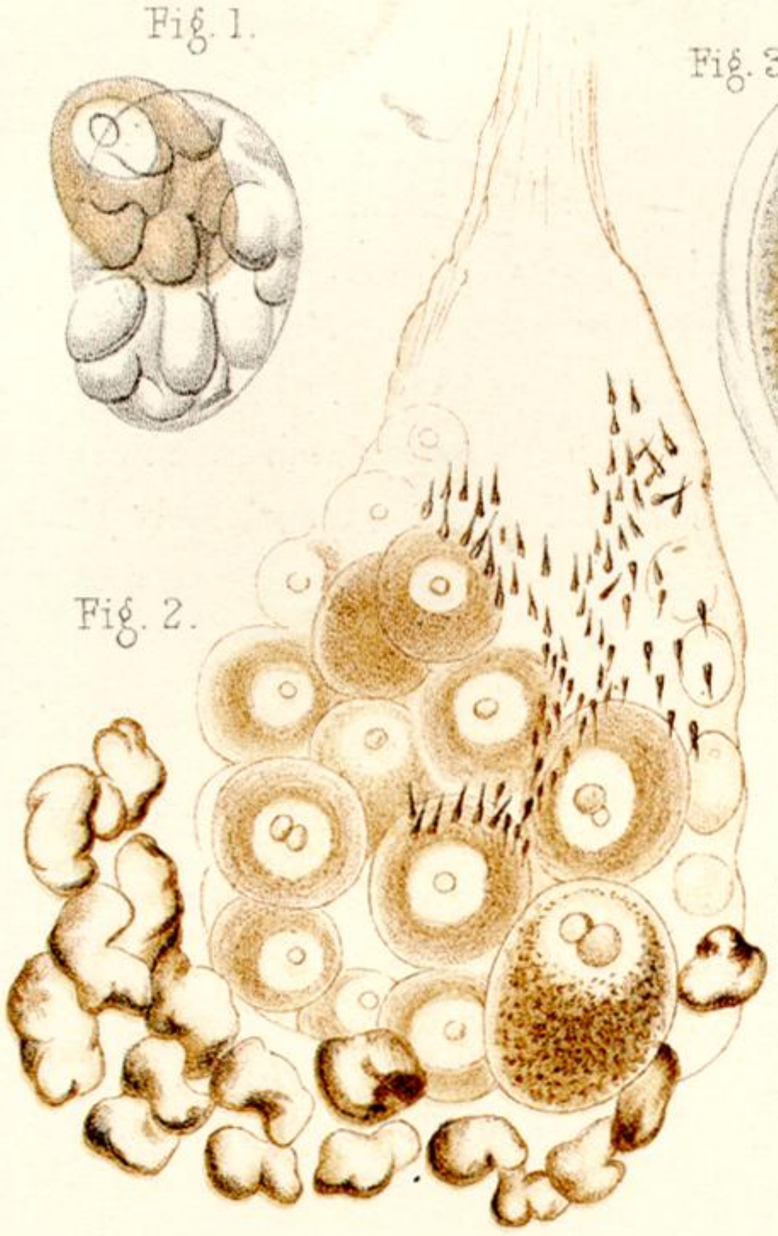

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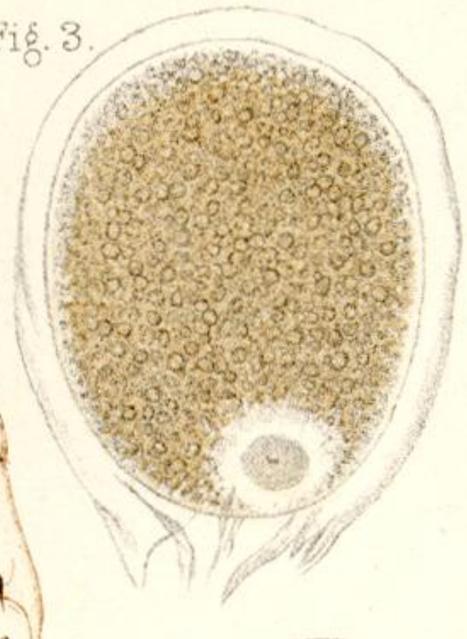

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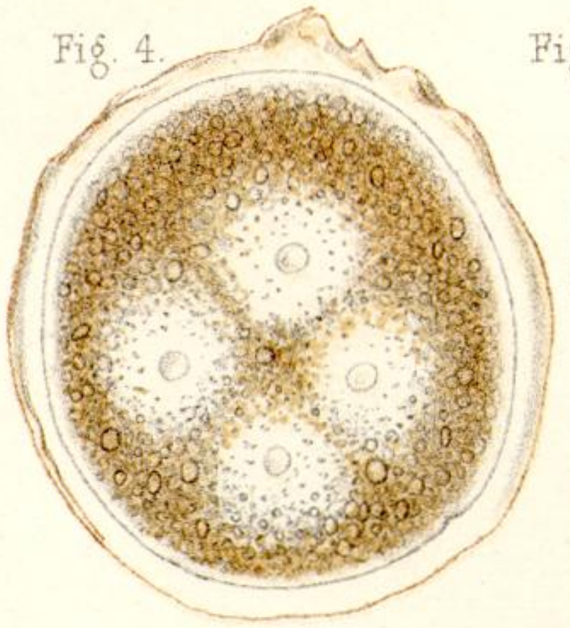

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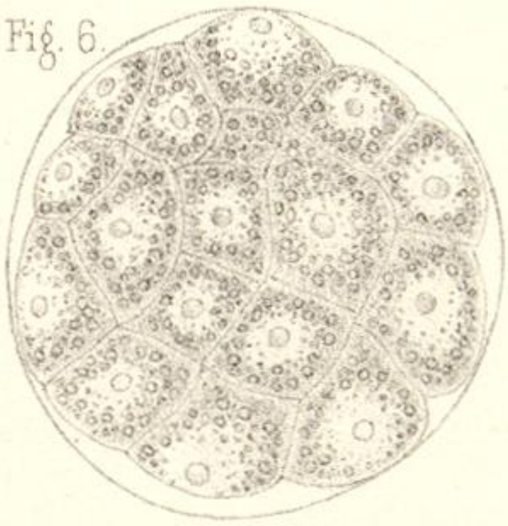

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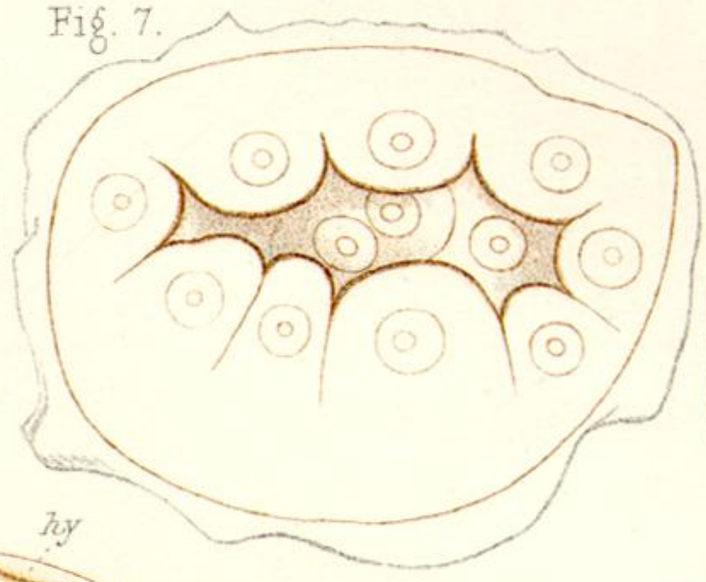

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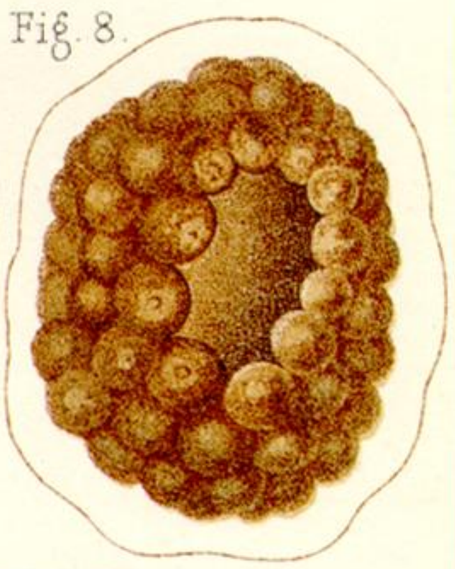

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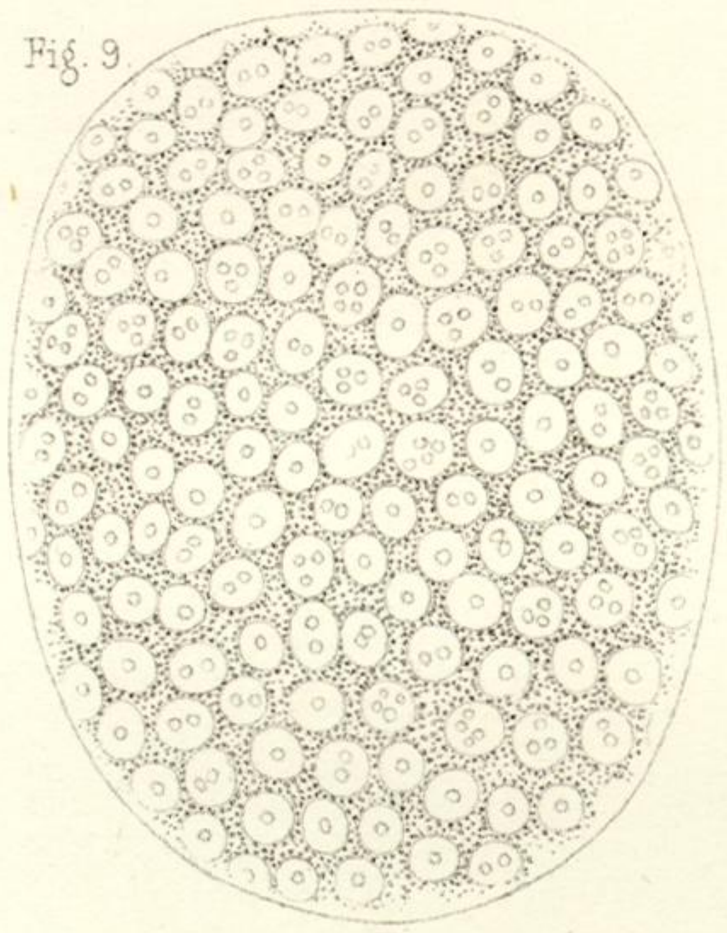

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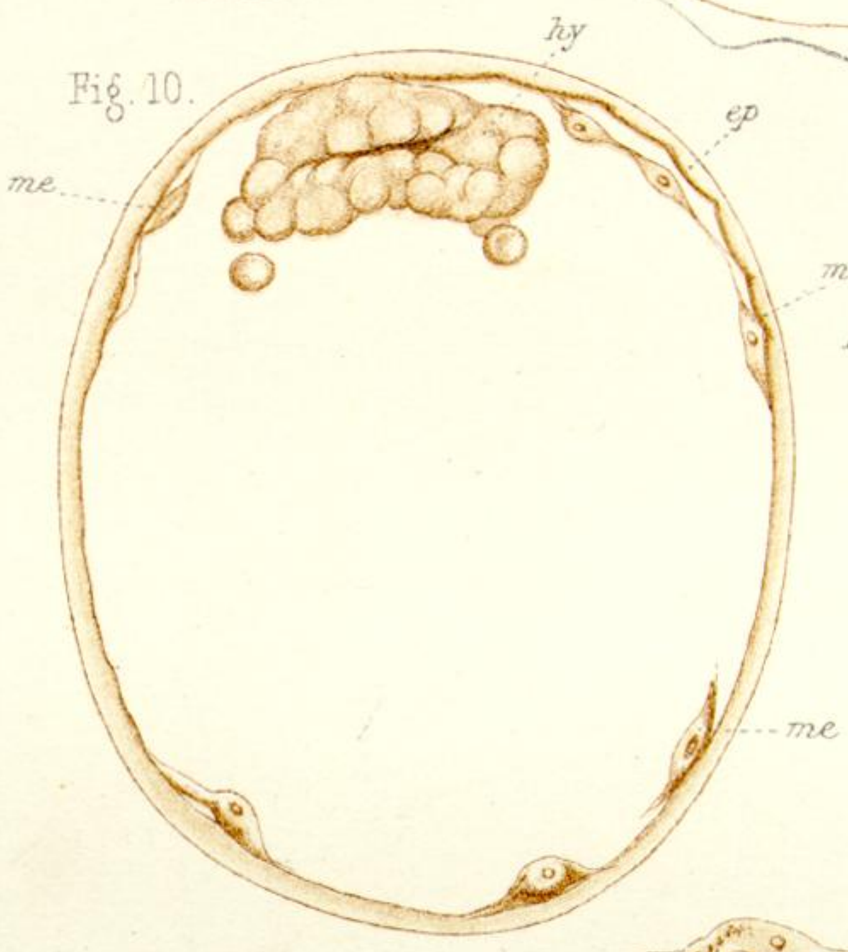

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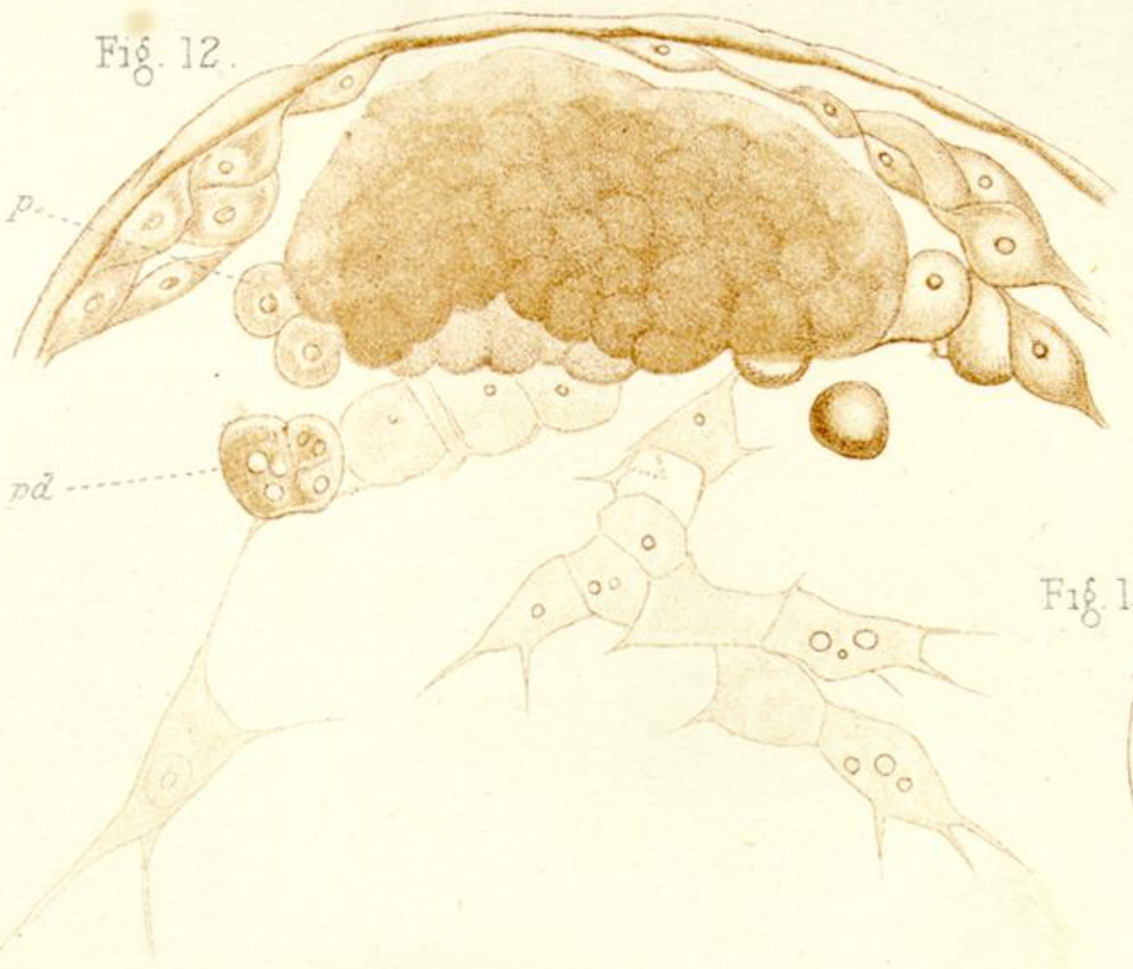

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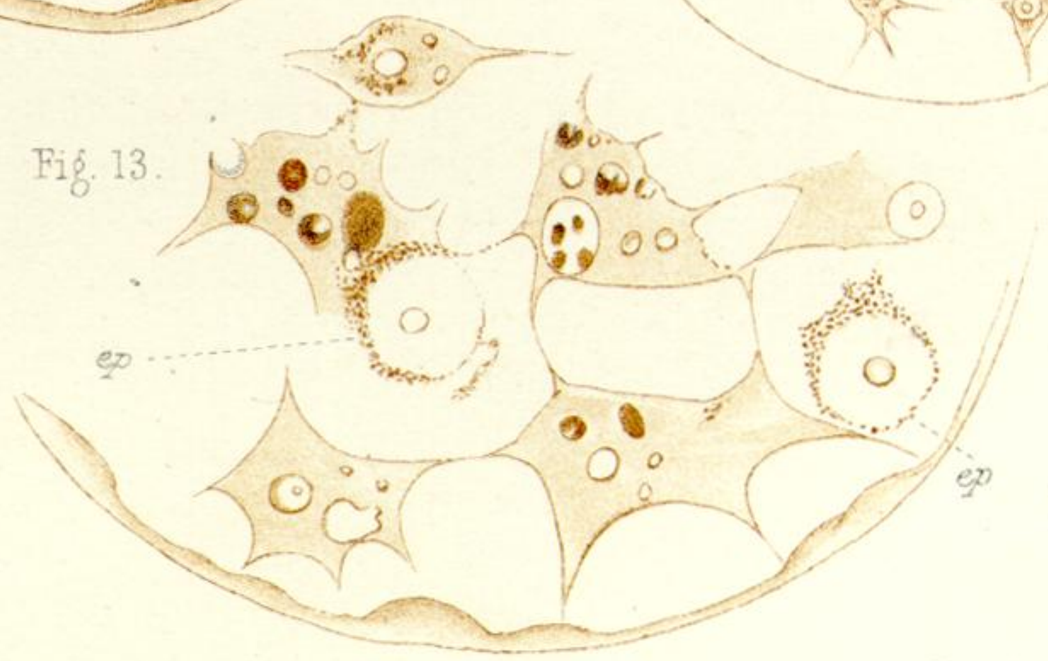

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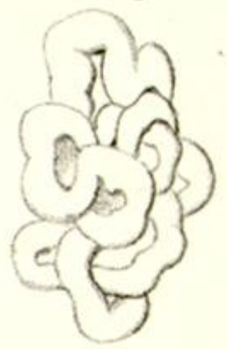
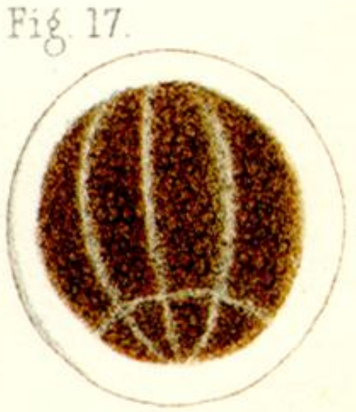


Fig. 15.

