X. *The Early Stages in the Development of* Antedon rosacea.

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[Plates 43–47.]

During the winter of 1886–87, while occupying the Cambridge table in the Zoological Station at Naples, I obtained an abundant supply of larvæ of *Antedon rosacea* in all the early stages of development.

As I have had no opportunity of examining larvæ from any other locality, the following description must be understood to refer solely to the Neapolitan form; for, though this and the British form are included under the common name of *A. rosacea,* it is possible that the discrepancies between Wyville Thomson's account of the larva (21)* and the one here given may indicate the existence of specific differences which have hitherto escaped notice.

Two stages of larval development are very clearly marked off from one another, (1) the free-swimming larva; (2) the fixed larva, usually known as the pentacrinoid. Perrier, however (19, p. 118) subdivides this second stage into (*a*) the "cystid," or stalked form without arms; (*b*) the "phytocrinoid," still stalked, but provided with arms and cirri.

This convenient nomenclature is adopted in this paper, in which the development is only traced to the end of the cystid stage; but the term pentacrinoid, instead of being dropped as Perrier suggests, may, I think, conveniently be retained to denote any stalked larva, whether cystid or phytocrinoid.

The orientation of the larva presents some difficulties. Wyville Thomson assumed that the oral end of the pentacrinoid was the anterior end, and that the stalk was posterior, and in this he has been generally followed. But recently Barrois (4) has put forward the hypothesis that the stalk really represents the præoral lobe, and that this larva, like many others, fixes itself by its anterior end.

Being persuaded that Barrois's view is by far the more probable, I have adopted it in this paper, in spite of the confusion which it is likely to cause in comparing my account with those of previous writers. But, since the proper discussion of this

* The numbers in parentheses refer to the entries in the Literature List at pp. 296, 297.

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question is impossible before the facts of development are known, I must defer such discussion to the end of the paper.

Preservation.—Only the early stages of development gave any trouble, and for these a mixture of corrosive sublimate (two parts) and acetic acid (one part), as recommended by BATESON for *Balanoglossus*, gave the most satisfactory results. Several other preservatives gave excellent anatomical results; but, owing to the presence in the larva of large quantities of food-yolk, I was unable after them to obtain any satisfactory staining which would exhibit the histology.

Of the copulation described by JICKELI (12) I could obtain no decisive evidence, though I was on more than one occasion led to suspect its occurrence. I am, however, certain that it is not usually nearly so complete as he describes, and that it need not last more than a few hours; moreover, the falling off of the pinnules of the female after the extrusion of the eggs is certainly not a normal occurrence, and, as far as my experience goes, never occurs while the animals are supplied with plenty of well-aërated water. Indeed, the position of the eggs—namely, on that side of the pinnule which is turned towards the apex of the arm—would lead us to the same conclusion; for it is evident that this position affords them great protection so long as the pinnule remains attached. Some peculiarities with regard to the times of laying may be mentioned here. Often several weeks would elapse without a single fertilised ovum being obtained, and then suddenly several adults would be brought in on the same day, each with a number of eggs on almost every pinnule; and, what was more remarkable, every embryo, not merely on the same parent, but on all the adults brought in on the same day, would be in the same stage of development. This enabled me not only to preserve hundreds of embryos at the same time, with the certainty that all were of the same age, but also to predict with accuracy the age of any larvæ which were brought in in the course of the next three or four days. Until late in April, when laying became infrequent and irregular, I met with only a single exception to this rule, that exception being, so far as I could learn, due to the specimens having been brought from two separate localities, instead of, as usual, from one.

The Ovum.—The eggs are always laid, till late in the season, in the morning, probably not much before 8 A.M., and are attached in masses to the pinnules by a sticky secretion, which makes it extremely difficult to detach them without injury. Each ovum is about 0·3 mm. in diameter and of a pink colour, and each is enclosed in a transparent and close-fitting vitelline membrane. The embryo usually remains enclosed in its membrane and attached to the pinnule of the parent till the sixth or seventh day, though in this respect they are subject to considerable variations.

In consequence of the extreme opacity of the ovum and the difficulty of staining the nucleus in the presence of the food-yolk, I made no observations on the fertilisation of the ovum.

Segmentation.—The first cleavage furrow usually makes its appearance soon after

mid-day, probably at least three hours after fertilisation, and divides the ovum into two equal parts. Segmentation then proceeds in a perfectly regular manner, the segments being equal in size, and the divisions occurring at intervals of about an hour. Very soon the segments begin to range themselves round a central cavity, but the blastosphere is not complete till fully twelve hours after the first cleavage. PERRIER (19, p. 119) describes and figures a blastosphere of about 64 cells, in which four cells are distinctly larger than the rest, and he regards these four cells as indicating the commencement of an invagination; but neither in this stage nor in any subsequent ones do I find such inequalities to be normal, though undoubtedly one can always find at any stage ova in which segmentation has been somewhat unequal. In reality invagination does not take place till a considerably later stage than that figured by PERRIER, and even at the time of its commencement I could detect no inequality in the size of the cells composing the blastosphere. In size and form the cells of the blastosphere do not appreciably differ from those of the epiblast shown in fig. 1 (Plate 43).

The Gastrula.—About twenty hours after fertilisation a depression makes its appearance at one point in the spherical blastosphere, and gradually deepens until a typical gastrula is formed. The blastopore attains its greatest dimensions about the middle of the second day of development; it then gradually narrows to an elongated slit, which shortens and, finally, about forty hours after fertilisation, closes completely.

The difficulty of rupturing the vitelline membrane without injuring the embryo makes it hard to determine whether the gastrula is ciliated or not: but, as far as I could make out, no cilia are developed till after the closure of the blastopore.

In the early stages of invagination the cells of the hypoblast are considerably smaller than those of the epiblast, owing, apparently, to their more rapid division. This is seen in fig. 1, which represents a section through an embryo about twenty-four hours old. All the cells at this stage are crowded with yolk-spherules, but as yet there is no mesoblast, and the segmentation cavity is filled only with a coagulable fluid.

Very soon after the stage represented in fig. 1 the mesoblast makes its appearance. At first the cells composing it arise only from the apex of the archenteric invagination, but as it increases in quantity more and more of the hypoblast becomes involved in its formation. Whether these mesoblast cells are simply budded off from the hypoblast, or are pushed out bodily from the archenteric epithelium, I was unable to determine.