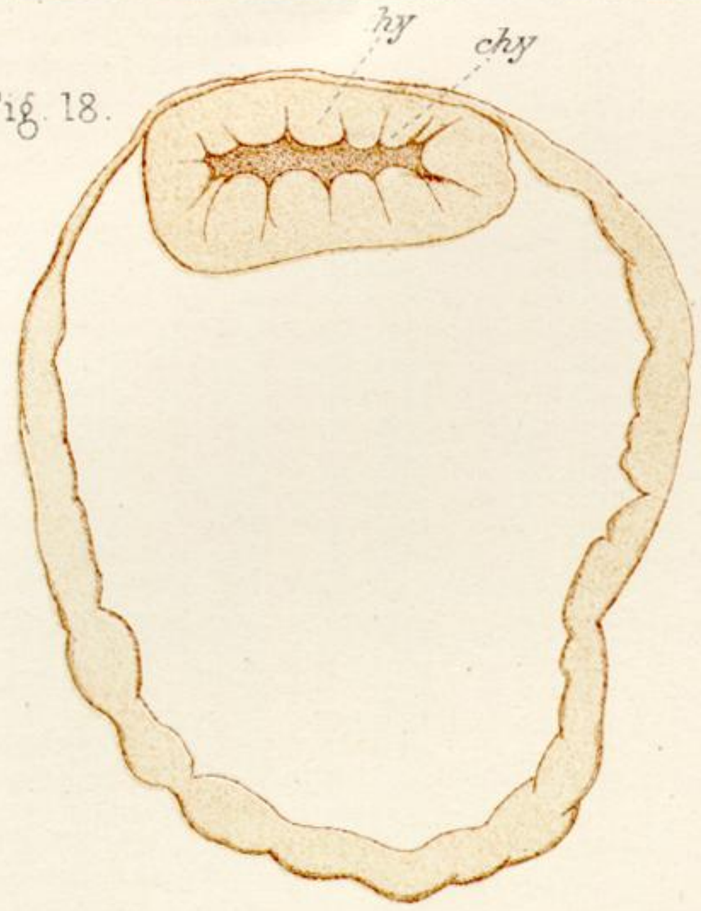
Fig. 16.

Fig. 17.



DEVELOPMENT OF PISIDIUM PUSILLUM.

Fig. 18.



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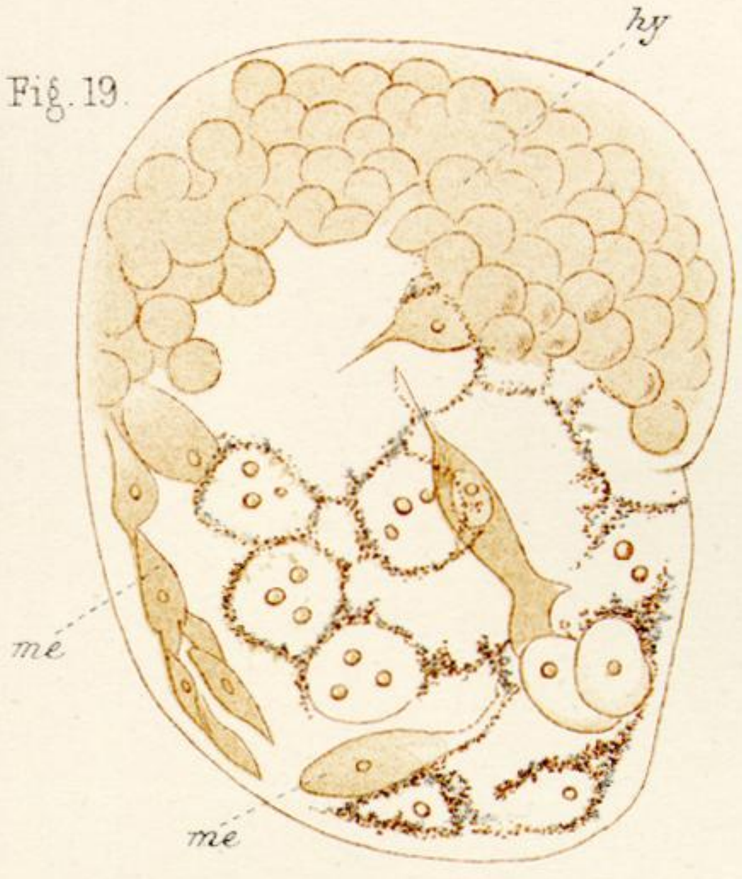

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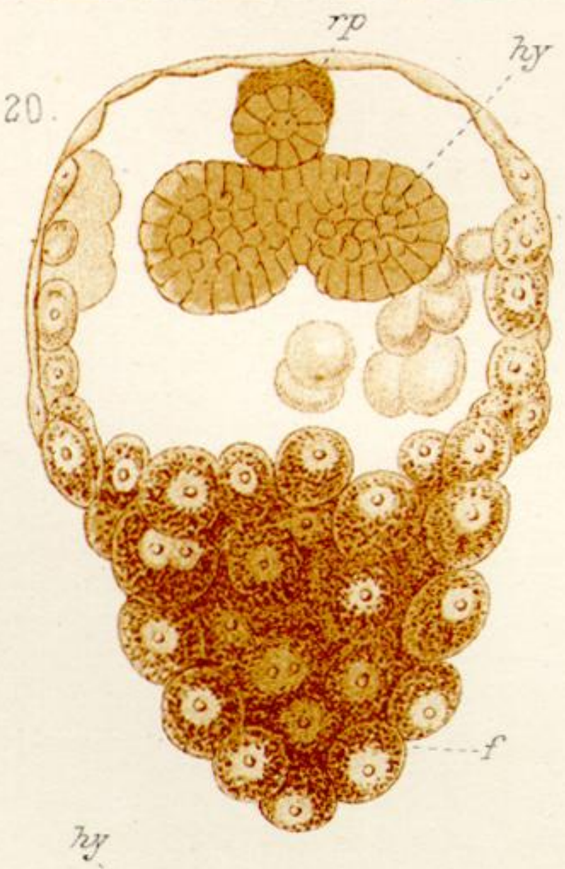

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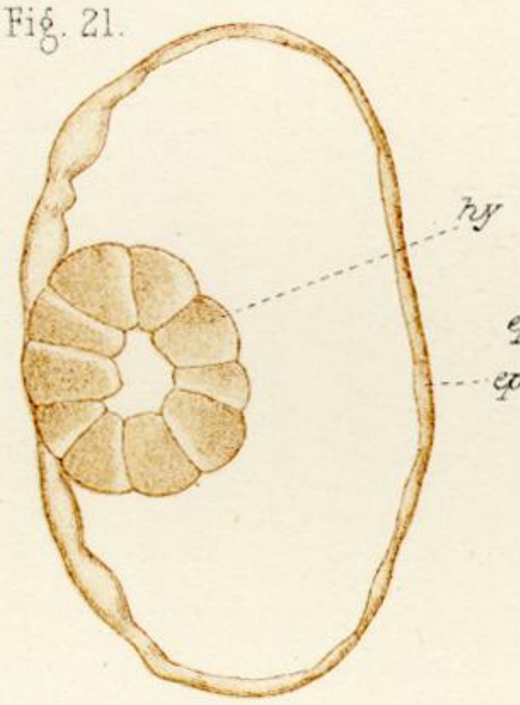

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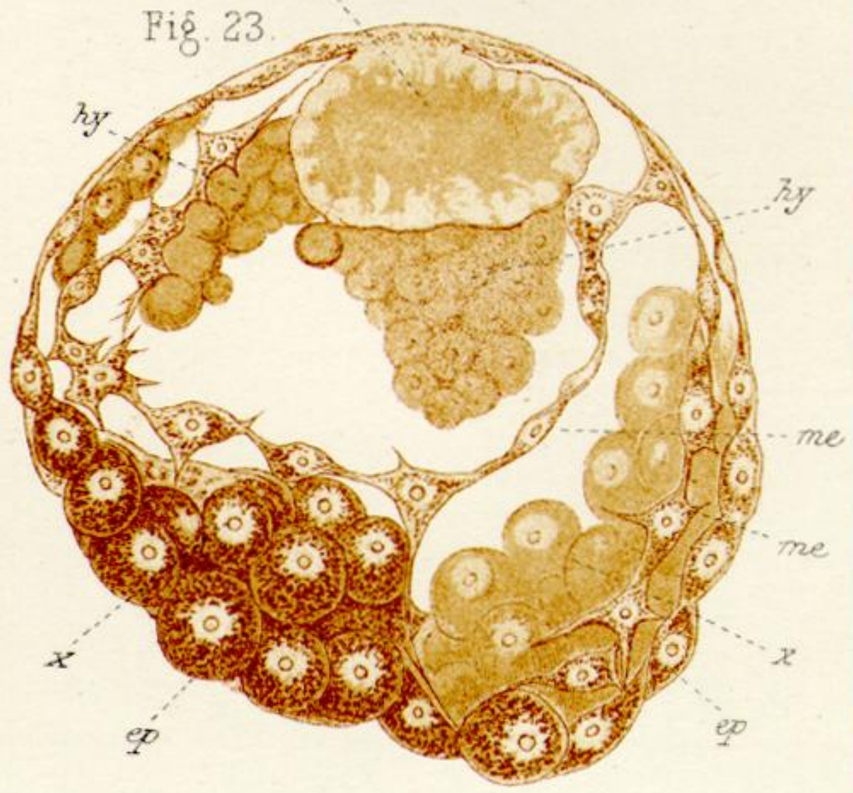

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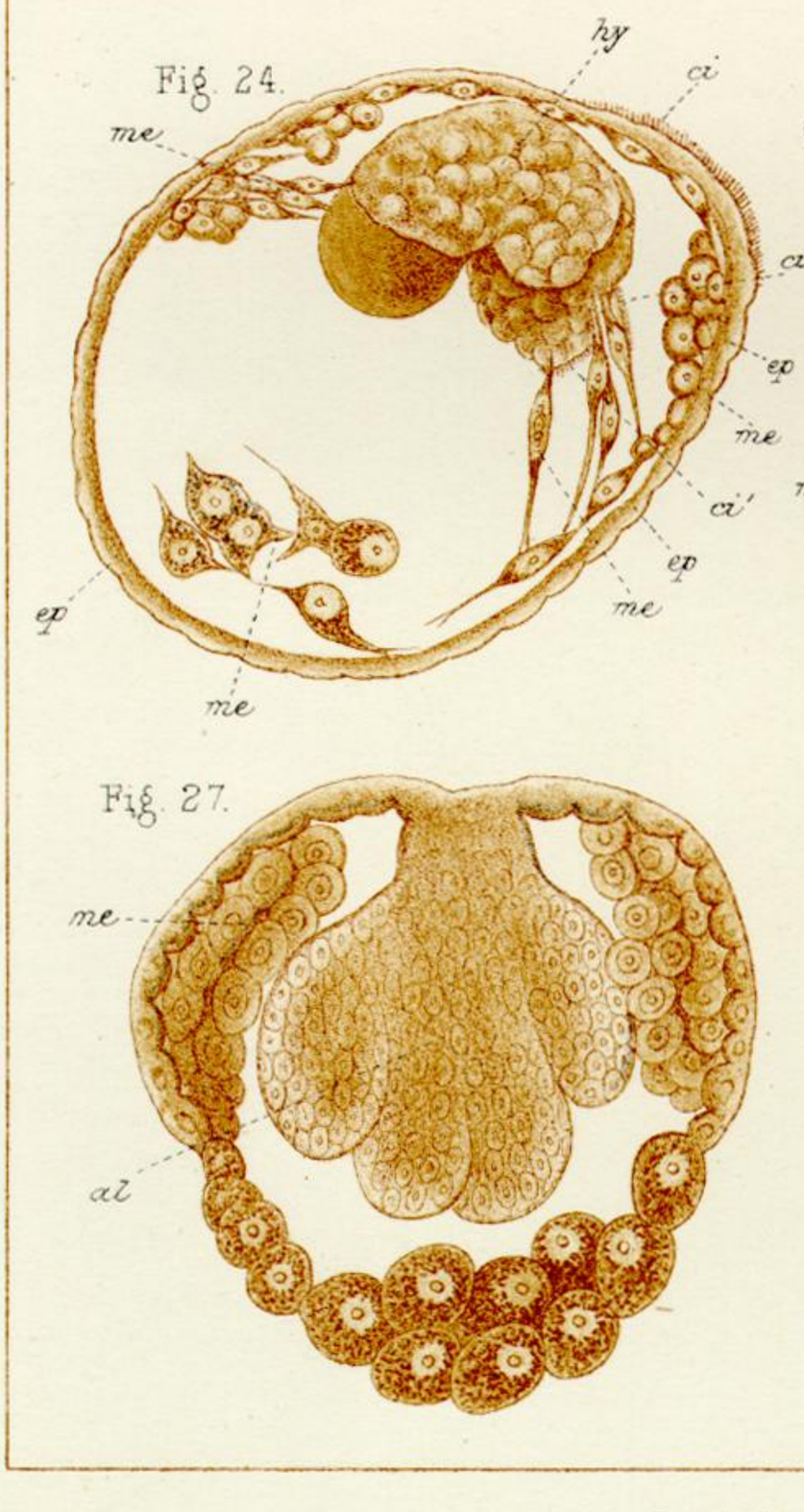

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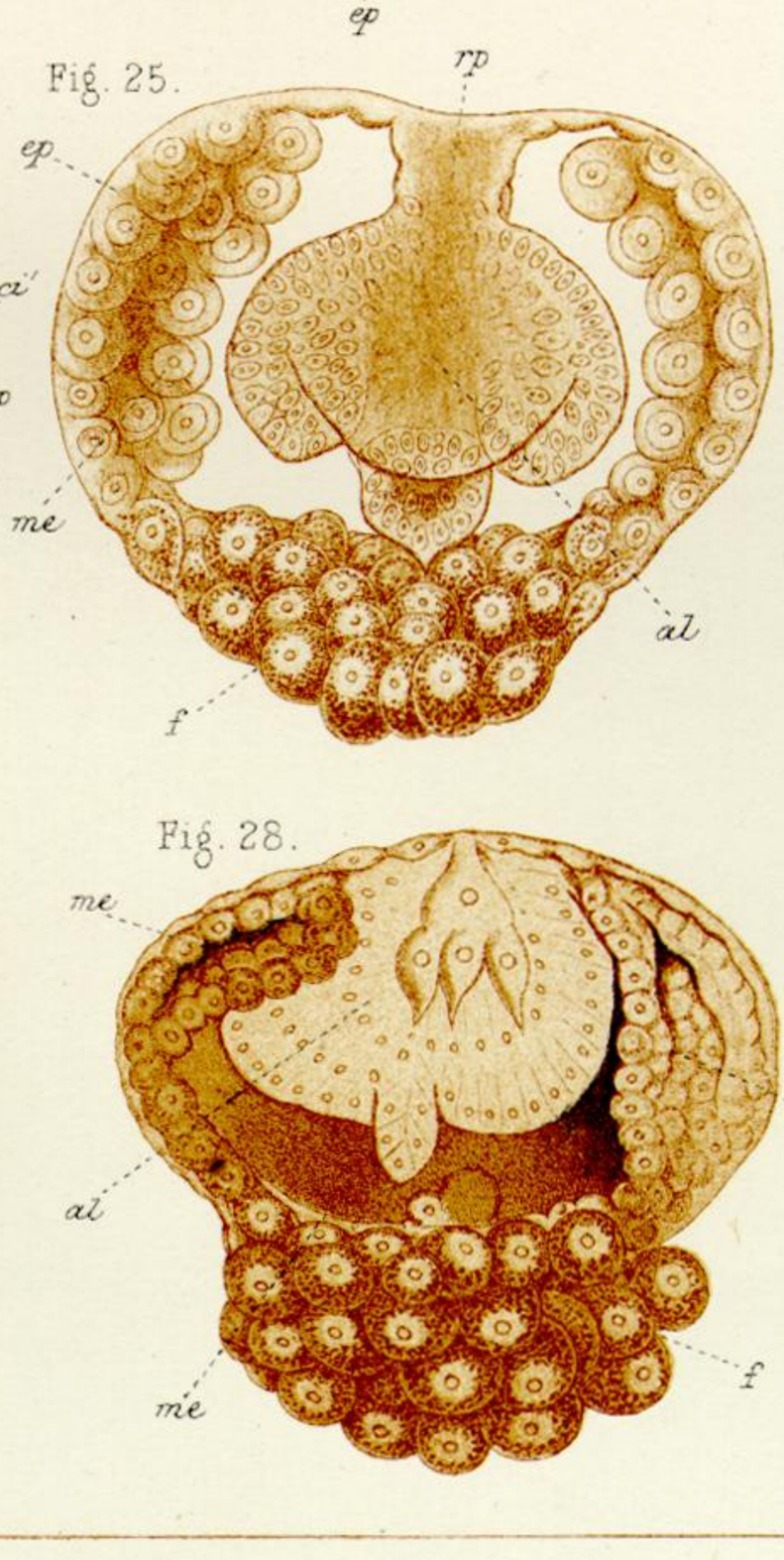

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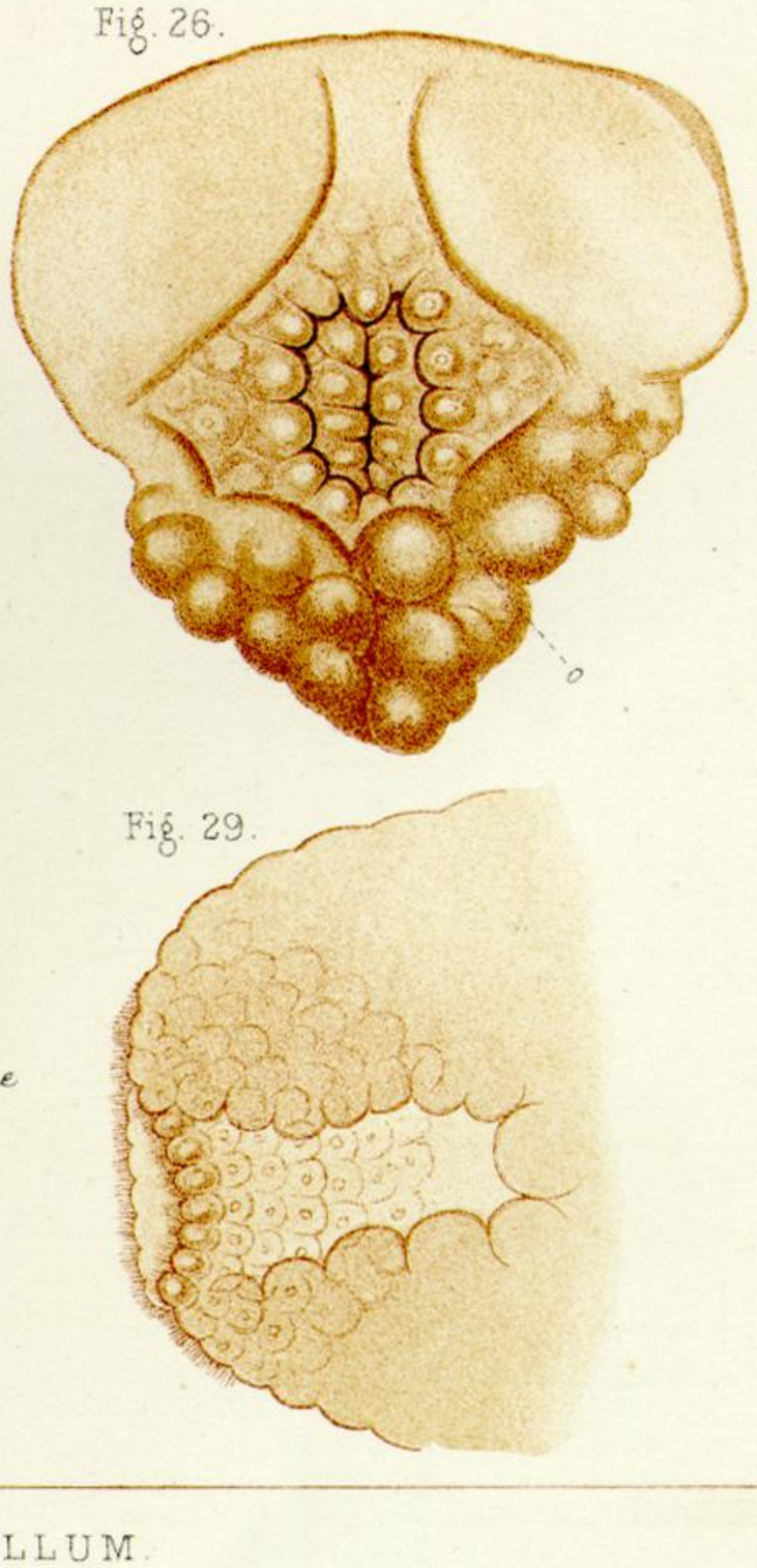

Fig. 27.

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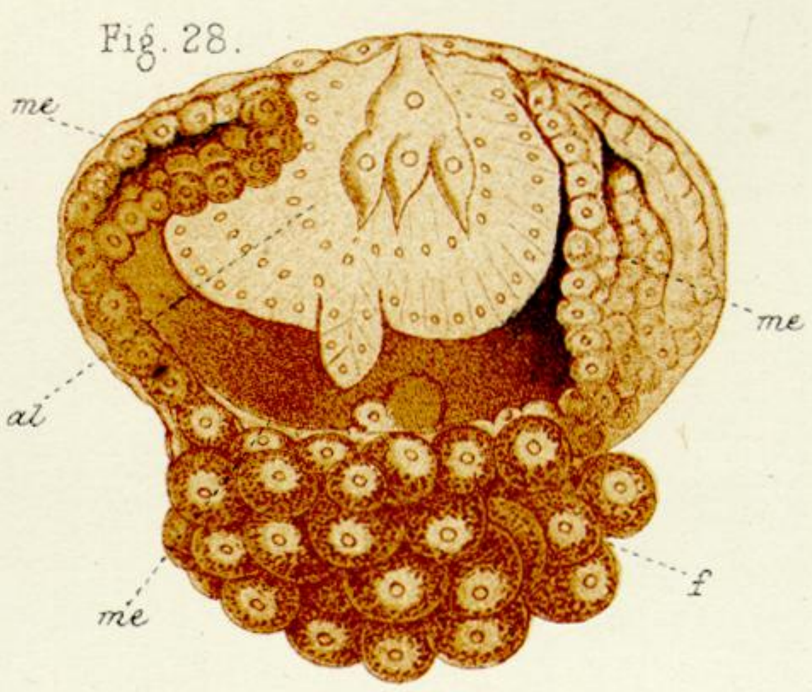
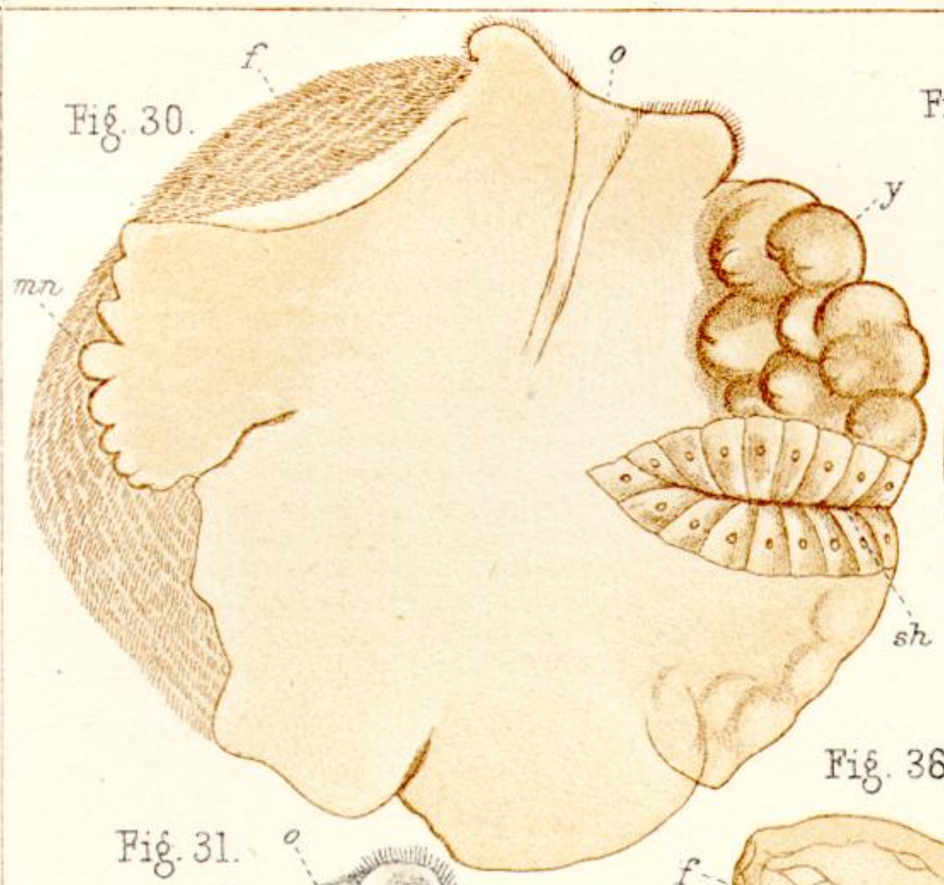


Fig. 29.

DEVELOPMENT OF PISIDIUM PUSILLUM.

Fig. 30.



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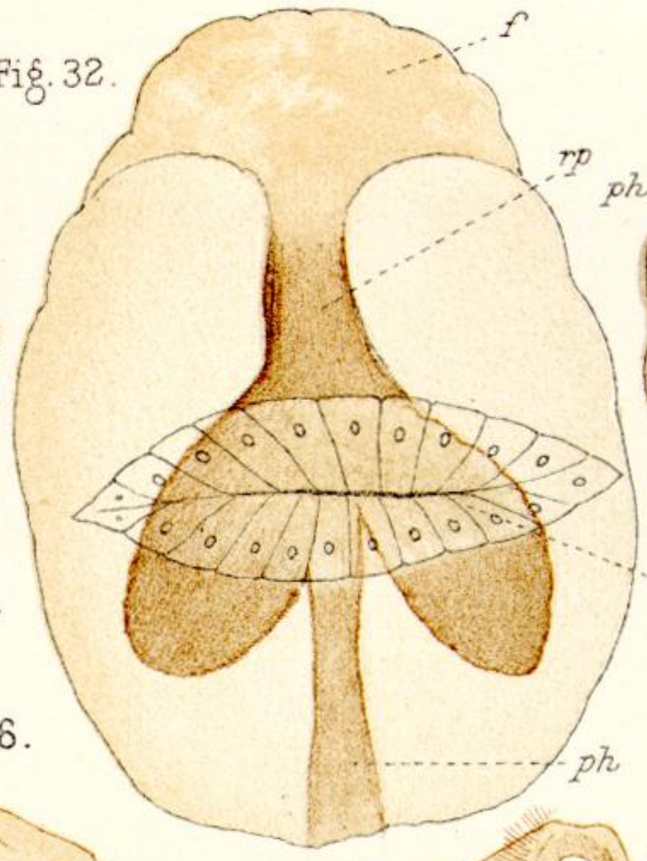

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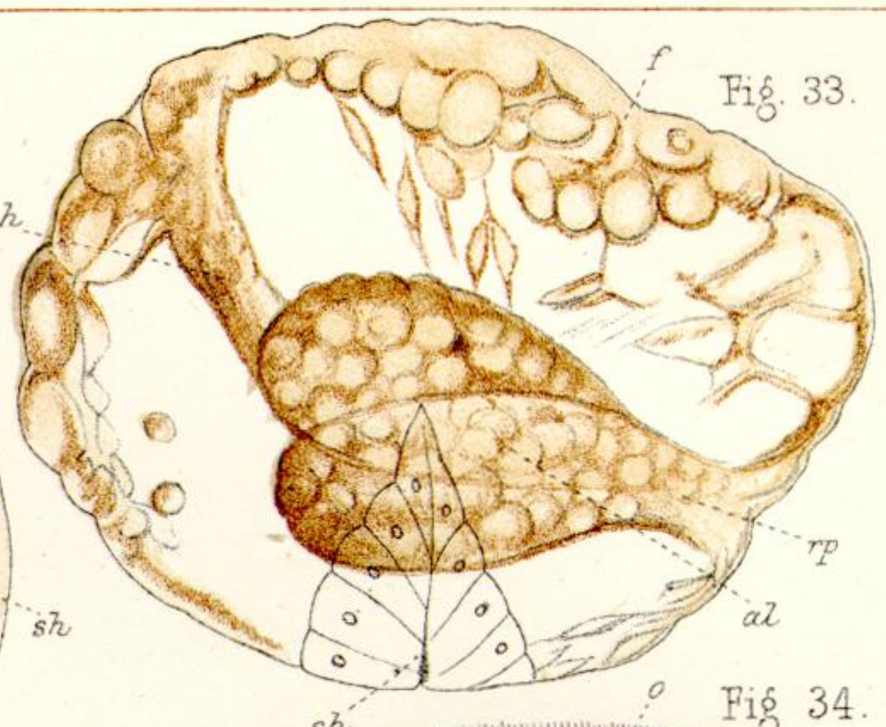

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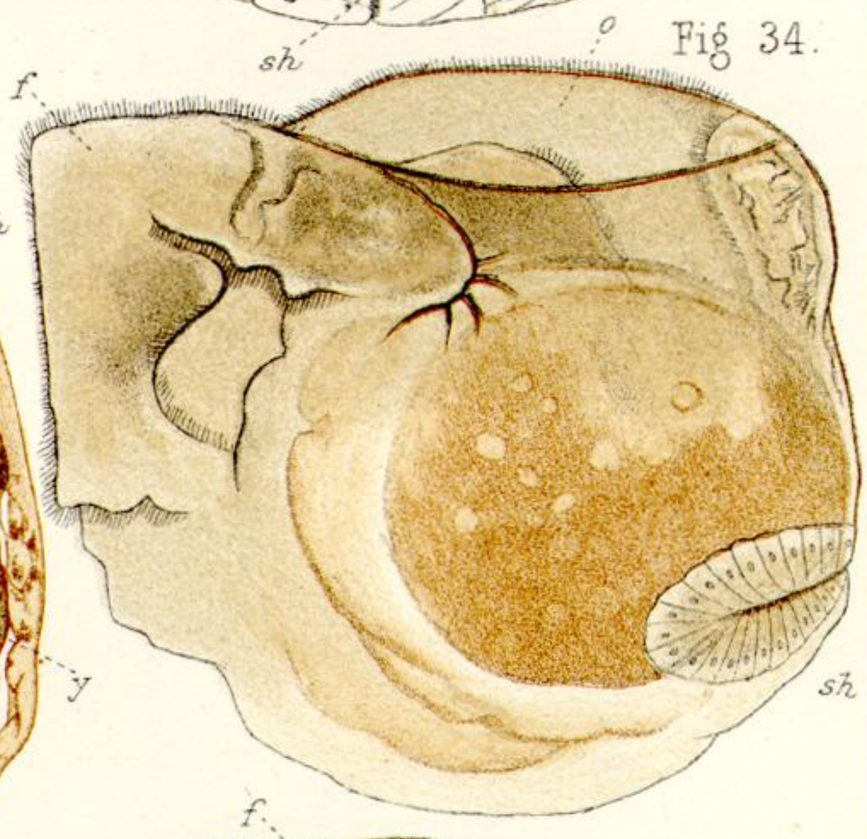
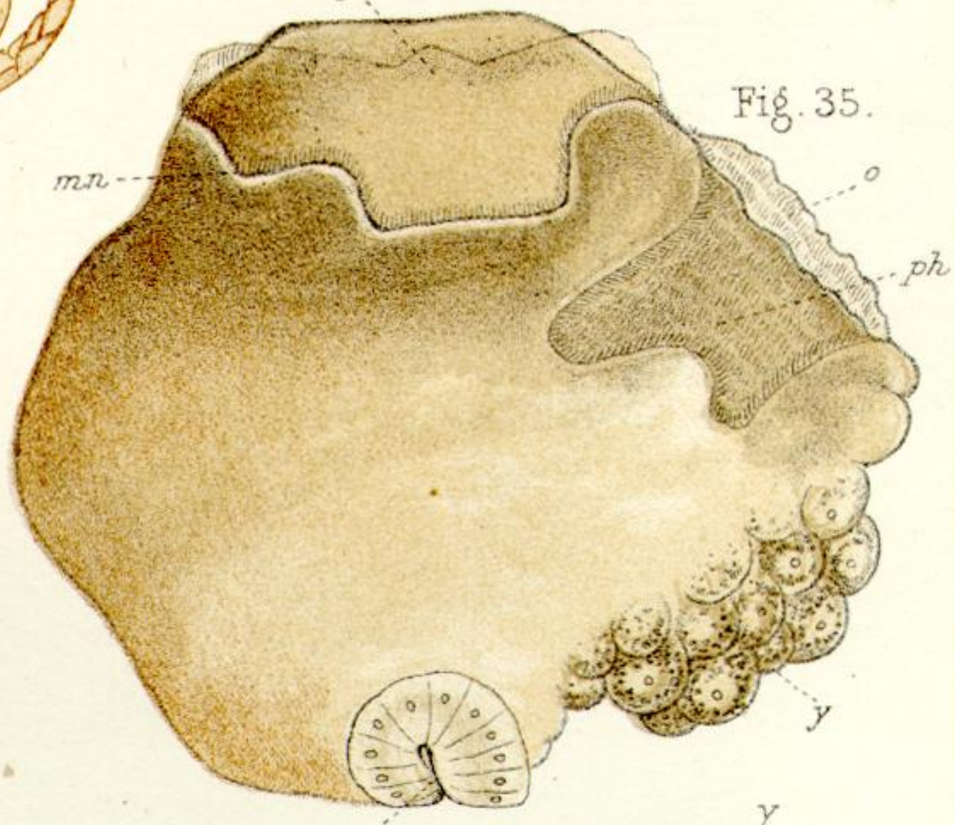


Fig. 31.

Fig. 36.

Fig. 35.



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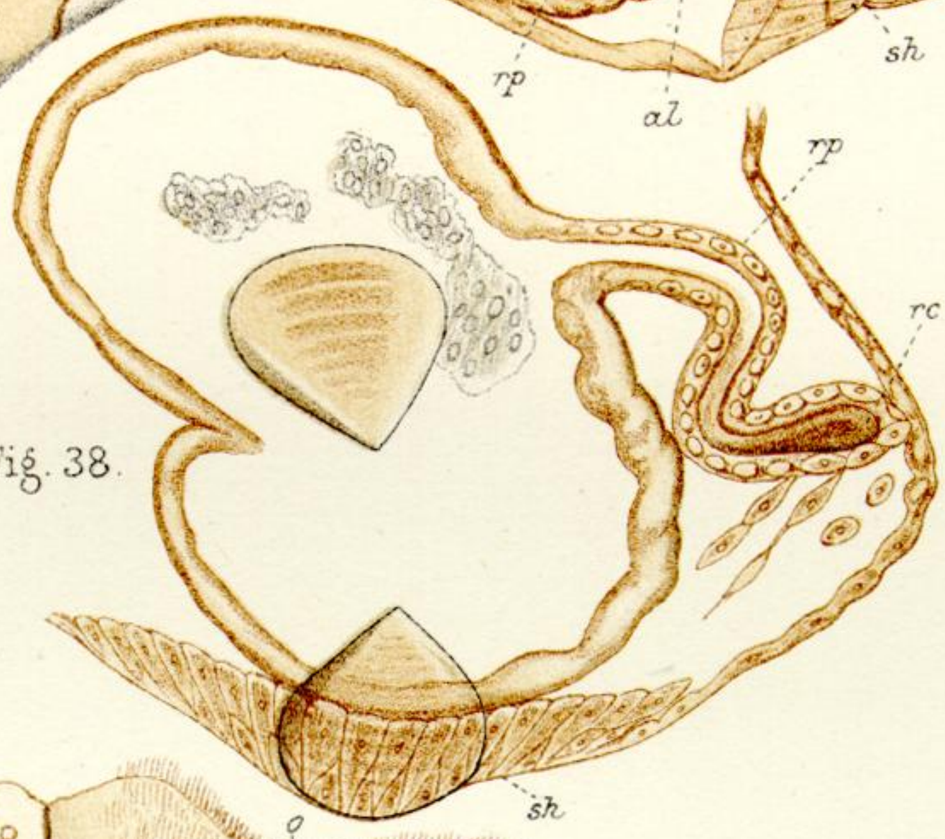


Fig. 35.a

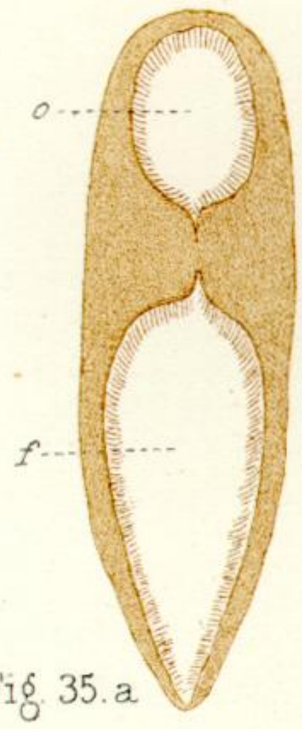


Fig. 37.