In the meantime the epiblast cells have greatly diminished in height, though evidently undergoing rapid division; and, as I could never observe any direct formation of mesoblast from the epiblast, it seems probable that there is a constant invagination going on all this time at the lips of the blastopore, by which fresh hypoblast cells are continually added as fast as the old ones are used up in the formation of the mesoblast; for the height of the hypoblastic epithelium does not greatly diminish, and the size of the archenteric cavity seldom increases after the

mesoblast makes its appearance, and often appears to decrease. The closure of the elongated blastopore appears to proceed from one end only, and leads to considerable changes in the symmetry of the gastrula, as will be evident from fig. 2, and from the diagram, fig. 55 (Plate 47), in which the former outline of the blastopore is indicated by dotted lines.

It must, however, be admitted that my sections of this stage are not wholly satisfactory. Fig. 3, in which the blastopore is already closed, certainly represents a normal stage; but it is just possible that the section represented in fig. 2 belongs to an abnormal larva; and in this case fig. 55, in which I have attempted to connect diagrammatically fig. 1 with fig. 3, must be given up.

Long before the end of the second day the epiblast cells have attained a minimum height, as seen in fig. 2, though perhaps in this figure they are even unusually low, a better idea of their normal height being obtained from fig. 3.

It may be well here to offer a few remarks upon the gastrulæ observed by GÖTTE (11). In the earliest stage observed, in which a certain amount of mesoderm was already present, he describes four ciliated bands; and in the next stage, corresponding to my fig. 2, he finds also a depression on the ventral side near the pole, which he considers posterior; so that, according to him, almost all the external features which characterise the complete free-swimming larva are already present at this early stage. I have already stated my inability to detect any cilia whatever at this stage: a little later (early on the third day) I find a uniform coating of cilia, but ciliated bands were never visible before the fourth day. With regard to the ventral "Grübchen" figured by GÖTTE, I can only say that I believe it to be accidental. The embryos are so closely packed on the pinnule of the parent that they frequently press against and distort one another. These distortions are not permanent, and at once disappear in an isolated living larva; but they are often preserved in hardened specimens, and I have, among my sections, several instances of such accidental depressions arising in various parts of the body.

Third Day.

By the beginning of the third day the blastopore has closed completely. The larva is still spherical or slightly elongated, and in specimens set free from the vitelline membrane it is seen to have a uniform coating of cilia.

The archenteron has a lenticular form, and in longitudinal sections of slightly elongated larvæ is seen to be flattened antero-posteriorly, and to occupy only one-half of the larva, that half being, on the orientation here adopted, posterior (fig. 3). It is of course important to determine the relations of the blastopore to the regions subsequently recognisable in the larva; but the extremely early closure of the blastopore and the absence of any marked external features at this stage make this determination by no means an easy matter. GÖTTE described the blastopore as

closing in the middle of the ventral side (11, p. 588); but we have already seen that the "Grübchen" which he relied upon as indicating the ventral side was probably accidental. BARROIS (3), on the other hand, says that the blastopore closes terminally at the pole which he still calls anterior, but which, in correspondence with his later suggestion, is here called posterior. I cannot pronounce a decided opinion upon this point, though I am strongly of opinion that the point of closure is not terminal, but subterminal, as represented in fig. 2. I am convinced that it is not so near the middle of the ventral line as GÖTTE represents it, and, indeed, I do not feel sure that it is on the ventral side at all. The analogy of other Echinoderm larvæ would lead us to regard the ventral position as more probable; but if, on the other hand, the line along which the blastopore closes is to be considered as lying between the future mouth and the final point of closure, then it would appear that this final point must be considered dorsal, for the larval mouth, as will subsequently be shown, appears in the middle of the ventral side.

It is to be hoped that the investigation of the development of some other species of Crinoid may set this question at rest.

Very soon after the closure of the blastopore a transverse constriction appears in the archenteron, and before the end of the day divides its cavity into two approximately equal parts, anterior and posterior, of which the former is, if anything, slightly the larger. Both cavities are flattened antero-posteriorly, and in transverse section the posterior cavity is usually somewhat oval, subsequent changes showing this to be due to a dorso-ventral compression. This stage is represented in fig. 4, in which the elongation of the larva is already well marked.

So far as I am able to make out, no further production of mesoblast takes place from the walls of the posterior vesicle, which is an enterocele pouch, though a certain amount appears still to be formed from the anterior part of the anterior vesicle or mesenteron.

Fourth Day.

By the fourth day the embryo has nearly lost its pink colour, and has become white or faintly yellow. When set free from the vitelline membrane (a process which is sometimes extremely easy, but usually requires some violence) it is found to be somewhat more elongated than on the previous day, and, though still ciliated all over, provided with several transverse bands and a terminal (anterior) tuft of elongated cilia. These ciliated bands will be described in connection with the next stage of development, in which they are much more clearly marked. Besides these we can usually distinguish two slight depressions, marking the ventral side of the larva. The anterior depression has a circular outline, while the posterior one, occupying the middle of the ventral surface, is larger, and is elongated in the direction of the long axis of the body. These depressions were named "pseudoproct" and "pseudostome" by WYVILLE THOMSON; but in this paper the former will be called the "præoral pit,"

and the latter the "larval mouth." Neither of them can be seen in a larva still confined within the vitelline membrane, and consequently they are rarely seen in sections, but their positions are indicated by two thickenings of the ectoderm, or, more usually, by a single thickening extending over the whole of the anterior pole and running back along the anterior two-thirds of the ventral surface. GÖTTE regarded the "larval mouth" as marking the position of closure of the blastopore, but in this, as already mentioned, he was almost certainly wrong.

Figs. 5, 6, and 7 (Plate 43) represent three longitudinal vertical sections through a larva at this stage; fig. 5 being through the left side, fig. 6 median, and fig. 7 through the right side of the same larva.

It will be seen that the enterocele pouch has assumed the form of a dumb-bell, extending from left to right, and that the mesenteron is curving round the constricted part of this dumb-bell towards the posterior end. At the same time two new pouches are growing out from the anterior portion of the mesenteron, though, as yet, they are but faintly indicated; one of them, which is on the left hand side and ventral, is destined to form the hydrocele (fig. 5); while the other, which is the rudiment of an anterior unpaired body-cavity, is median (fig. 6).

The posterior enterocele pouch, which, by its constriction, gives rise to the right and left body-cavities, is now bounded by a definite columnar epithelium; but the cells bounding the mesenteron are much lower, and on its anterior side there is some indication of a continued formation of mesoderm. The hydrocele has a somewhat more definite boundary of elongated cells. The structure of the ectoderm is very difficult to make out, but appears to consist of a single layer of narrow, closely-packed cells, which are crowded with yolk-granules and, for the most part, stain deeply; though below the anterior ciliated tuft and along the region of the larval mouth the staining is usually somewhat less intense.