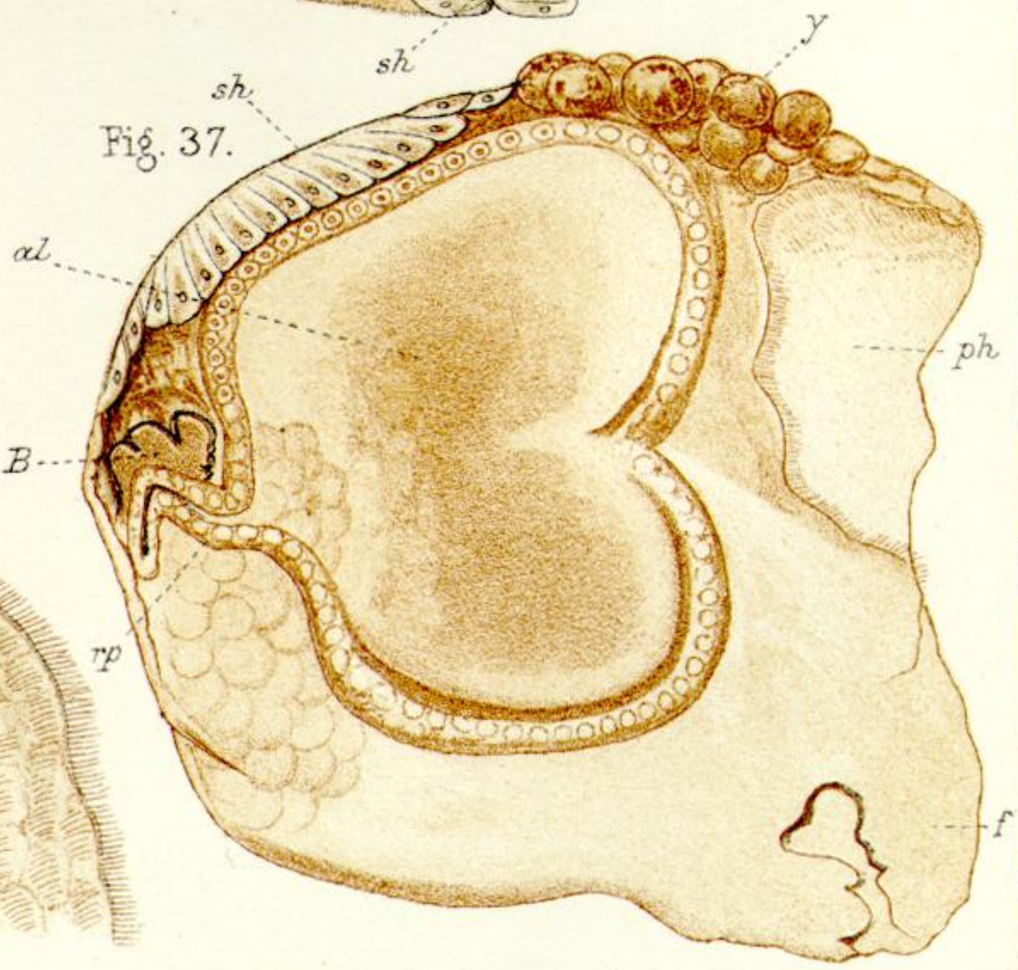
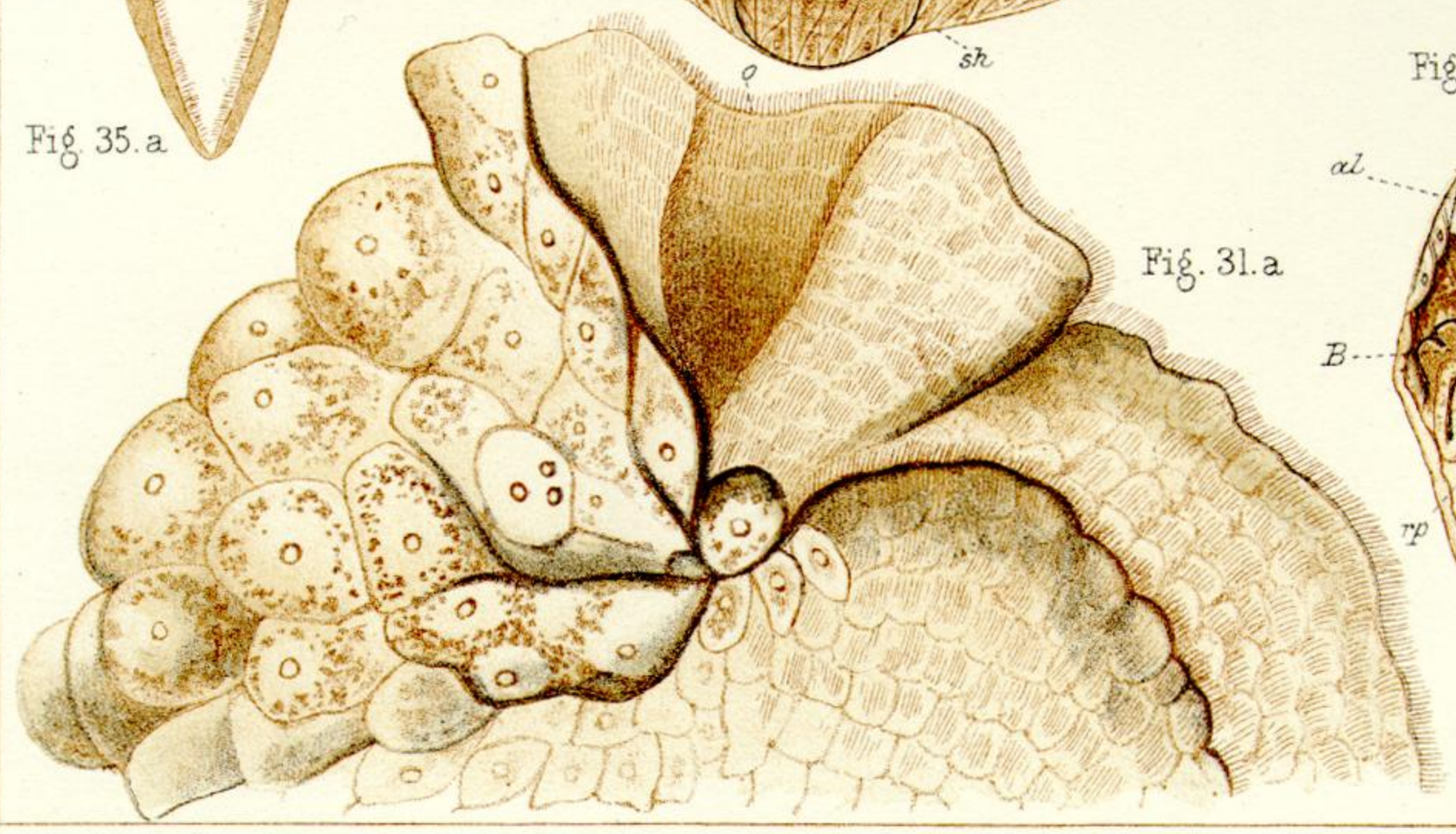
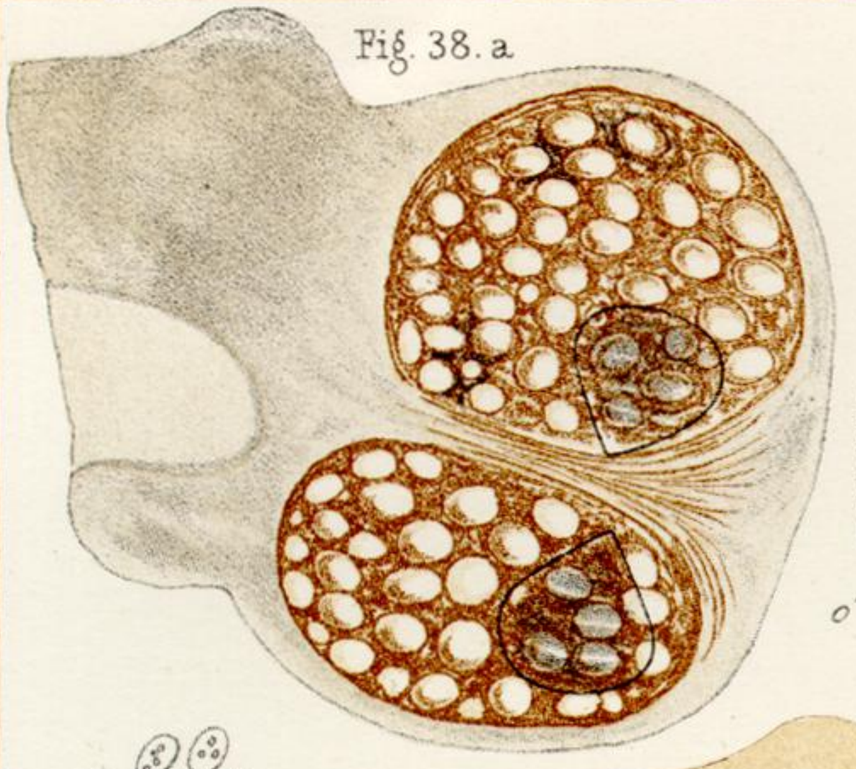


Fig. 31.a



DEVELOPMENT OF PISIDIUM PUSILLUM.

Fig. 38. a.



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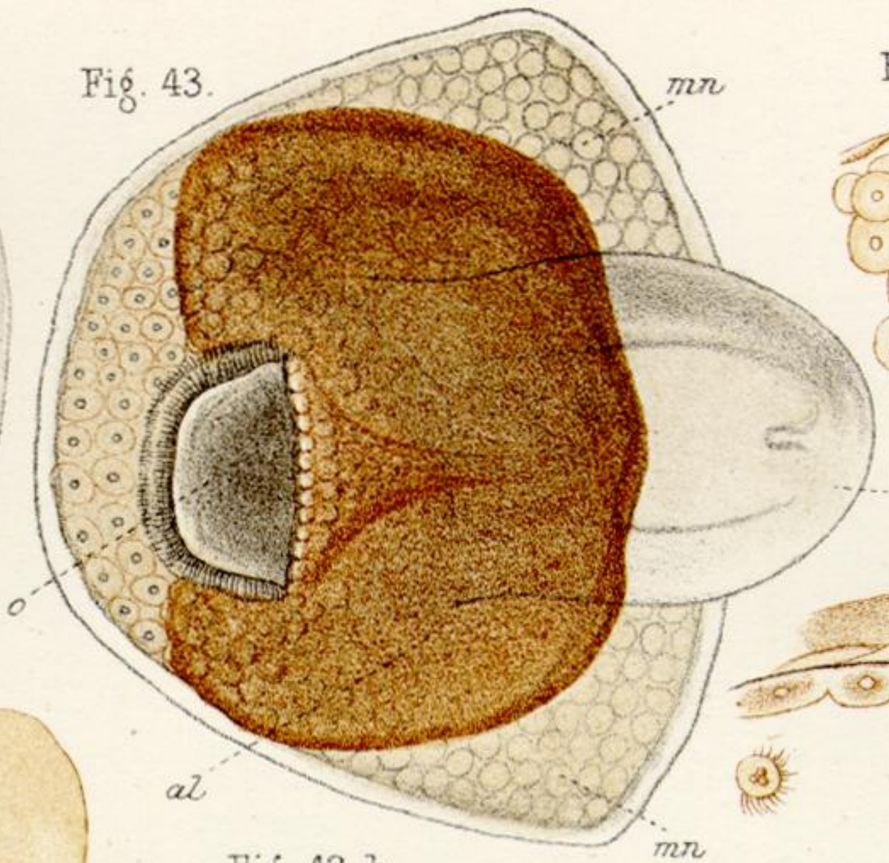


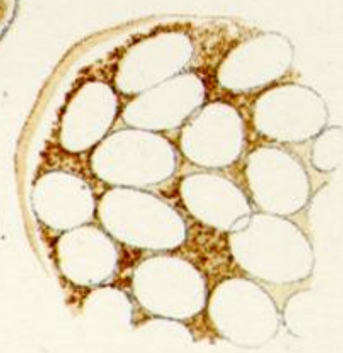
Fig. 44.

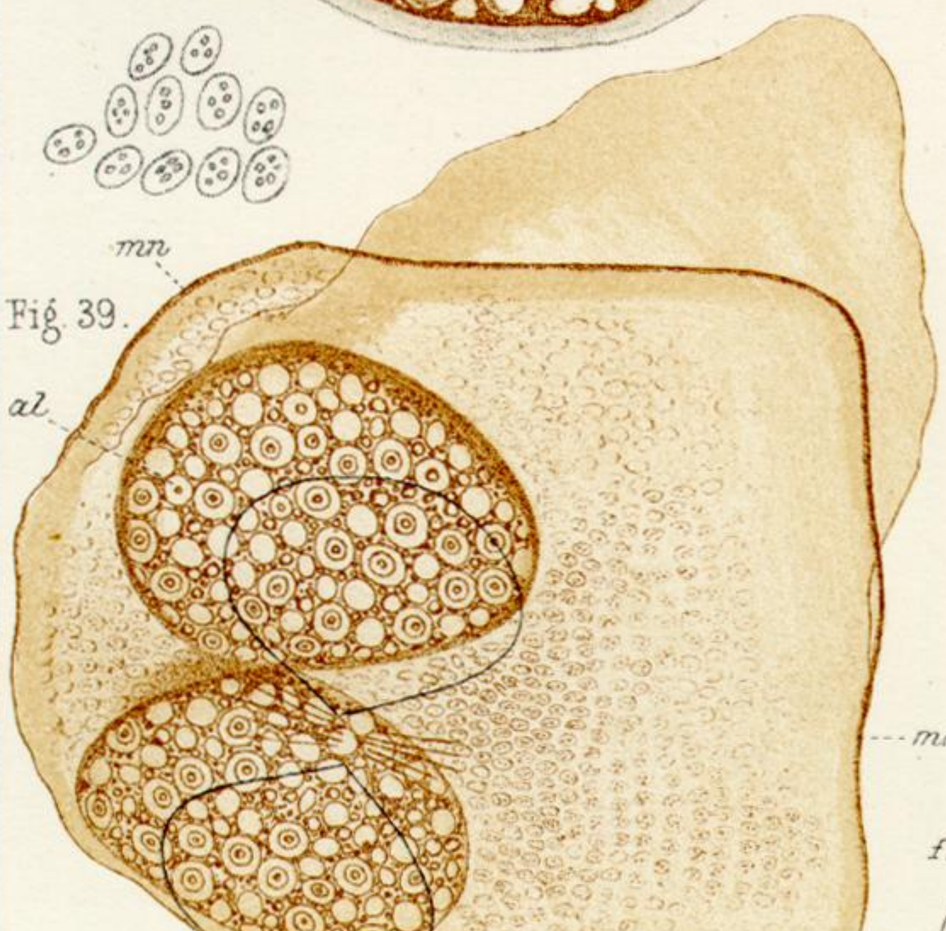
ep

Fig. 45.

Fig. 43. b.

Fig. 40.





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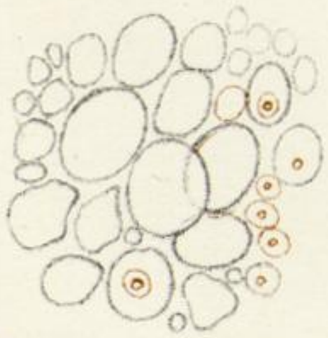

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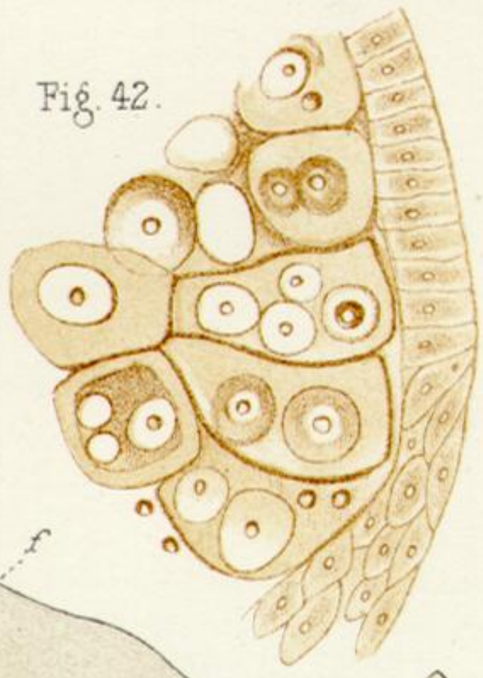

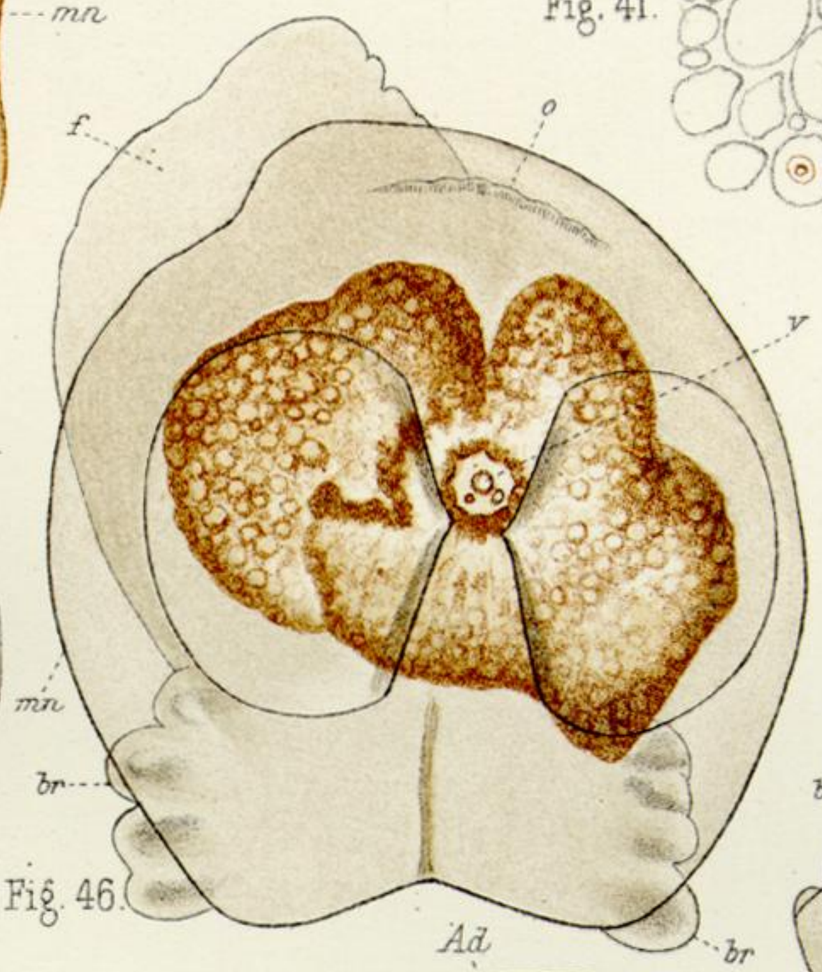

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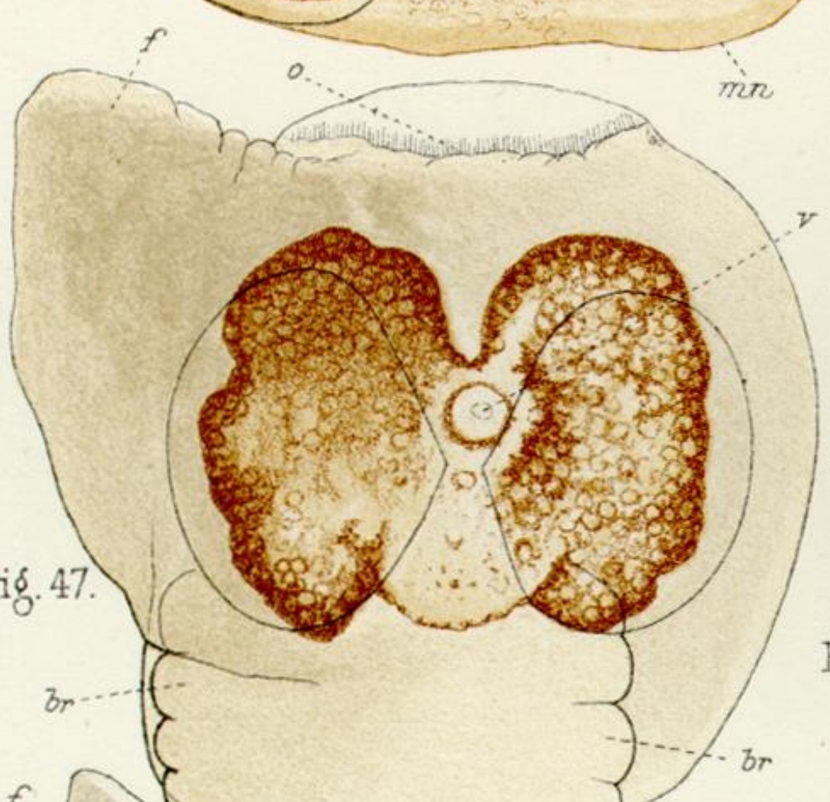


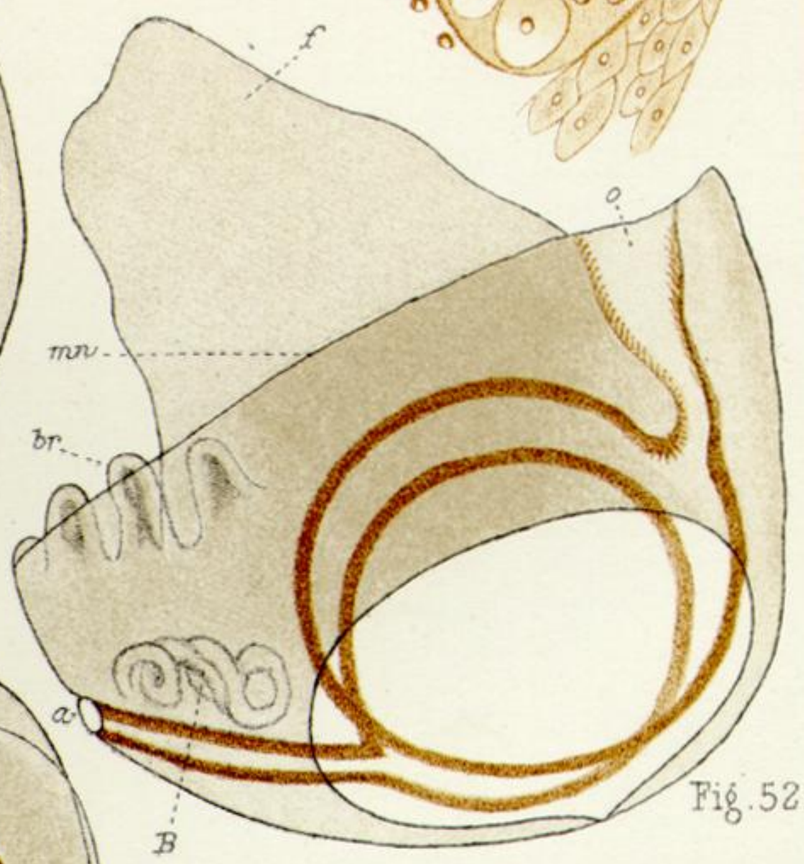
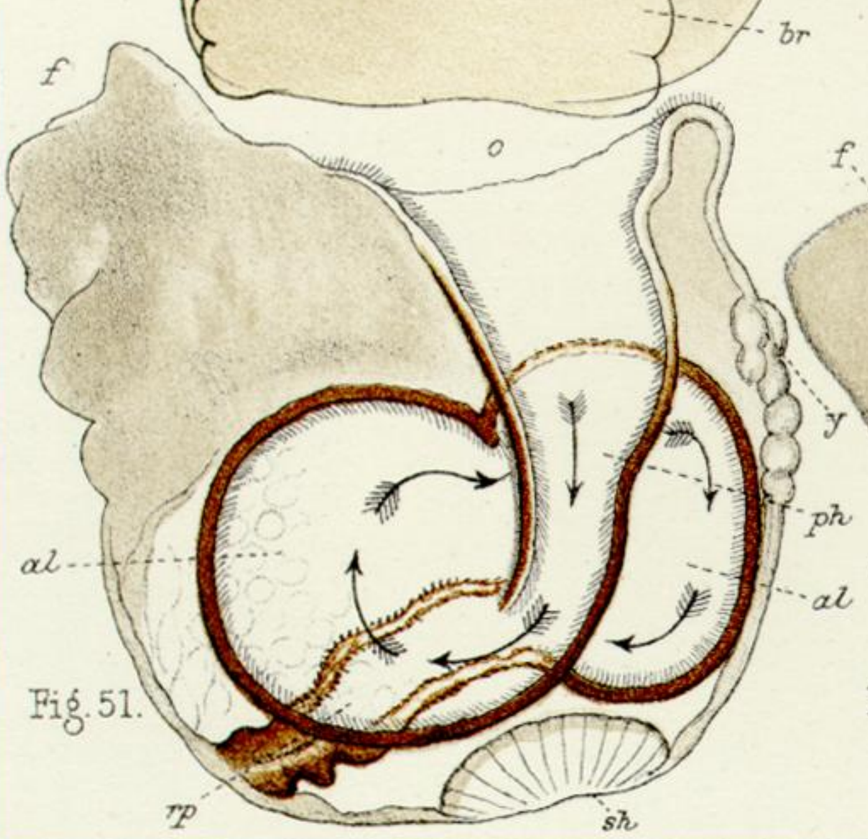


Fig. 52.

Fig. 46.

Ad

Fig. 50.



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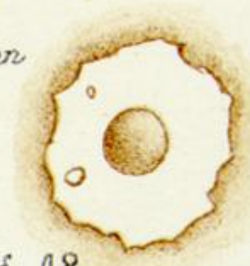

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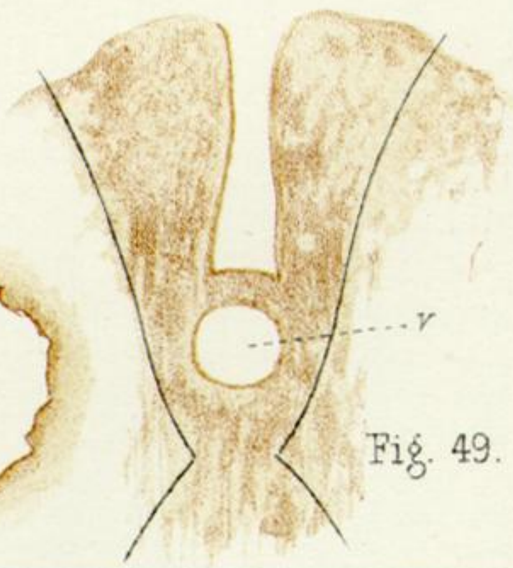


Fig. 49.

DEVELOPMENT OF PISIDIUM PUSILLUM.

Fig. 1.

Fig. 3.

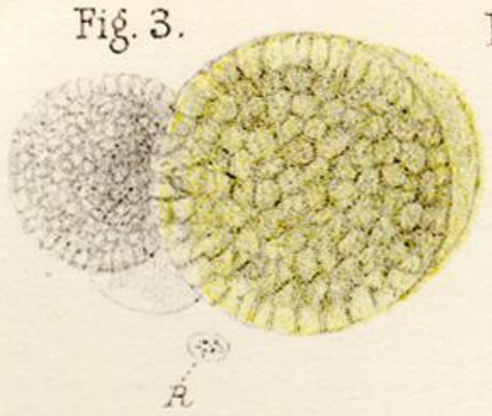


Fig. 4.

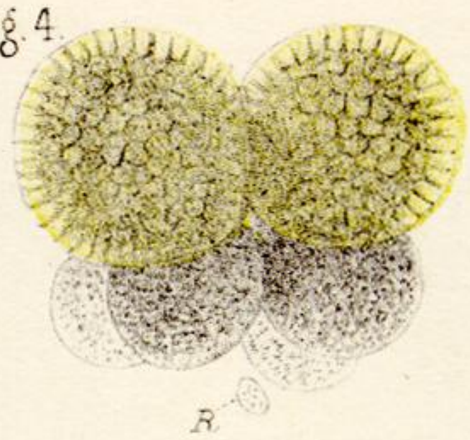


Fig. 5.

Fig. 6.

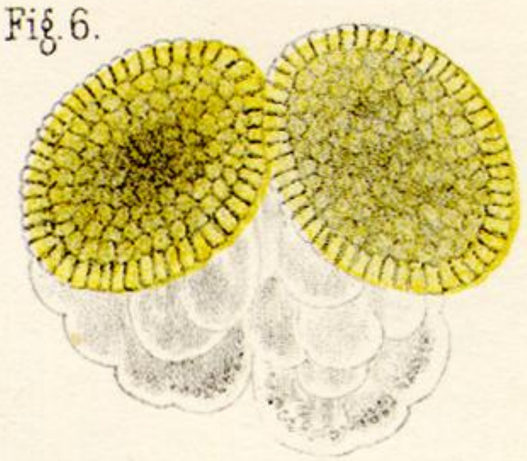


Fig. 2.

Fig. 7.

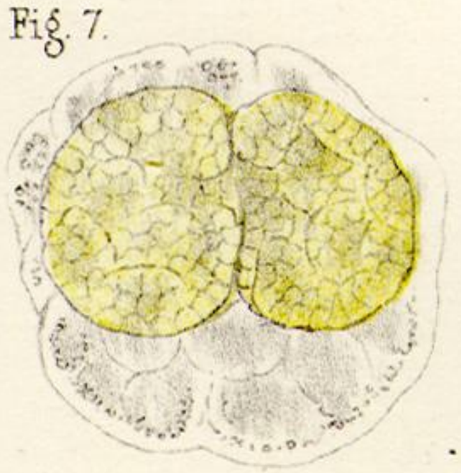
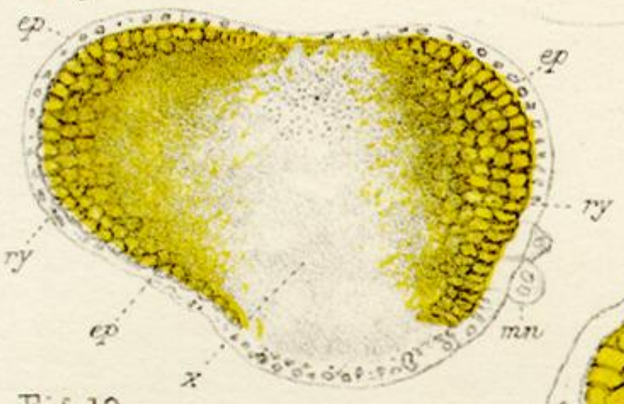


Fig. 8.

Fig. 9.



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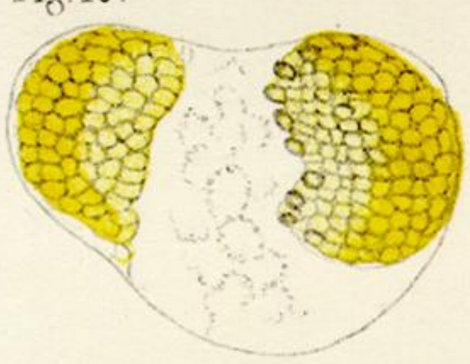

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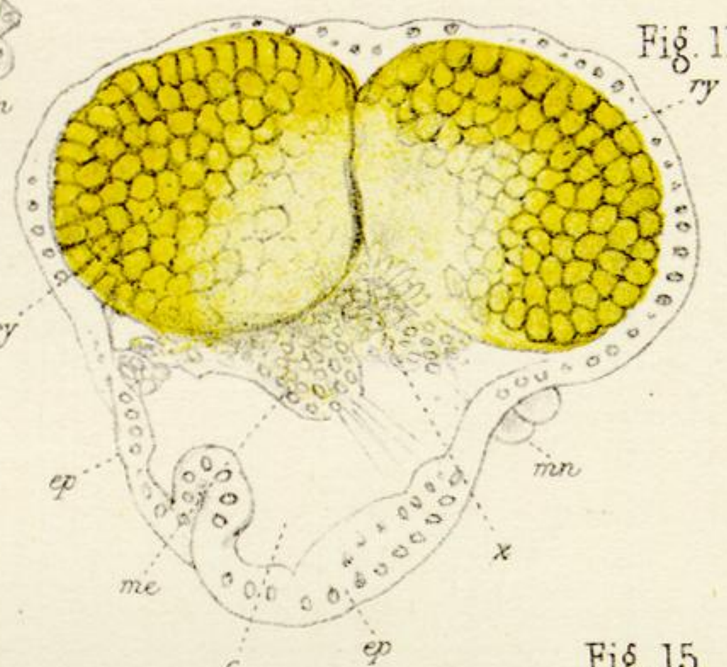
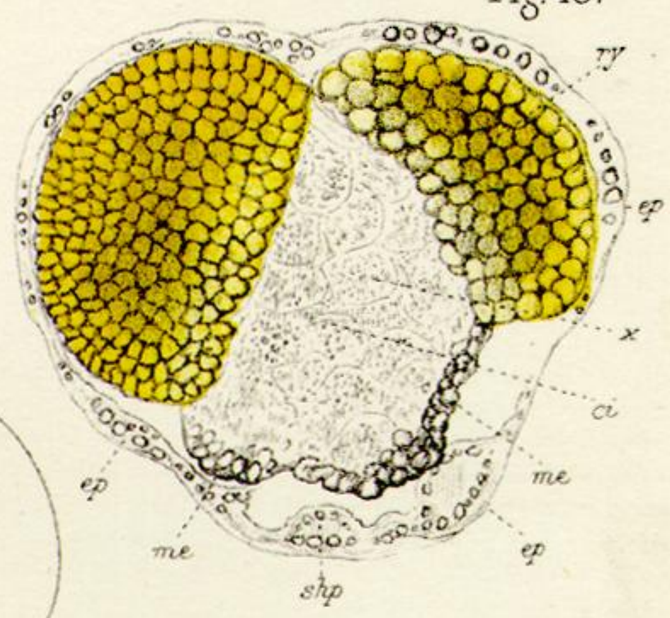


Fig. 1a.

Fig. 12.

Fig. 13.



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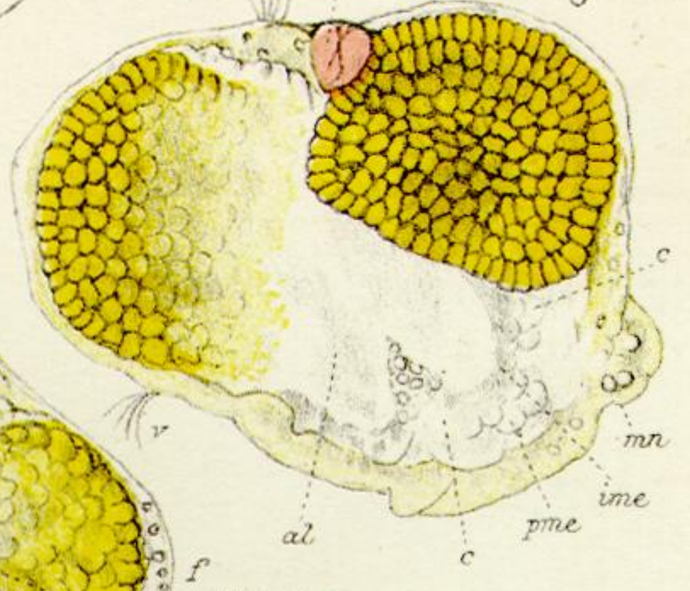

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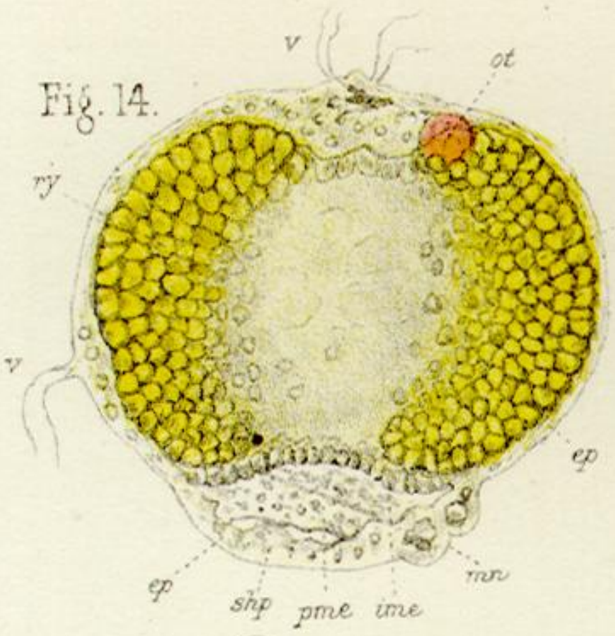

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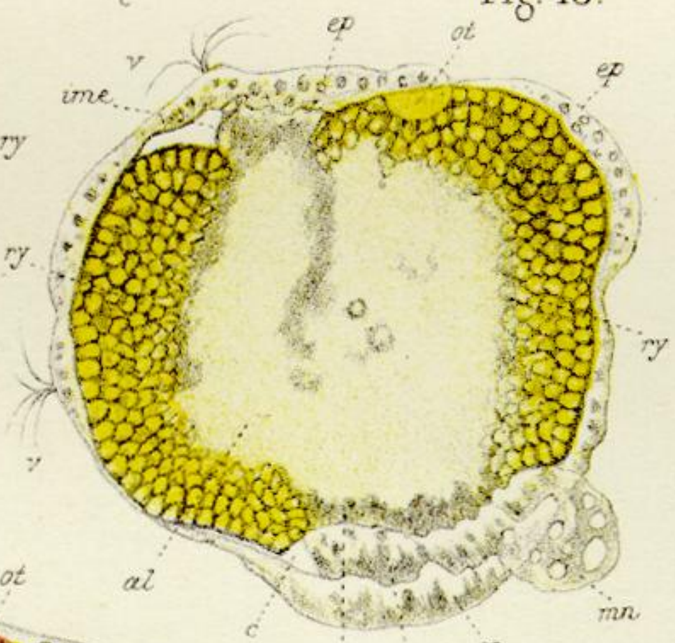

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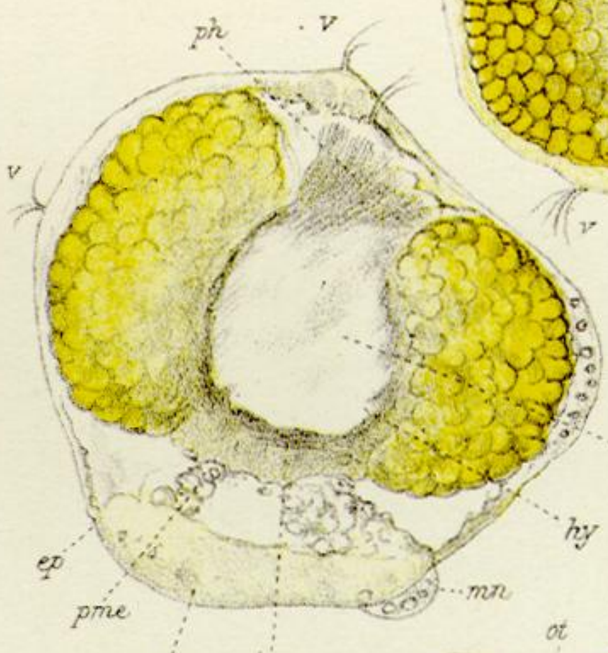

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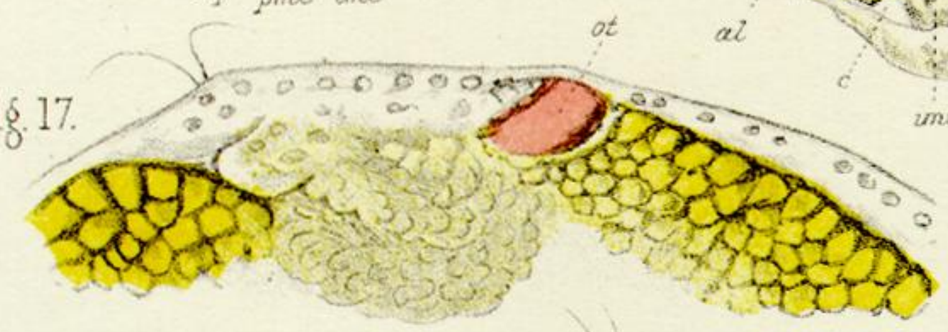
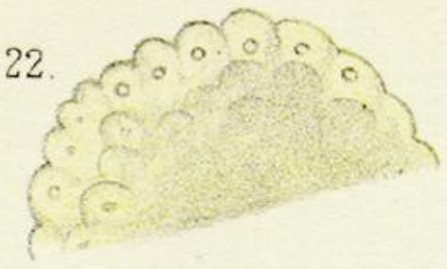


Fig. 18.

Fig. 21.

Fig. 22.



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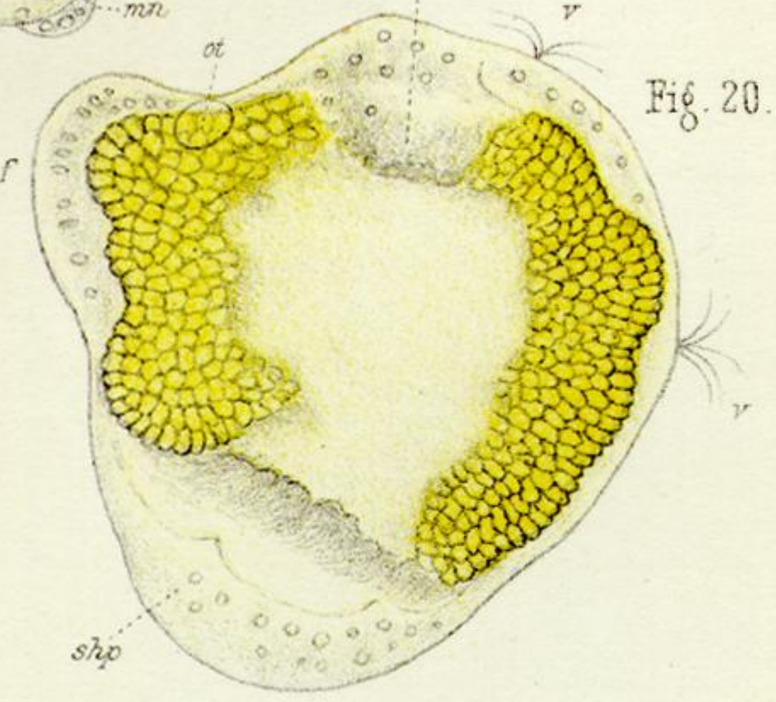
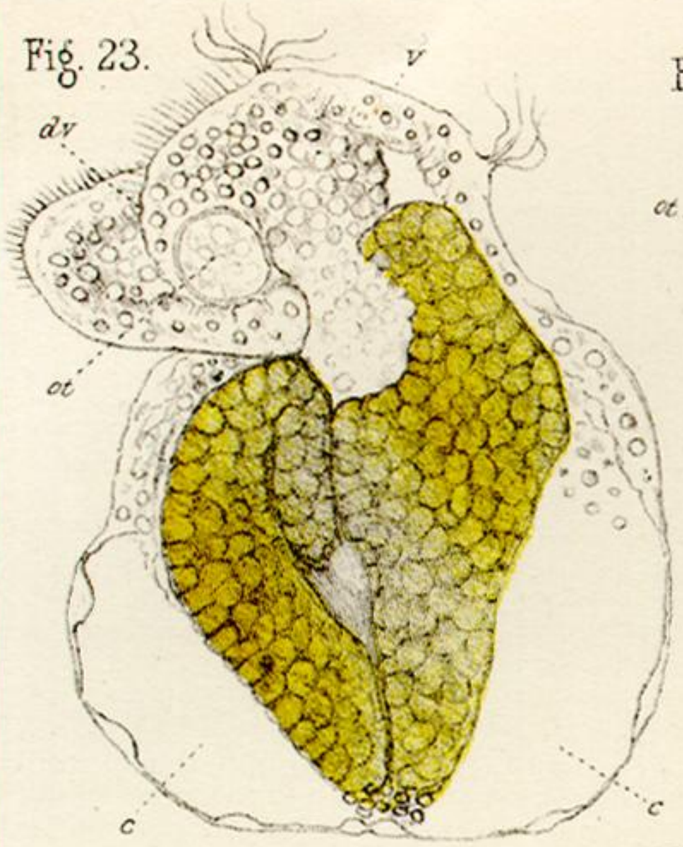


DEVELOPMENT OF APLYSIA DEPILANS.