As the day proceeds the separation of the right and left body-cavities becomes more nearly complete, while the two horns of the mesenteron, growing round the constriction which separates these cavities, at length meet and fuse behind it, so as to form a complete ring. At the same time the hydrocele and anterior body cavity become gradually constricted off from the mesenteron, though they remain freely open to one another till the next day.

Figs. 8, 9, and 10 (Plate 43) are taken from a series of approximately transverse sections through a larva three-and-a-half days old, seen from the anterior end. Unfortunately this series was so much overstained that the histology could not be satisfactorily made out, and no attempt, therefore, has been made to represent it.

From these figures the ring-like form of the mesenteron will be easily recognised. Owing to a slight obliquity in the plane of section, the anterior body-cavity appears to run towards the ventral side, but its real course, though somewhat ventral, is directly forwards, parallel with the thickened ectoderm of the larval month.

At a slightly later stage than is here represented the separation of the hydrocele

and anterior body-cavity from the mesenteron and of the right and left body-cavities from one another is complete, though the two last remain for a while connected together by a solid cord of cells, which perforates the mesenteron.

The growth of the mesenteron into a complete ring is so peculiar that for a long while I hesitated to regard it as normal; but I have traced it through so many different series of sections, cut in such diverse planes, that I can no longer doubt that it is the usual form of development, though what it may mean and how it may have arisen, I will not venture to suggest.

The description above given of the development of the various cavities differs in some important respects from those of GÖTTE and BARROIS.

GÖTTE describes the formation of three cœlomic pouches from the archenteron, two lateral and one ventral; the two former being the right and left body-cavities respectively, and the latter being the hydrocele (11 p. 590).

BARROIS (3) finds, as I do, that the archenteron first splits into two cavities, anterior and posterior; but in the nomenclature of these two cavities, and the subsequent fate which he assigns to them, his account differs widely from mine. According to him, after the closure of the blastopore follows—"L'étranglement de la vésicule endodermique en deux parties ; l'antérieure qui s'allonge pour se partager en vésicule aquifère et intestin, la postérieure qui s'étire en largeur pour se diviser en deux sacs péritonéaux. Ces derniers ne changent pas de place, mais se transforment en deux disques qui se rejoignent en un manchon tout autour de l'intestin."

If we remember that he still uses the old orientation, it will be clear that he describes as a growth of the two peritoneal vesicles round the intestine what I have described as a growth of the mesenteron round the posterior cœlomic pouch; that the hydrocele arises from the former and not from the latter is, I think, sufficiently clear from fig. 8.

Fifth, Sixth, and Seventh Days.

(1.) *External Form.*—By the fifth day the larva has acquired almost all the external features of the completely-developed free-swimming larva of the seventh day ; so that the following description applies in all but a few points (to be mentioned later) to any larva from four to six days old.

The general colour of the larva is usually yellowish-brown, but this colour is confined to the non-ciliated portions, so that the ciliated bands and the two ventral depressions (also ciliated), which are all white, are very clearly defined, their degree of distinctness varying with the amount of pigment developed elsewhere. The greatly elongated cilia of the anterior tuft also spring from a non-pigmented area. Besides the yellowish-brown cells the non-ciliated areas also contain a number of the so-called "yellow-cells." By reflected light, if much pigment is developed elsewhere, these cells are very inconspicuous ; but when teased out and seen by transmitted light they appear bright green, while the other ectoderm cells, in which but little

pigment is present, appear colourless. This green colour renders the name "yellow-cells" a very inappropriate one; but, since they have been so named in a recent controversy as to their nature, to which reference will be made later, I have thought it better to retain this name. WYVILLE THOMSON called them "oil cells"; but, as they do not appear to contain oil, this name is no improvement. It is worthy of note that these cells make their appearance long before the rupture of the vitelline membrane (fig. 13). The ciliated bands are five in number, and their cilia are somewhat shorter than those of the terminal tuft. No trace of cilia was to be found between the ciliated bands. The anterior band is incomplete ventrally, and irregular in its degree of development: usually it becomes lost at each side of the præoral pit (figs. 13 and 15), but sometimes it turns sharply forward, as if endeavouring to complete itself on the anterior side of this depression (fig. 14). On the dorsal side this band runs so close to the extremity of the larva that its cilia frequently show even from the ventral side, producing the impression that the whole anterior end is covered with short cilia (fig. 14).

Each of the other four ciliated bands completely encircles the larva, and the two posterior ones are simply transverse rings; but the two middle bands are only transverse on the dorsal side, being deflected from their course on the ventral side by the larval mouth, which lies between them, and with the ciliated lining of which the third band fuses posteriorly.

The larval mouth varies greatly in size, but is sometimes so deep as almost to cut the larva in two, and is always much deeper anteriorly than posteriorly.

The præoral pit, on the other hand, never attains any great depth, and is often so shallow as scarcely to be recognisable in sections.

The principal difference between the larvæ of the fifth, sixth, and seventh days is one of size, and especially of length. Within the vitelline membrane the larva is always compressed into a spherical, or nearly spherical, form (fig. 13); but when liberated it suddenly elongates to a considerable extent, usually, however, remaining for a time concave ventrally. If set free on the fifth or sixth day it continues to increase in size and to elongate itself, until it usually becomes quite straight (fig. 15); but if not liberated till the seventh day it seldom has time to straighten itself completely before it becomes fixed.

In most broods, but not quite in all, there appeared on the seventh day a circular white spot on the left side, between the third and fourth ciliated bands (fig. 15); as indicated in the figure, it marks the orifice of the "water-pore."

The larvæ examined by me at Naples differed in several respects from those described by WYVILLE THOMSON. The more trifling of these differences are probably due to his method of examining the larva as a transparent object by means of compression, which naturally led to distortion. But the absence of all mention of the anterior ciliated band in his account can hardly be explained thus; and since this band is also omitted in the figures given by BUSCH (5), who obtained his larva

in Kirkwall Bay in 1849, it is possible that it is altogether absent in the British form.

That GÖTTE did not notice it is less surprising, as he does not appear to have worked much with fresh material, and it is with difficulty recognisable in spirit specimens. Of the oral depression described by him as occurring between the fourth and fifth ciliated bands (11, p. 590) I could find no trace.

Although WYVILLE THOMSON asserts that the larva "swims with either extremity in advance indifferently" (21, p. 522), I find that in almost all cases the ciliated tuft is directed forwards; indeed, out of hundreds of larvæ examined, I never saw one swim in the opposite direction, except when it encountered an obstacle, in which case it would reverse its motion for a short distance, always, however, resuming before long its original course. The fact that when at rest the cilia all curve towards the anterior end is probably connected with this mode of swimming.

(2.) *Internal Anatomy.*—We left the larva at the end of the fourth day with a ring-like alimentary canal, and four cavities derived from it, namely (1), an anterior body-cavity, running forward into the præoral lobe, and at its posterior end turning slightly to the left to open into (2), the hydrocele, which is at present a simple vesicle; (3 and 4), the right and left body-cavities, which are still connected by a solid cord of cells passing through the mesenteron; but very soon this cord is completely absorbed, so that the mesenteron has no longer the form of a ring, but rather that of a disc flattened between the body-cavities.

Rather before this stage is reached an important change takes place in the positions of the right and left body-cavities. The latter, which lies immediately behind the hydrocele, shifts towards the posterior end, and at the same time towards the ventral surface; while the right body-cavity becomes more and more anterior and dorsal. In consequence of this change, the mesentery separating these two cavities, instead of being longitudinal, assumes an oblique position, which is more easily understood from figures than from a description.

Fig. 21 (Plate 44) represents a horizontal section, seen from the dorsal side, in which the right body-cavity is clearly more anterior than the left; the mesentery is visible on each side of the alimentary canal, and a line joining these two portions of it would represent its course across the back of the larva: in this specimen the mesentery is very decidedly oblique, but in many larvæ on the seventh day it appears, from this point of view, to have an almost completely transverse course. In a lateral view, however, it is always oblique, running from the ventral side backwards towards the dorsal side, as seen in fig. 59 (Plate 47), which is a diagrammatic view of a larva from the right side.

GÖTTE (11, p. 591) correctly describes this arrangement of the mesentery, but in accounting for it by a change in position of the body-cavities he has fallen into an error of no little importance, but one which, owing to the different orientation which he employs, is not easy to demonstrate. That which in fig. 21 I have marked "left body-cavity" receives the same name in his account, but then he regards this cavity

as occupying the anterior end of the body, and the side marked R in my figure is, according to him, left. I am not here concerned with the question whether his orientation is or is not correct; but I wish to call attention to the fact that if we both used the same orientation we should differ in our nomenclature of the body-cavities; in other words, if we interpret his account in terms of the orientation here adopted, it is the *right*, and not, as I have stated, the *left*, body-cavity which assumes a posterior position.

Besides fig. 21, which has already been explained, figs. 11 and 12 (Plate 43) also support my account. Fig. 11 represents a transverse section, seen from the posterior side, through a larva of the fifth day, passing through the posterior part of the larval mouth, the thickened ectoderm of which marks the ventral side. On the left side is seen the hydrocele, still opening into the anterior body-cavity; while on the right side lies the right body-cavity. The left body-cavity, being posterior to the hydrocele, does not appear in this section; but in fig. 12, representing a section near the posterior end, it is the principal cavity, and lies distinctly more on the ventral side than does the right body-cavity.

Returning now to the general anatomy, we find that the hydrocele and anterior body-cavity are undergoing some important modifications. In fig. 11 they still communicate with one another, but at a slightly later stage I have searched in vain for any such connection. The hydrocele grows towards the right side, and then, curving towards the posterior end, and again towards the left side, it forms a horse-shoe-shaped curve, open towards the left, and lying between the mesenteron and the ventral ectoderm. At first it does not extend much beyond the middle ventral line, but later on it extends very nearly to the extreme right, and forms an almost complete ring, from the ventral surface of which spring the rudiments of five tentacles (fig. 61, Plate 47). After separating from the hydrocele the anterior body-cavity grows towards the ectoderm on the right side, at the level of the blind end of the hydrocele, and finally opens to the exterior between the third and fourth ciliated bands by the "water-pore" already mentioned. The walls of the pore itself are certainly formed by ectoderm cells, but there appears to be no regular invagination of the ectoderm to meet the cœlomic outgrowth. This pore is usually not formed till just before the larva fixes itself. It is clearly the homologue of the "dorsal pore" of other Echinoderm larvæ, but I have avoided this name for it, since in *Antedon* it is distinctly lateral.

So far I have only given a general outline of the changes in the anatomy of the larva between the fifth and seventh days. It will now be well to enter into a more detailed description of a fully-developed free-swimming larva of the seventh day, mentioning such points as have hitherto been purposely omitted, and comparing my results with those of previous observers. The two diagrams (figs. 59 and 60) will be found useful in connection with the following description.

The anterior body-cavity varies considerably in dimensions. It usually forms a

conspicuous cavity at the anterior end of the mesenteron, but elsewhere it is quite narrow. Its continuation forwards, where it usually lies close to the ectoderm of the larval mouth, and rather on the left side, is seldom easy to trace for any distance; though that it sometimes has a considerable length is evident from fig. 18 (Plate 44). It is lined throughout, except close to the pore, by an epithelium of much-flattened cells, the pore itself and a small portion of the tube below it being bounded by a cubical epithelium bearing cilia.

The form of the hydrocele has already been sufficiently described. It has a high columnar epithelium with deeply-staining nuclei.

The mesenteron is flattened on the ventral side, where it adjoins the hydrocele, but is convex dorsally (fig. 17). It lies far from the larval mouth, and indeed shows no trace of any communication with the exterior; for, as already mentioned, I have been unable to find the ectodermic depression described by GÖTTE as the mouth.

The left body-cavity, which fits like a cap over the posterior end of the mesenteron, extends forwards in the median ventral line only as far as the posterior border of the hydrocele (fig. 17): it nowhere intervenes between this organ and the ventral ectoderm, but on each side of the former it extends forwards almost to the level of the water-pore. Dorsally, as already mentioned, it does not extend very far forward. Its epithelium, and that of the right body-cavity, is considerably flattened at this stage. While the left body-cavity is for the most part ventral, the right body-cavity is almost wholly dorsal. On the right side, it is true, it nearly reaches the ventral side (fig. 59), but on the left it extends no further than the water-pore. It tapers away rapidly as it passes forwards, and at the anterior end of the mesenteron exists only as a small cavity having a semi-lunar form in transverse section, the convexity being towards the dorsal surface. In the centre of the mass of mesoderm which stretches from this point to the extreme anterior end, there runs at this stage a cord of slightly elongated cells. No trace of this was present on the fifth day, and even on the seventh day it seldom extends much more than half way from the mesenteron to the anterior pole. It usually has a more or less strong ventral curvature, in correspondence with the curvature which, as already mentioned, most larvæ show, until they have been for some time free from the vitelline membrane. In longitudinal sections it is generally possible to trace the right body-cavity forward into this axial cord; and in favourable transverse sections it is even possible to make out that this extension of the body-cavity is divided into five extremely minute cavities, arranged round a central strand (fig. 19). This central strand or *axial organ* runs back to the anterior end of the mesenteron, and it is around it that the right body-cavity assumes the horseshoe-like form above described. Owing to their extremely small size, these five tubular cavities, which clearly form the rudiment of the *chambered organ*, could not be satisfactorily traced back individually into the body-cavity; but, from the fact that two of them appear in horizontal sections (fig. 21), and only one in longitudinal vertical sections (fig. 17), and from certain changes which the right body-cavity