Fig. 23.



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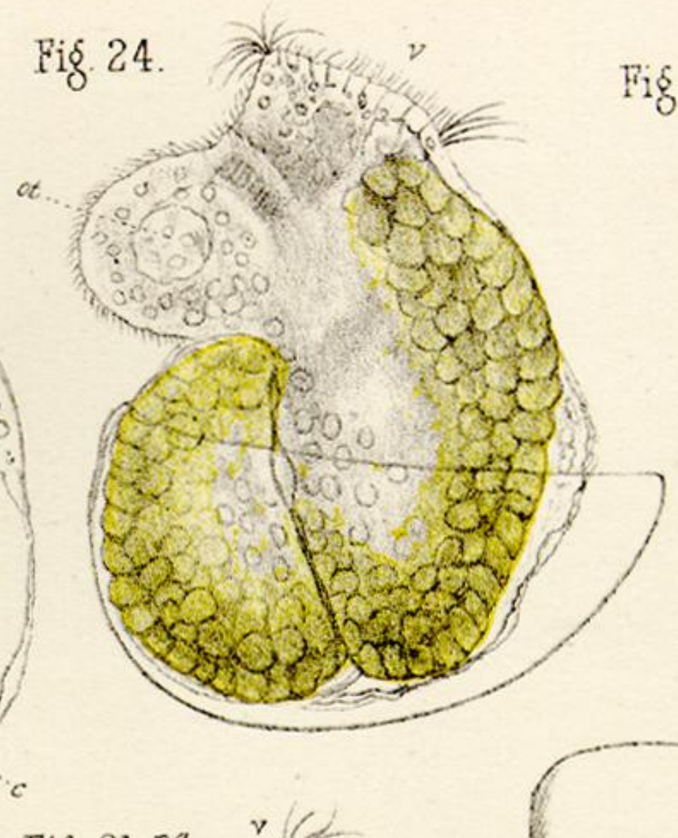

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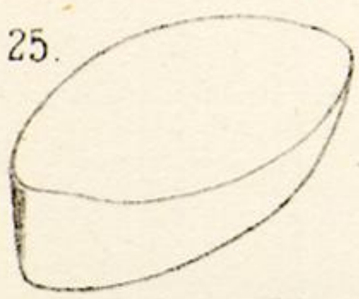

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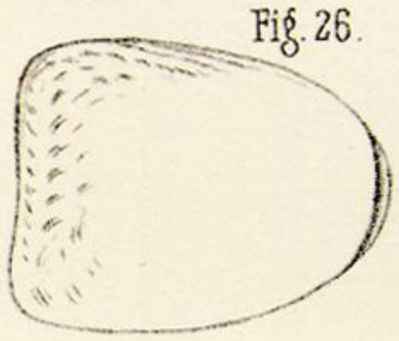

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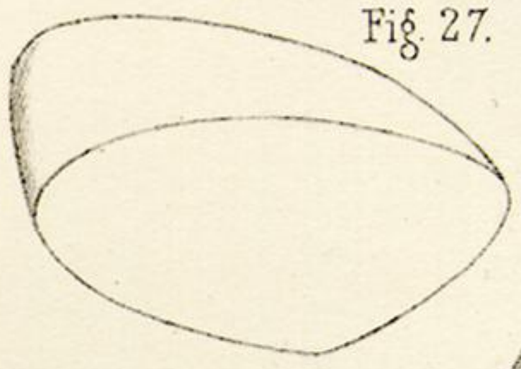


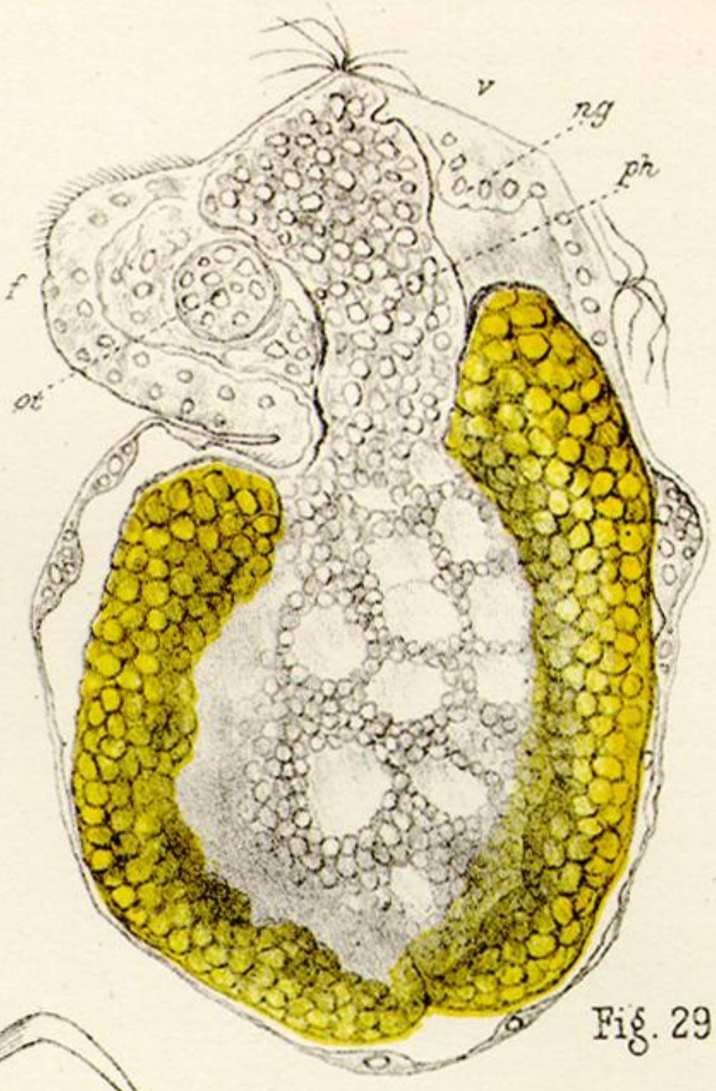
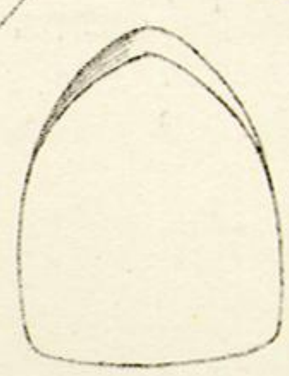


Fig. 29

Fig. 28.



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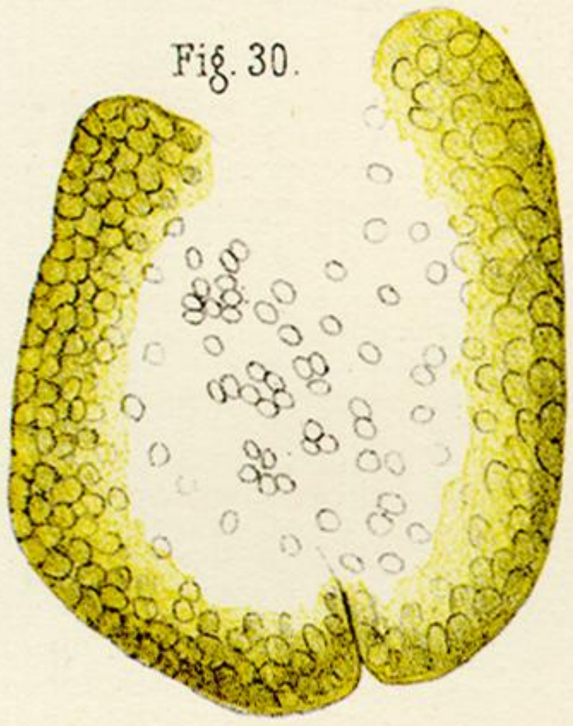

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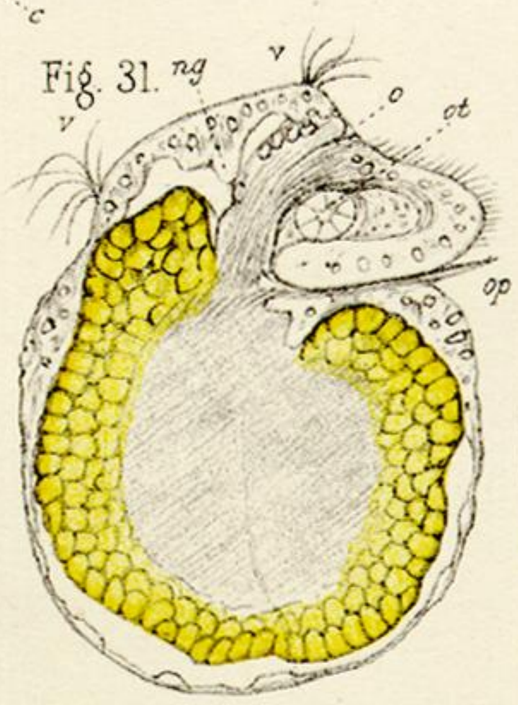

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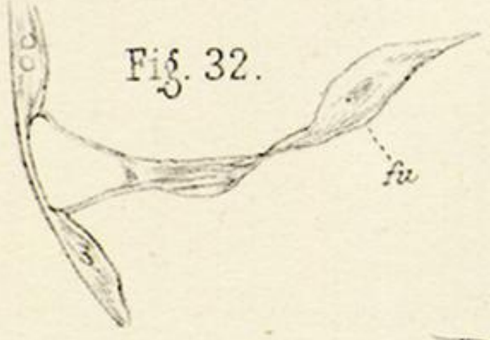

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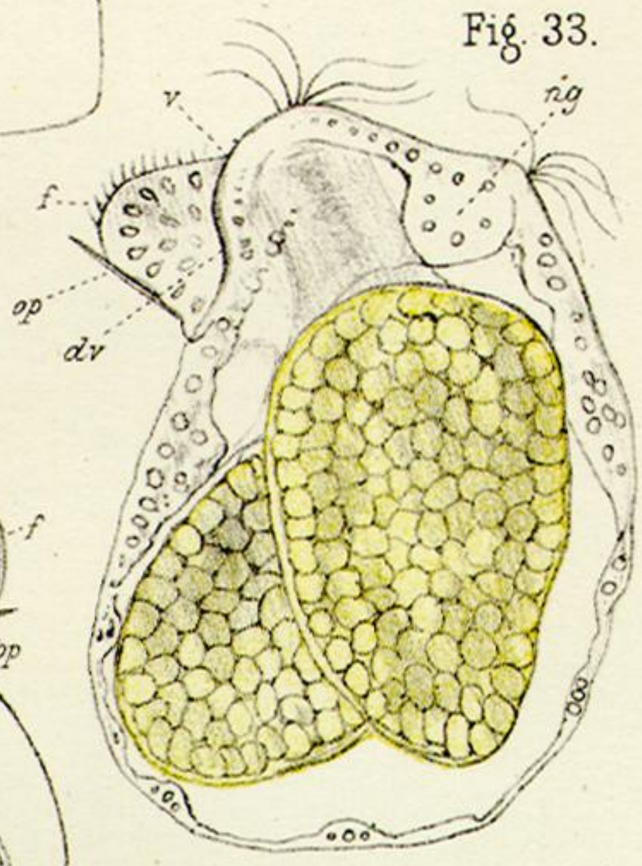

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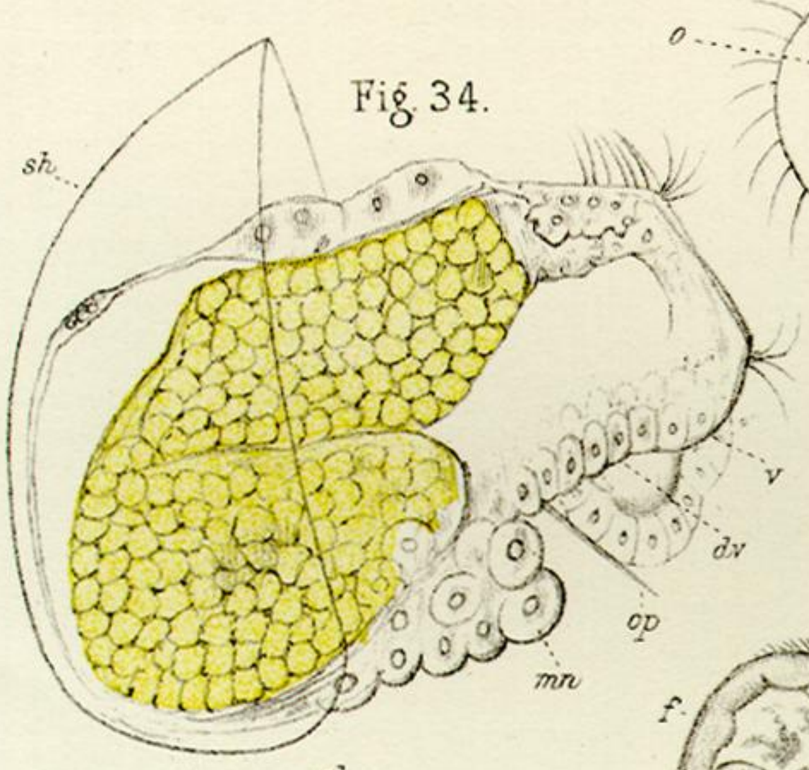
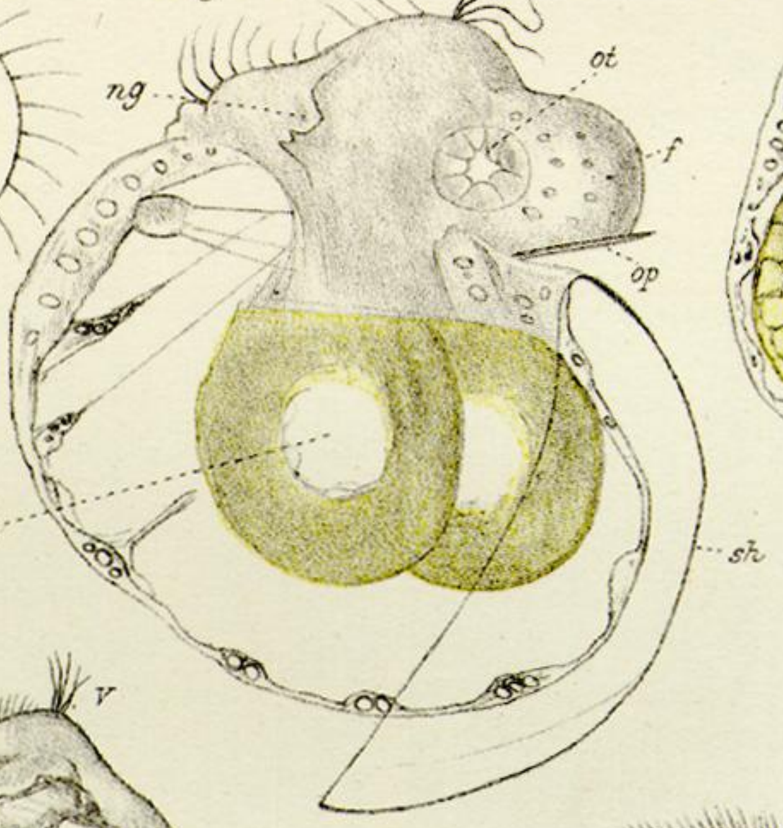
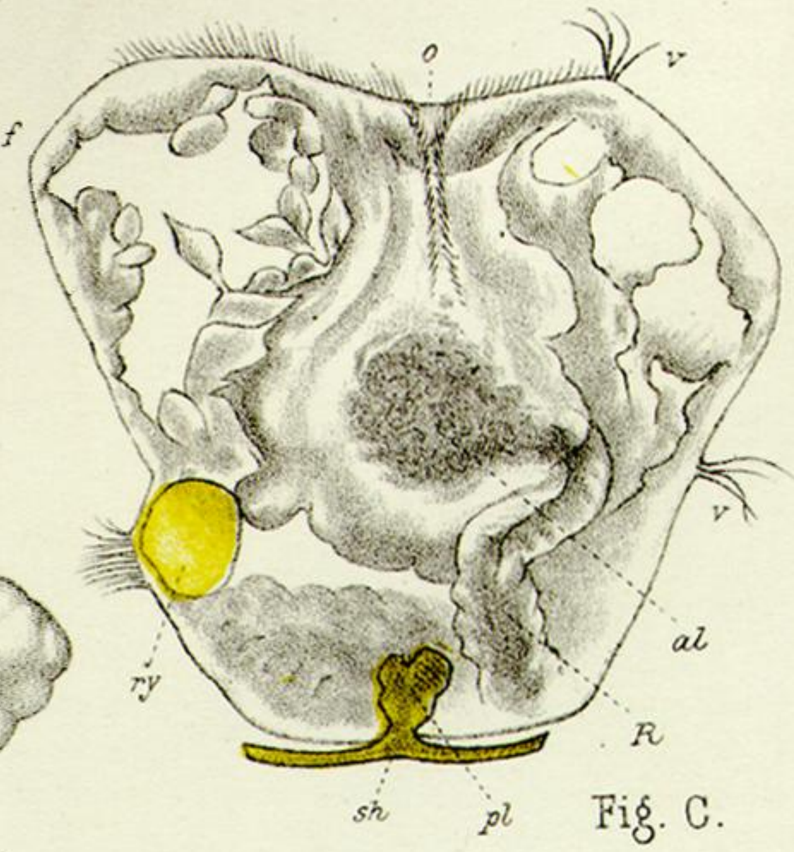


Fig. 35.

Fig. 36.