undergoes at a later stage, I am led to believe that the diagram (fig. 56, Plate 47) represents their mode of origin; two appear to come off on the right side and three on the left, one of the latter forming in fig. 19 the median ventral chamber. Fig. 56 is orientated for comparison with fig. 57 (which will be explained later), and is seen from the posterior end.

BARROIS (3) denies altogether the existence of any forward prolongation of the cœlom into this region of the body; but, since it seldom exists till a few hours before fixation, and is much obscured afterwards, this is not very surprising. Far more suprising is the fact that the anterior body-cavity and its pore seem also to have escaped his notice.

GÖTTE, on the other hand, figures an enormously wide prolongation, into which a tapering cord of splanchnic mesoderm runs from the mesenteron. He gives no explanation of how this state of affairs arose, and I have no doubt that he has really confused together the anterior body-cavity and the forward prolongation of the right body-cavity.

PERRIER, however, accepts GÖTTE'S figure (11, Plate 25, fig. 10) as correct, and attempts to prove from his own sections of the cystid that the chambered organ arises from the fusion along certain lines of a central cord of splanchnic peritoneum with a surrounding sheath of somatic peritoneum (19, pp. 123, 139, and 163). But, as I shall show later, he has overlooked the presence of a longitudinal mesentery, which on his view would be difficult to account for.

The histology of the ectoderm remains to be described. The cells of the ciliated bands are easily recognisable in section, not merely by their arrangement, but also by their small, deeply-stained nuclei, situated for the most part at the inner ends of the cells, and by the marked striation of their outer borders. The nuclei of the non-ciliated cells, on the other hand, are large, stained but slightly, and are situated near the middle of the cell. Among these cells are scattered the "yellow-cells," but these are rarely distinguishable in sections. In fig. 12 they are recognisable by their shrunken and distorted walls, which have a yellow colour after staining with borax carmine; but these peculiarities are probably due to the preservative used (picro-hydrochloric acid), and are by no means always present They sometimes stain deep blue with GRENACHER'S hæmatoxylin, but the colour is rapidly removed by acid; and, unless decolorisation is checked at precisely the right moment, they are indistinguishable from the surrounding cells. If a living larva be teased out in sea-water, all the ectoderm cells are seen to be filled with refractive yolk-spherules, and the "yellow-cells" differ from the rest only in their colour, which however is not equally developed at all. The yellowish-brown pigment of the other cells appears to be entirely superficial, is not dichroic, and is rarely present in sufficient quantities to be recognisable in individual cells. If a yellow-cell be broken up, we see that the colour is contained in a diffuse form in the yolk-spherules, and innumerable gradations can be found between absolutely colourless spherules and others of a vivid green. The

addition of acetic acid at once destroys the colour, clears up the spherules, and brings the nucleus into view; and then the "yellow-cells" are absolutely indistinguishable from ordinary ectoderm cells. Osmic acid also destroys the colour, but does not blacken the contents; so that THOMSON'S name of "oil-cells" is without foundation. GÖTTE professes to have seen these cells in his sections, and figures them accordingly; but, since in his figures they are made to occur in the larval mouth, from which they are certainly absent in the living animal, I do not feel confident that what he figures were really the yellow-cells at all.

The cells bearing the anterior tuft of cilia differ considerably from those of the ordinary ciliated bands, though they too have a striated border (fig. 23). The cells of the præoral pit, however, though generally resembling those of the ciliated tuft, have no striated border. Between the ciliated tuft and the first ciliated band the ectoderm is peculiar in containing a number of long narrow cells, which stain deep purple with GRENACHER'S hæmatoxylin, and retain this colour tenaciously in acidulated alcohol. The anterior and deeper half of the larval mouth contains cells which also stain deep purple, but they part with their colour much more readily, and they have strongly striated borders. They are seen in longitudinal section in fig. 22 stained with hæmatoxylin, and in transverse section in fig. 24 stained with borax carmine, which has but little effect upon them. The posterior half of the larval mouth is lined by narrow, closely-packed cells, which are easily distinguished in sections stained with GRENACHER'S hæmatoxylin (fig. 22).

Round the edge of the præoral pit and down the sides of the larval mouth there runs a narrow groove (figs. 22 and 24) which is filled with excessively fine longitudinal fibres. A deep layer of similar fibres, running for the most part from side to side, underlies the whole of the anterior pole (fig. 23): they are apparently ectodermic, though where they occur there is seldom any marked line of separation between the ectoderm and mesoderm. From the position and general appearance of these fibres it seems most probable that they are part of a nervous system, and that some at least of the peculiar ectodermic structures connected with them are of a sensory nature.

The Skeleton.—The first rudiments of the skeleton make their appearance early on the sixth day, but, owing to the opacity of the larva, they can only be seen in specimens cleared in turpentine and balsam, or partially macerated in potash. In the youngest specimen observed there were already fourteen calcareous nodules, representing five orals, five basals, a dorsocentral, and three stem-joints, but the last-named plates rapidly increase in number. The most anterior plate is the dorsocentral, which lies deeply embedded in the tissues, almost exactly in the centre of the body. From it the stem-joints, which as yet are exceedingly minute, lead back in a longitudinal series towards the anterior end of the mesenteron. The five basals and five orals are of about the same size as the dorsocentral, but much more superficial, lying immediately beneath the ectoderm. Each series of five plates is arranged in the form of a horseshoe, widely open towards the ventral surface, and set obliquely to the long

axis of the larva; in fact, each horseshoe may be described as approximately parallel to the mesentery separating the right and left body-cavities, the basals being developed round the former, and the orals round the latter cavity. As a consequence of the fact that they share not only the longitudinal but also the lateral obliquity of this mesentery, the left ventral plate of each series is distinctly nearer the anterior end of the larva than is the right ventral plate of the same series: thus the left ventral basal generally lies at about the same level as the dorsocentral, while the right ventral plate of the same series lies at about the level of the posterior stem-joint.

I could discover no indication that the dorsocentral, basals, and orals, were developed in any particular order, though it is probable that all of them are developed before the stem-joints. At first all these plates are simple amorphous nodules, but as they increase in size most of them branch out and assume the form of triradiate or quadriradiate spicules, all the rays lying in one plane; and later, by further branching and anastomosis, each forms a flat reticulate plate, lying in the case of the basals and orals parallel with the ectoderm, and in the case of the dorsocentral nearly transverse to the long axis of the body. Fig. 47 (*a*), though really representing another plate, will serve to illustrate the form of an oral or basal on the sixth day; while fig. 49 represents one of them on the tenth day.

The stem-joints differ from the dorsocentral and other plates in form. Each is at first a slightly-curved plate, smooth on the concave side (which is directed ventrally), and scalloped on the convex or dorsal side (fig. 47, *b*); but as it increases in size it grows more and more round to the ventral surface, and eventually forms a complete ring (fig. 51), though this does not usually happen till after fixation. At the same time the processes of the convex side grow out more and more, and anastomose with one another.

New stem-joints are constantly being formed at the posterior end, and push the dorsocentral nearer to the anterior end; and consequently the anterior stem-joint is always the oldest and most developed. As is seen in fig. 19, each joint, in its growth into a ring, surrounds the chambered organ.

The number of stem-joints of course varies with the age of the larva, but the process of formation appears to be quite continuous, and no pause at a stage with eight plates, such as is described by GÖTTE (11, p. 597), could be observed.

Early on the seventh day some new plates make their appearance at the posterior end of the series of stem-joints; they are three in number (rarely four or five), and in form resemble small basals, though they are developed at a much deeper level than these plates, and are usually nearer the posterior end of the body than the two ventral basals. One of these plates is shown in fig. 47 (*a*); and their position with respect to the basals and stem-joints is seen in fig. 45, in which the plates themselves are represented diagrammatically, though their position is carefully copied from actual specimens. These three "underbasals" are at first equal in size, but after a while two of them begin to grow more rapidly than the third, eventually attaining to about double its size.

In order to explain the true positions of these underbasals, we must have a definite nomenclature for the five radii, into which the body of the larva becomes marked out by the appearance of the interradial basals and orals. Fig. 54 is a diagram of the disc of an adult endocyclic Crinoid seen from the oral side, illustrating CARPENTER'S system of nomenclature (see 6, p. 89). Taking the anal interradius as a fixed point, he names the radius opposite to it A, and then, passing round the animal in the same direction as the winding of the alimentary canal, he calls the other radii B, C, D, E. This nomenclature is adopted in this paper, with this difference, that the radius A is made to depend not on the anus, which is not yet present, but on the water-pore, which, as we shall see, lies in the cystid with the anus in the interradius C D. This pore is shown in figs. 45 and 58, and is seen not to be at present directly connected with any one of the skeletal plates.

In fig. 58 the animal is supposed to be seen from the posterior end, with the larval mouth directed away from the observer. This orientation is intended to facilitate comparison with the figures of the later stages. We now see that the smallest underbasal lies, not in the dorsal interradius AE, but in the radius A, opposite the interradius of the water-pore.

It is not a little curious how all the plates seem, as it were, to avoid at first the ventral side. This is not so well marked for the orals and basals in fig. 58 as it was at an earlier period, but it is still true of the underbasals and stem-joints; and in the rare cases in which five underbasals were developed they appeared, so far as I could see, to be ranged in the form of a horseshoe, quite as widely open ventrally as that of the basals and of the orals.

FIXATION OF THE LARVA AND TRANSITION TO CYSTID STAGE.

External Form.—As already mentioned, the majority of larvæ are not set free from the vitelline membrane till the seventh day of development. Such larvæ, after swimming actively for about twelve hours, attach themselves to any suitable surface by means of a præoral pit, which then rapidly flattens out into a disc. It is clear, therefore, that the whole ventral side of the larva lies almost parallel with the surface of attachment. For convenience in section cutting, I allowed the larvæ to fix on thin sheets of celloidin; and this method, for which I am indebted to my friend Dr. G. J. VOSMAER, has the advantage that the changes undergone by the ventral surface of the larva subsequent to fixation can easily be followed under the microscope through the transparent celloidin, without disturbing the animal. Fig. 16 is a drawing of a rather unusually large larva made in this way about an hour after fixation. In this figure the ciliated tuft and anterior ciliated band are still present, but these very soon disappear; the four remaining bands, however, not only persist for two or three hours, but usually continue to exhibit a certain amount of motion. A little later all the ciliated bands disappear, and the larval mouth, after first becoming very shallow, gradually narrows and disappears.

At the same time the posterior end gradually rises up, so that the long axis of the larva makes a larger and larger angle with the surface of attachment, and the anterior end, which, though flattened dorso-ventrally, was formerly the widest part of the body (fig. 20), becomes narrow and rounded; so that the whole animal assumes the form of a gradually-tapering club, attached by a flattened disc at its narrow end. Up to this time the larva has remained extremely opaque, but it now rapidly becomes more transparent, and the calcareous plates can be faintly seen even when the larva is viewed as an opaque object.

The larva has now assumed all the characters of the well-known cystid, and the subsequent external changes are correctly figured in THOMSON's paper (21).

This observer's account of the fixation differs slightly from mine. He describes the two ventral depressions, and most of the ciliated bands, as disappearing before fixation; and the larva figured by him as the latest free-swimming form has already the shape of a complete cystid (21, Plate 25, fig. 1). There may, of course, be some difference in this respect between the English and Neapolitan forms; but such larvæ as he has figured did occur frequently, though not normally, among my specimens. They were not, however, as I believe, really unfixed: for in each one that was specially examined some small object, such as a grain of sand, was found imbedded in the tissues at the anterior end (end of stalk); but this object not being sufficient to anchor the larva, the latter had continued to swim about, and had retained its cilia at a later stage than it would otherwise have done. Such larvæ were never observed to undergo any further process of fixation; but, sooner or later, lost their cilia completely, and sank helplessly to the bottom of the tank, where they perished in the débris. Altogether, the larvæ showed a singular want of discrimination in their choice of positions for fixation; besides numbers which thus perished from attaching themselves to objects too small to support them, some attached themselves to the pinnules of the parent, where they never managed to adhere very long; and others to their own cast-off vitelline membranes, which were soon eaten up by bacteria and infusoria.