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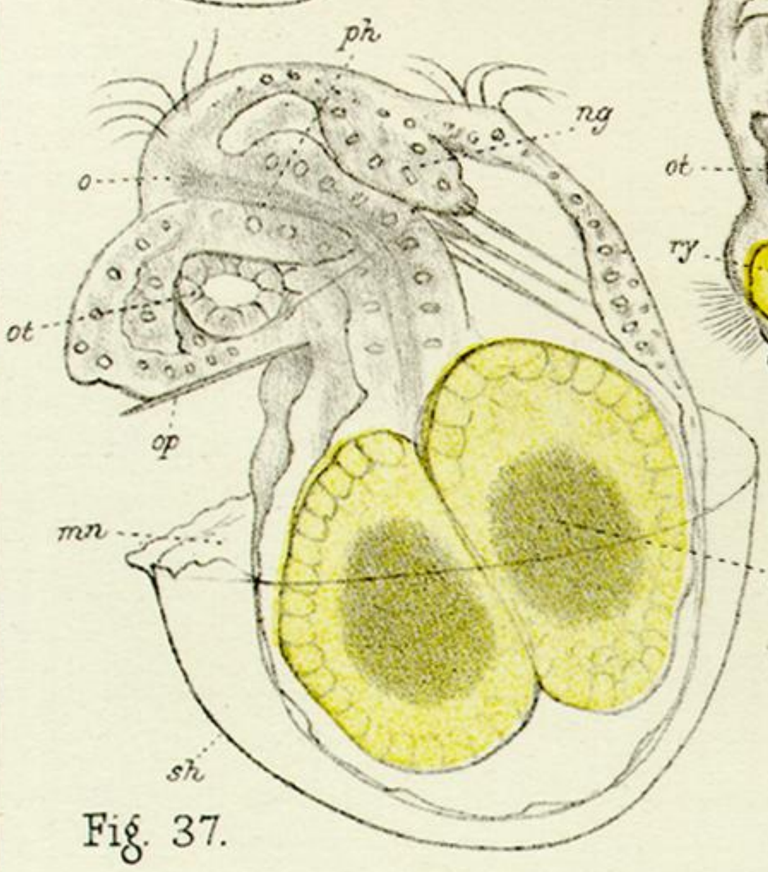


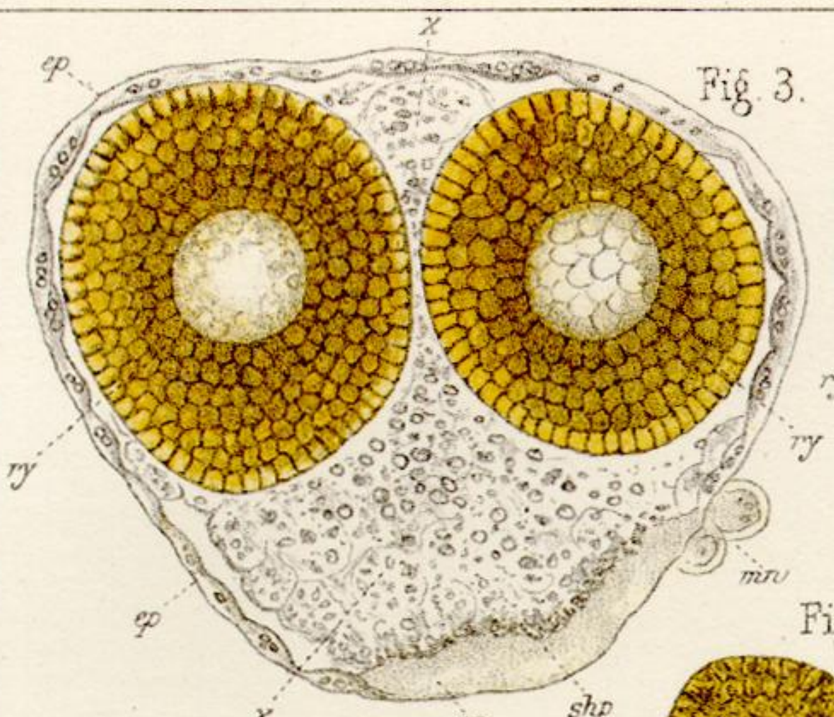
Fig. B.

Fig. A.

Fig. C.

23 - 37 APLYSIA. Figs A, B, C, PLEUROBRANCHIDIUM.

Fig. 3.



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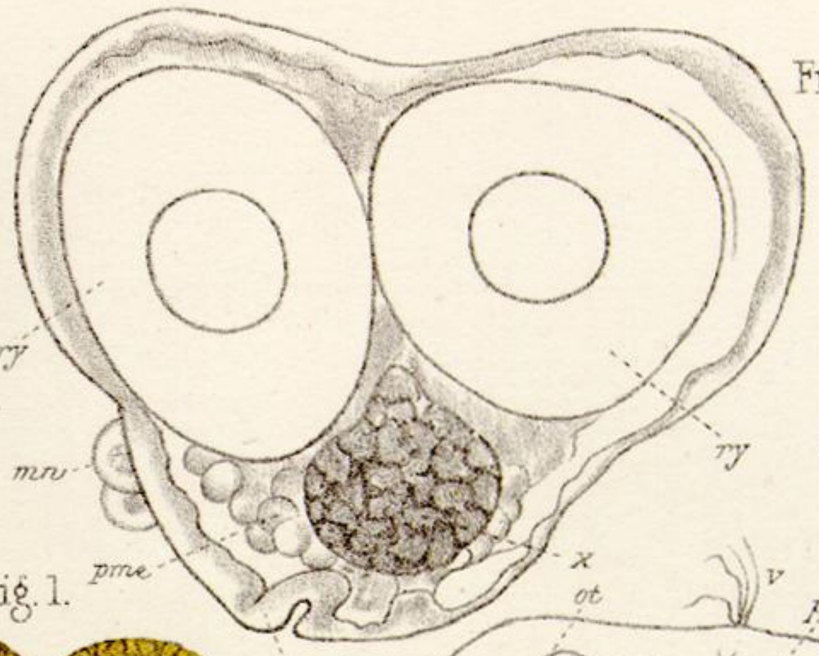
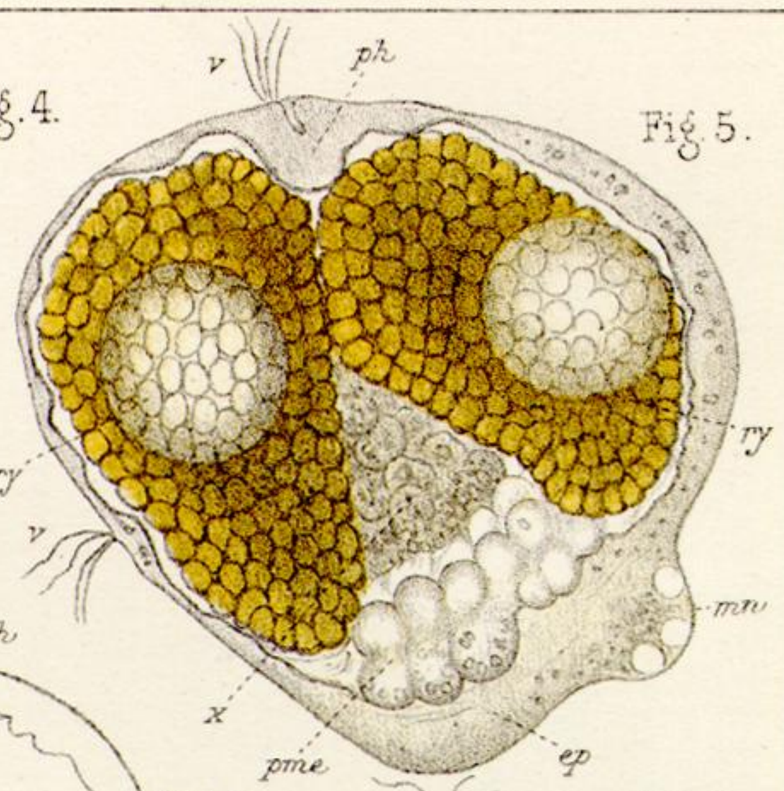


Fig. 4.

Fig. 5.



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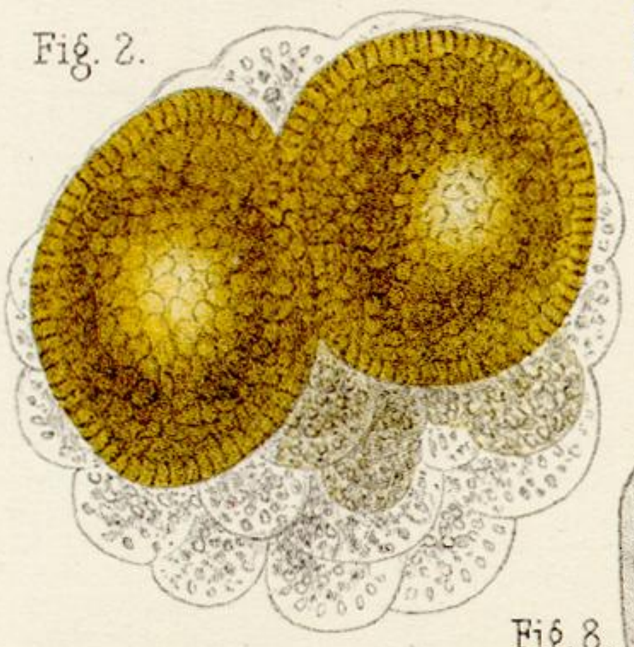


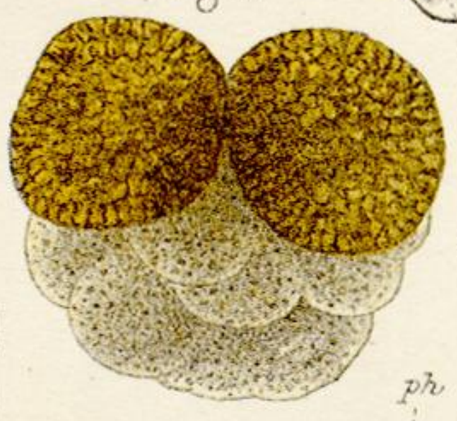


Fig. 8.

Fig. 10.

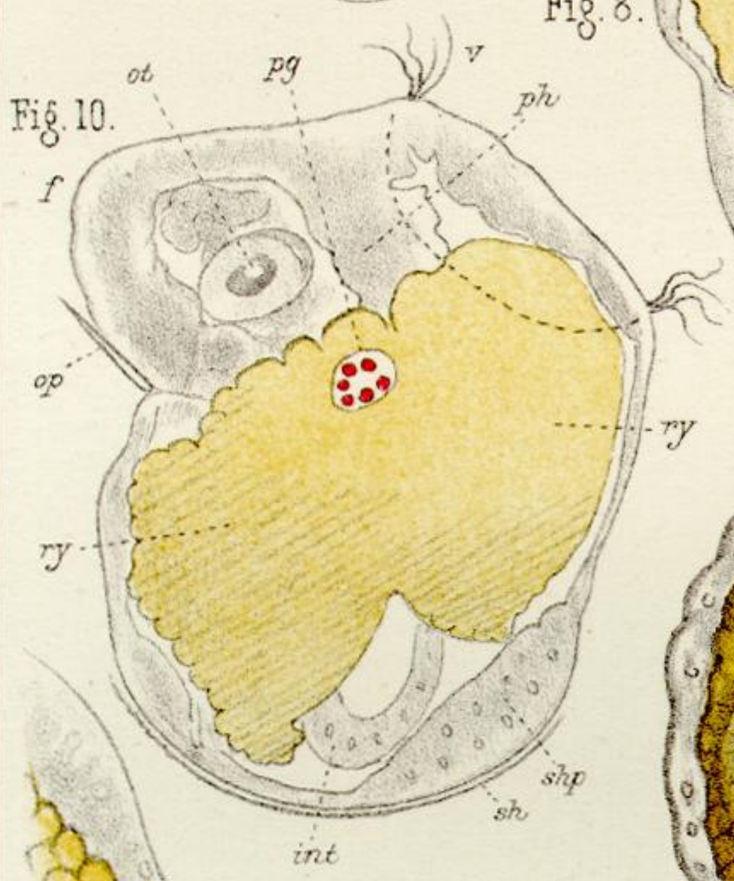
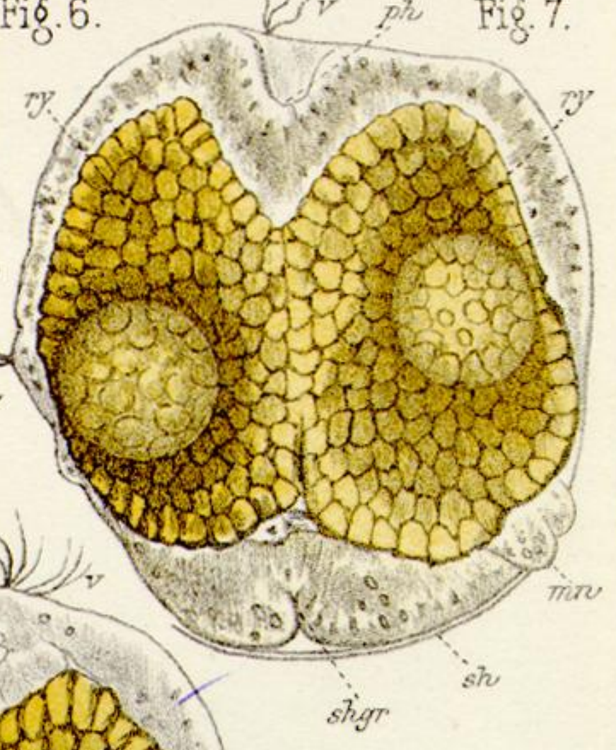


Fig. 6.

Fig. 7.



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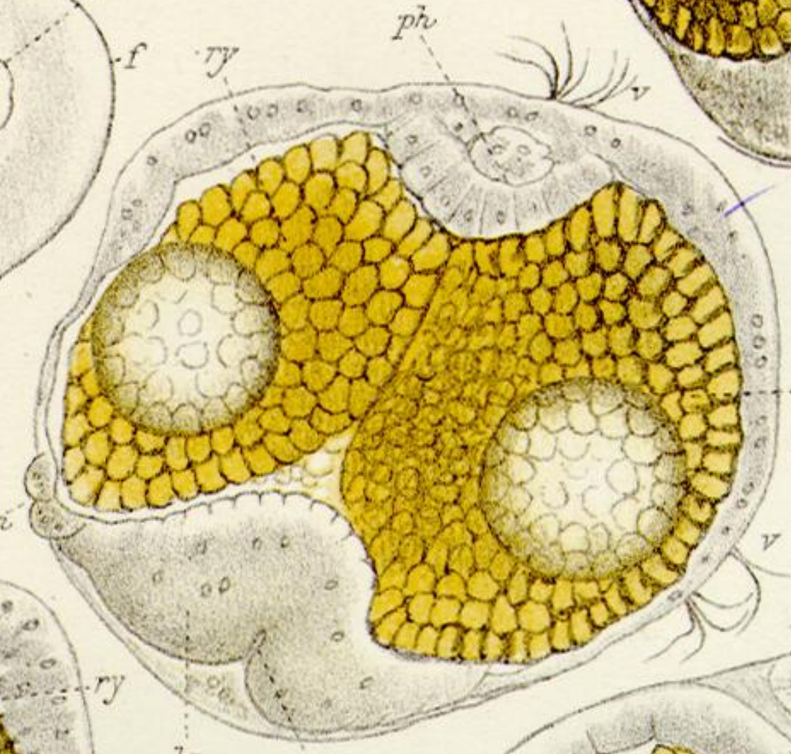


Fig. 11.

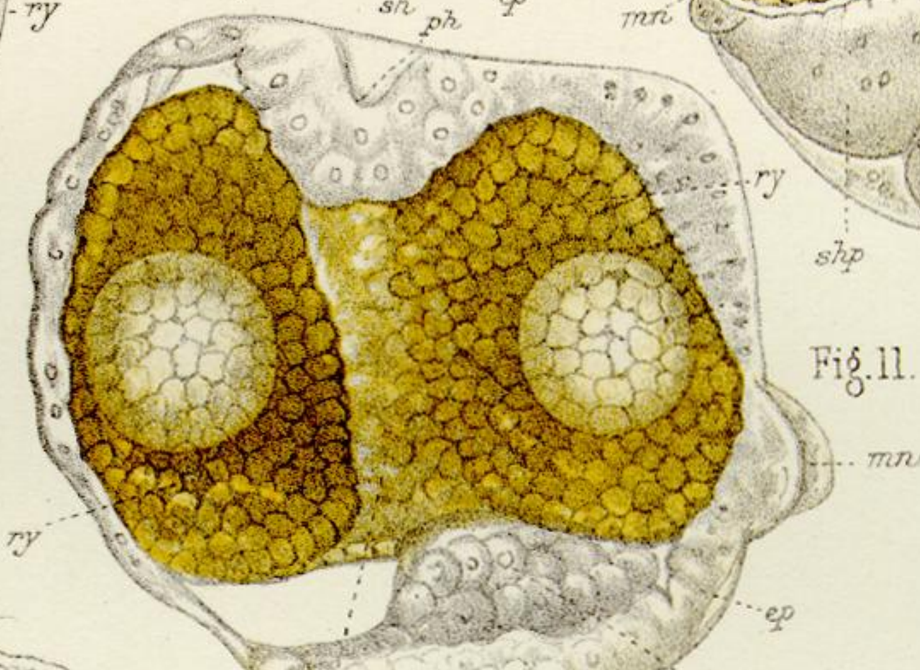


Fig. 12.

Fig. 13.

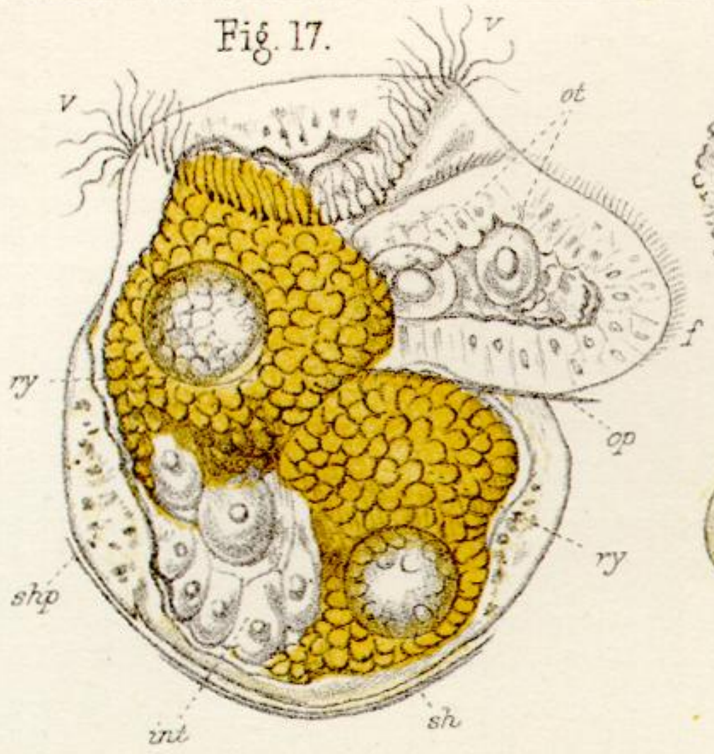
Fig. 14.

Fig. 15.

Fig. 16.

DEVELOPMENT OF PLEUROBRANCHIDIUM.

Fig. 17.