Another frequent source of destruction of larvæ may be mentioned here. As previously stated, the ease with which the vitelline membrane can be broken is subject to considerable variations. Some whole broods are set free with ease on the fourth day; but in most broods, not only in my tanks, but also in the sea, the majority were not set free till the seventh day, and a considerable number were unable to free themselves even on the ninth or tenth days—long after the majority of larvæ had become fixed. Such prisoners, when at length liberated, were seldom able to fix themselves, and if they did so, usually exhibited considerable abnormalities of form; more often they remained unattached, and either grew into monstrous shapes or remained perfectly spherical. Some of the last-named forms I have liberated as late as the eleventh day; and, though they had lost the two ventral depressions, they still

retained some of their cilia in active motion. The internal anatomy of such forms would afford an interesting study, but I have not yet had time to investigate it.

The reason of so much variation in the consistency of the vitelline membrane, leading so often to considerable loss of life, is not easy to see, but it may possibly be connected with the varying conditions to which these animals are exposed. Thus, if the membrane were always of the same strength, a sudden storm might set all the larvæ free at too early a stage of development, and so deprive them of the protection afforded by the pinnules of the parent; while, if the membrane were strong enough to resist such a storm, a continued calm might leave a greater number unable ever to free themselves than at present occur. What value there is in this suggestion must be determined by the examination of other larvæ exposed to the same varying conditions.

Internal Anatomy.—The first changes which occur after fixation are principally histological, and it is not for some hours that the general internal anatomy alters much.

The ectoderm soon loses its distinctness from the mesoderm, the ciliated bands degenerate (fig. 20), and histolysis, setting inwards from the ectoderm, rapidly spreads to all the tissues, and results in the obliteration of almost all the previously existing histological differentiation. The details of this process of histolysis are extremely difficult to follow; and both in its mode and degree of action and in the relative times at which it affects different organs it appears to vary considerably. About six hours after fixation the larval mouth has flattened considerably, and presents the very peculiar appearance represented in fig. 26, which should be compared with the section through the same region in a free-swimming larva (fig. 24). The central part, which stains but slightly, no longer shows any cell-outlines, but is traversed by a fine network of threads, and contains a few extremely minute cells, whose nuclei stain intensely, and which may very possibly be phagocytes; while at each side of the groove there lies a deeply-stained mass, containing a few large but inconspicuous nuclei and an enormous number of small deeply-stained nuclei, which apparently belong to cells similar to, but perhaps usually larger than, the phagocytes (?) in the centre. Similar cells have already attacked the ciliated bands in fig. 20.

Some hours later a transverse section through the larval mouth presents the appearance shown in fig. 27. The fine network has disappeared, while the large nuclei have spread towards the centre; the whole mass stains deeply, but no true epithelium appears to be formed. In both this and the previous stage the striated border seen in fig. 24 is still represented by a hyaline region. Besides these details we notice in fig. 27 that two lateral folds are growing across the larval mouth to meet one another in the middle line: they meet and fuse first at the posterior end of the groove, but, their fusion extending rapidly forwards, we find, less than twelve hours after fixation, a completely closed cavity running along the ventral surface, which is shown in longitudinal section as the vestibule in fig. 28. In this figure, and in all subsequent ones of fixed larvæ, the position of the larva has been reversed, and the

præoral lobe (stalk) directed towards the observer, since less confusion is likely to arise from this than from altering the orientation of the pentacrinoid larva, with which previous writers have made us familiar.

In the meantime, usually before the invagination of the larval mouth, a number of very minute cells are proliferated into the mesenteron from the centre of the water-vascular ring (fig. 25): these cells soon completely fill the cavity of the mesenteron, where they remain for a considerable time. Since their deeply-stained nuclei are fairly conspicuous, it is surprising that in their figures both Götte and Perrier should have drawn a pale granular mass, which looks much more like a coagulum than a mass of cells. Perrier, indeed, distinctly states (19, p. 122) that this mass colours almost as completely as the cells of the epithelium of the stomach; he does not, however, represent it so in any of his figures, but generally leaves the stomach empty, while in one place (19, Plate 1, fig. 3) he has drawn, instead, several cells of enormous size—a condition which meets with no support either from his other figures or his description, and one which I cannot but regard as wholly imaginary.

Returning now to fig. 28, we see that soon after the invagination of the larval mouth the cavity so formed, which we may call the vestibule, pushes its way rapidly backwards, so that part of it comes to lie opposite the water-vascular ring, while the mass of cells forming its floor envelopes this ring, and fuses with the similar mass occupying the cavity of the mesenteron. Histolysis has by this time invaded the epithelial linings of the various cavities, so as very greatly to obscure their limits.

Hitherto the larva has been lying almost parallel with the surface of attachment; but now, by a rapid growth of the part between the disc of fixation and the vestibule, the long axis of the body becomes more nearly perpendicular to this surface, and at the same time all the internal organs are, as it were, rotated to the posterior, or, as I shall in future call it, the *oral*, pole. By this change the vestibule and the water-vascular ring come to lie transversely to the long-axis of the body (fig. 29), while the body-cavities also undergo some important changes. The anterior body-cavity has greatly diminished in size, and it is only in very thin sections that its lumen is at all distinguishable: it is no longer continued into the præoral lobe, but the whole of it has followed the general rotation, and now lies entirely in the inter-radius CD, near the oral pole. The left body-cavity is also much smaller than before, and, having been pushed from the ventral side by the movement of the vestibule, it now lies entirely on the dorsal side, immediately below the mass of cells forming the floor of the vestibule. The position and form of the right body-cavity are but little altered; and, though its five-chambered continuation forwards is no longer visible in sections, it probably still exists, and certainly re-appears a little later (fig. 29). Both right and left body-cavities now grow rapidly round to the ventral surface; but, as the larva has now reached the true cystid stage, further details as to its anatomy may conveniently be postponed.

Götte, as is well known, described the left body-cavity as splitting into two parts,

one of which formed the vestibule, while the other remained as body-cavity, and grew round the œsophagus: the latter is the left body-cavity of my account, and the real origin of the former is, I think, sufficiently proved by my figures.