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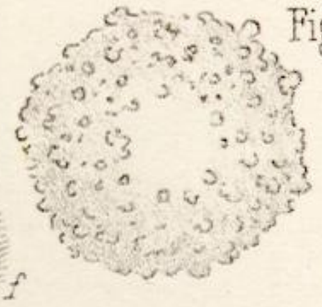

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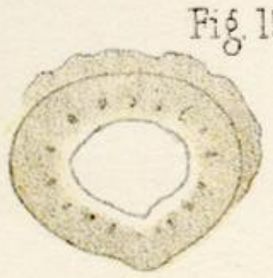

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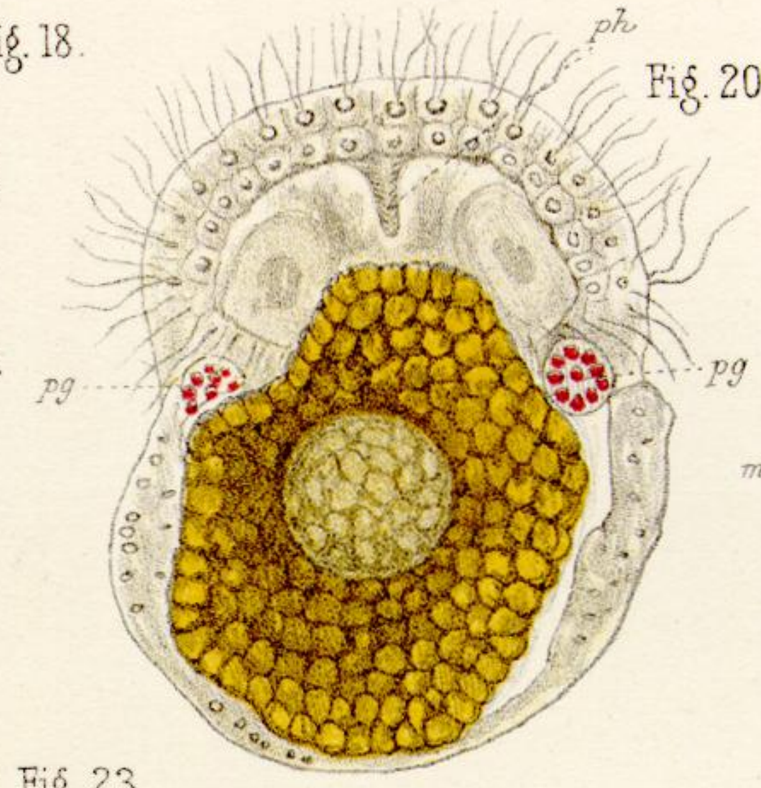
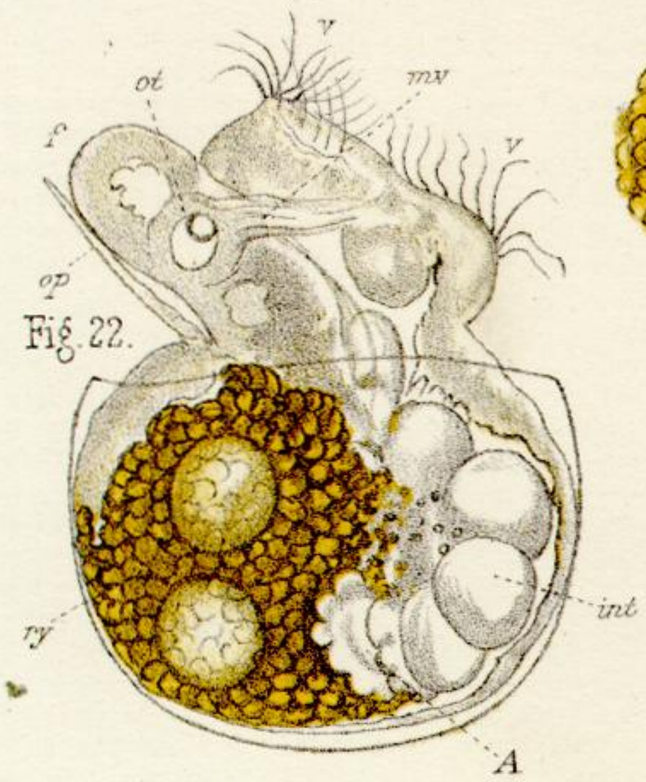


Fig. 21.

Fig. 22.



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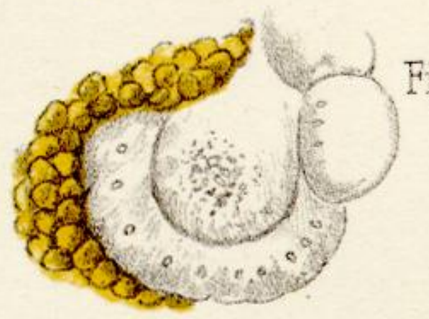
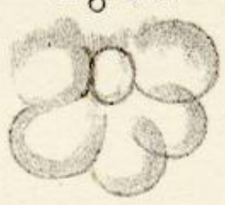


Fig. 24.

Fig. 25.



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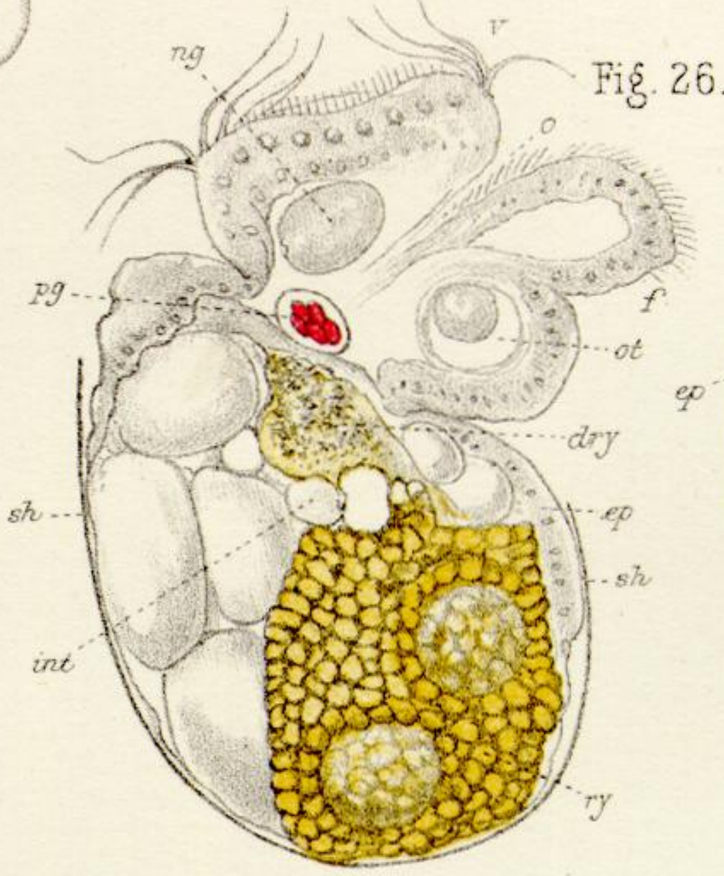

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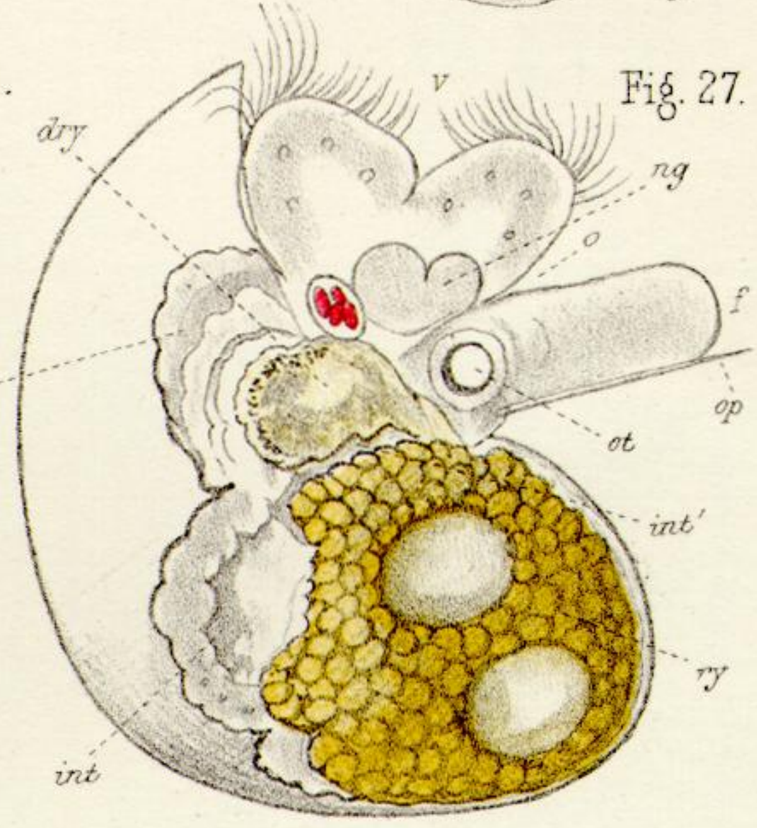

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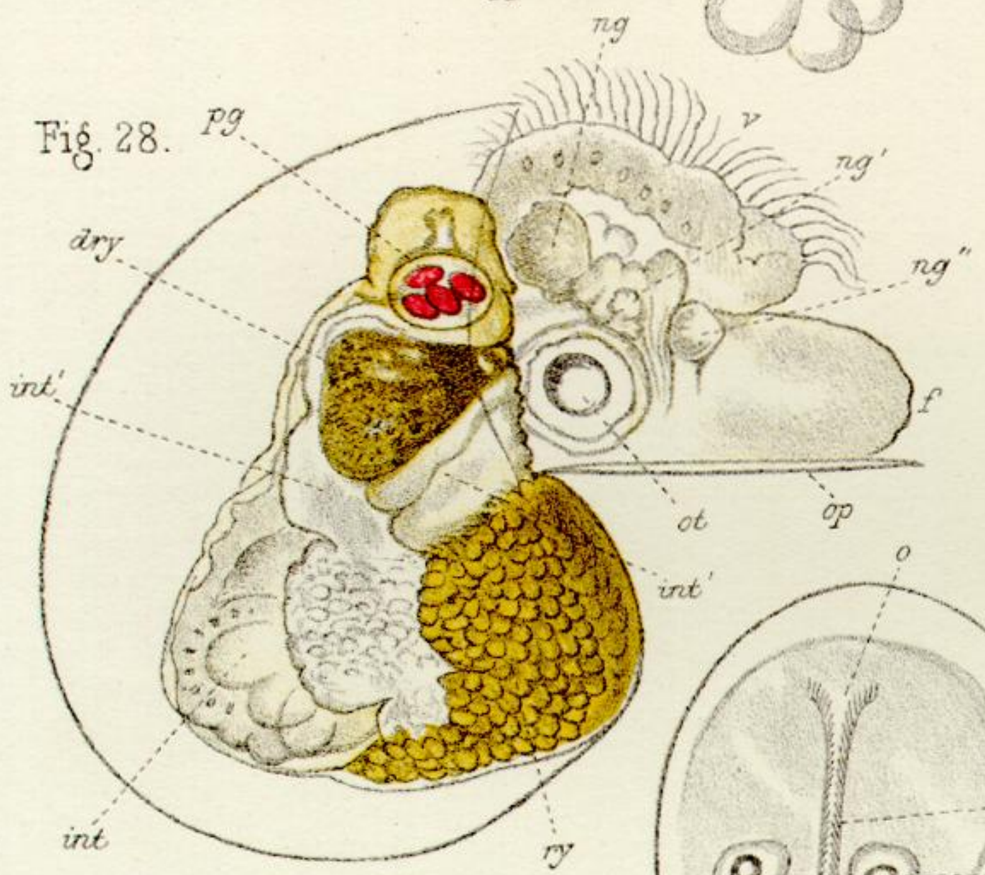

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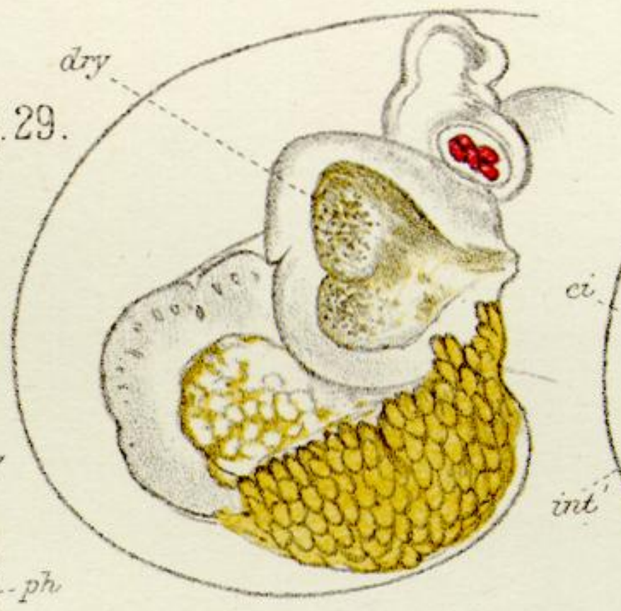

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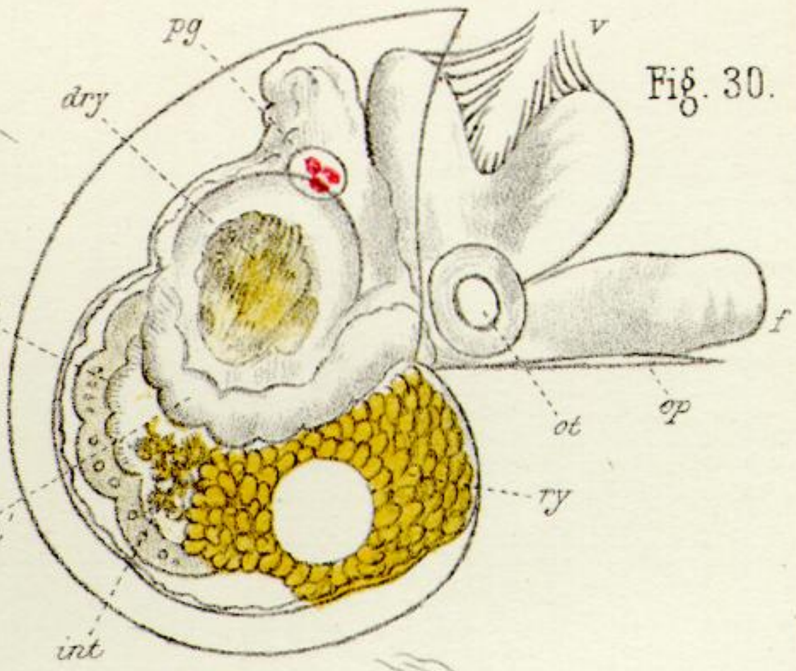

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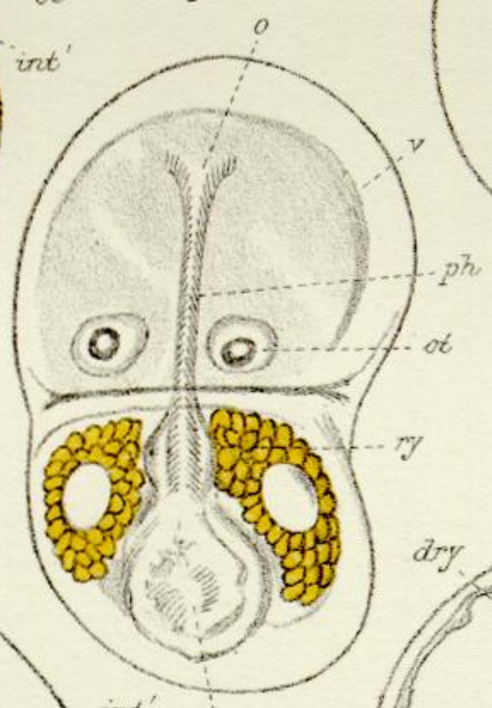

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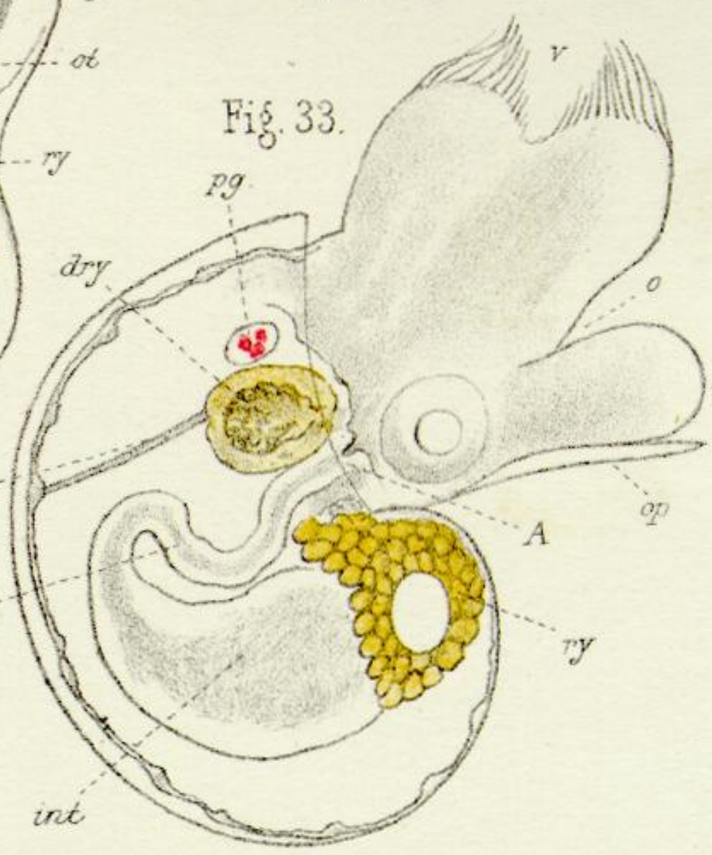

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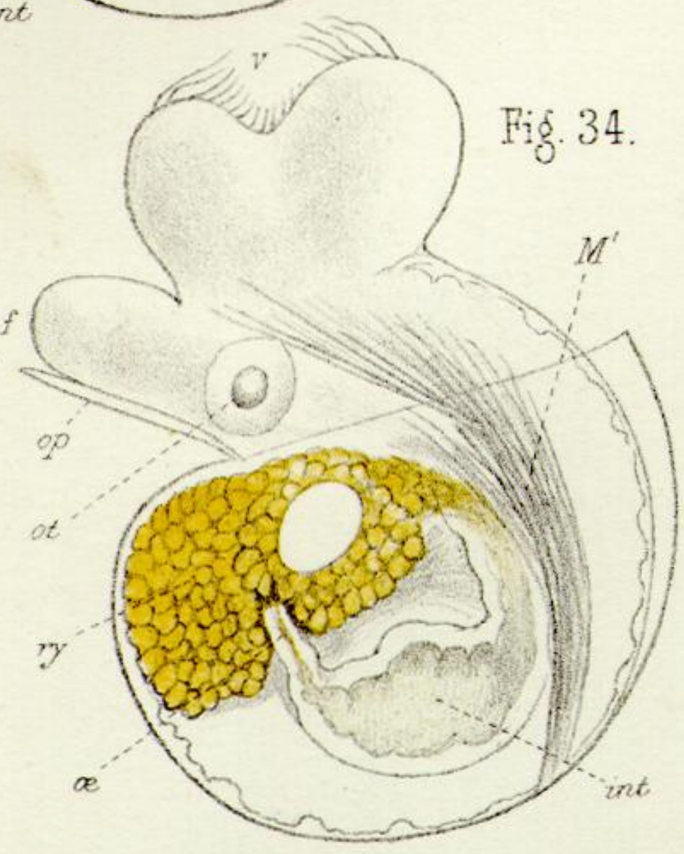
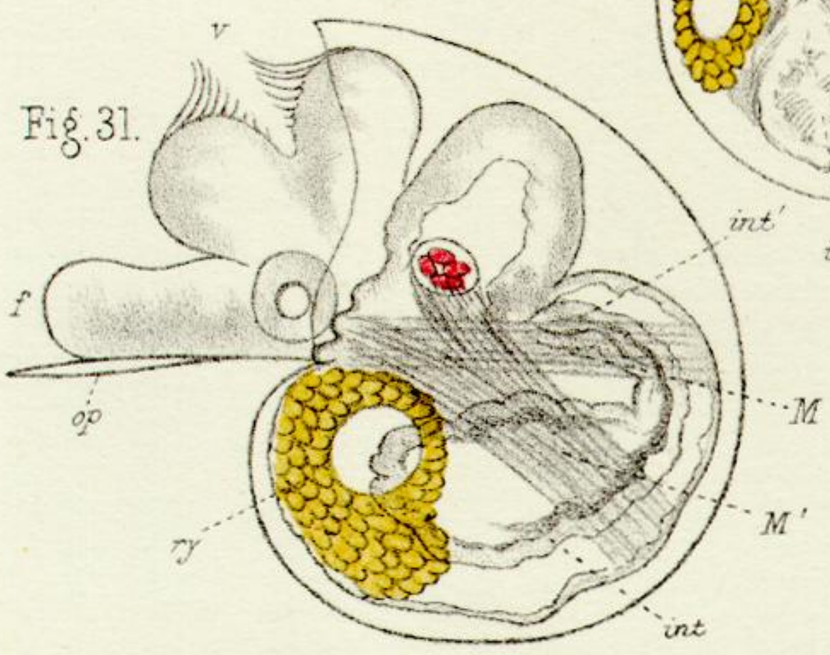
Fig. 31.