BARROIS (3) has already observed this mode of origin of the vestibule, but he gives no figures, and I cannot discover from his very brief note what his views are as to the origin of the left (or, as we may now call it, the *oral*) body-cavity. PERRIER evidently thinks (19, p. 124 note, and p. 281) that BARROIS derives this cavity from the vestibule, thus repeating GÖTTE'S error in a slightly different form; but I cannot feel sure that this is a correct representation of BARROIS'S views, since all that he says is that the right and left body-cavities do not change their places, but form "un manchon autour de l'intestin." This does not seem to me to justify PERRIER'S statements; but, at the same time, it does not account for the presence of two body-cavities, one oral, and the other aboral, such as we find in the cystid.

PERRIER himself believes in the common origin of the vestibule and oral body-cavity; but his figures of this stage show that he has unfortunately only obtained larvæ which had escaped late from the vitelline membrane, and which were consequently somewhat deformed; and in these forms, as I know from experience, the relations of the cavities are excessively difficult to make out, the oral body-cavity in particular being sometimes almost entirely obliterated by the excessive growth of the mass of cells forming the floor of the vestibule. I must, however, protest against the representation of a communication between the vestibule and the oral body-cavity in fig. 11 of PERRIER'S memoir: since this communication, if it ever existed, is, by his own admission, lost long before the stage there represented is reached.

Fig. 29 is interesting as illustrating the way in which GÖTTE'S error as to the origin of the vestibule probably arose. The roof of the vestibule, the walls of which are all still undergoing histolysis, is marked off by a clearly defined line from the tissues which separate it from the exterior, and which have recovered from histolysis. In this section the vestibular cavity, which is still narrow, is only cut in a small portion of its course, and in the next section is not seen at all: in such a case the line marking the boundary of the histolysed mass might be taken as the margin of the vestibular cavity; and, since it runs down almost to the oral body-cavity, these two cavities might easily be supposed to be in connection with one another (cp. 11, Plate 26, fig. 14).

THE CYSTID.

Since the right and left body-cavities no longer occupy a lateral position, they have been spoken of in the foregoing description as aboral and oral respectively. The use of the words "anterior" and "posterior" in this connection was purposely avoided, partly from the confusion which they would create in comparing my account with those of previous writers, and partly because, as we shall see, they have been, and may still be, applied to very different regions of the body. The oral surface (free

end) has always been regarded as ventral, and it would be unwise to alter this nomenclature. CARPENTER, in introducing the alphabetical nomenclature of the radii for descriptive purposes, regarded the anal interradius as posterior : but this arrangement, though almost the only one possible so long as the adult alone is studied, is open to several objections when we come to apply it to the larva. The evidence for these objections will be given later, but obviously the late appearance of the anus makes this structure an inconvenient one to rely upon; and for this reason, as already explained, the interradius of the water-pore is in this paper made the fixed point for the nomenclature of the radii. The other principal objections are :—(1) We have reason to believe that the anal interradius is variable ; (2) even assuming, as has been done in this paper, that the anus normally occurs in the interradius CD, this interradius is almost ventral in the free-swimming larva (fig. 58), and never at any time has any claim to be considered posterior.

This question, as to which part of an Echinoderm should be considered anterior has already been discussed by LUDWIG for *Asterina gibbosa* (16), and the conclusion arrived at by him, expressed in terms of CARPENTER's alphabetical nomenclature, is that the interradius BC is anterior, supposing, that is, that in *Asterina*, as in *Antedon*, the primary water-pore marks the interradius CD.

Now in the free-swimming larva of *Antedon* the arrangement of the calcareous plates suggests that the præoral lobe is not interradial at all, but in the radius C, and the mouth apparently is in the same radius. Theoretically I should be disposed to agree with LUDWIG that the præoral lobe was interradial, and to regard its radial position in *Antedon* as secondary ; but the twisting of the ambulacral and anti-ambulacral fields in *Asterina* makes it a very unsatisfactory subject for the determination of this point : and, until we have further evidence, I prefer to treat radius C as anterior in my description and figures of the pentacrinoid larva of *Antedon*. The change from this to LUDWIG's orientation, if it has to be made, will not be a great one ; whereas the adoption of CARPENTER's orientation of the adult would probably lead us far from the truth.

PERRIER's suggestion that the anal interradius should be considered dorsal (19, p. 154) seems to have nothing to recommend it.

The Body-cavities.—The growth towards the *anterior* (formerly ventral) surface of the oral and aboral body-cavities leads to the formation not only of the transverse mesentery, corresponding in part to the oblique mesentery which formerly separated them (cp. figs. 59 and 60), but also of two longitudinal mesenteries. The oral (left) body-cavity forms a mesentery in the interradius CD (*oral longitudinal mesentery*), in which, as will be presently mentioned, an important structure, the water-tube * runs. The aboral (right) cavity on the other hand forms a mesentery which is some-

* Throughout this paper I have used the name "water-tube" instead of "stone-canal," as the latter is liable to convey the erroneous impression that the tube in question is calcified. The old name has unfortunately been allowed to remain on the plates.

what oblique, being, where it meets the transverse mesentery in the radius C, and at its other extremity, where it joins the stem, in the interradius BC. This is the *aboral longitudinal mesentery.* Its course can be made out from figs. 30 and 31, in which it is cut transversely at two different levels; and from fig. 35, which shows it in longitudinal section throughout its length.

The Water-vascular System.—Hitherto the hydrocele has been spoken of as forming a ring; but it must be remembered that still, as on the seventh day, this ring is incomplete opposite the water-pore. The anterior body-cavity is now, as we have seen, quite small, and lies entirely in the body-wall; and, since it is no longer anterior (except so far as the interradius CD may be considered anterior), it will be better to change its name, and speak of it, as PERRIER does, as the "*parietal canal.*" By the time the cystid phase is reached the hydrocele has cleared itself completely from any histolysis which may have involved it during the previous stages; but both it and its five outgrowths lie completely imbedded in the histolysed mass of cells which form the floor of the vestibule, so that there are at this stage no distinct tentacles (fig. 29). Very soon, however, this mass of cells splits into five broad lobes, which may be looked upon as five primary tentacles; but as at the same time each of the five primary pouches of the hydrocele splits at its free end into three, we have already the rudiments of fifteen tentacles: at a slightly later period each of these fifteen tentacles projects freely and independently into the cavity of the vestibule.

On the ninth day the epithelium of the hydrocele is very high, and its lumen small; but the lumen steadily increases at the expense of the epithelium, until by the fourteenth day the latter has become quite flat, while other changes have taken place, which will be described later. The tentacles long retain a more columnar epithelium.

As soon as ever the cystid form is reached the anterior blind end of the hydrocele (see fig. 61) grows aborally and outwards in the oral (left) longitudinal mesentery; in fact, since it is present before the latter is fully formed, it may be looked upon as determining the position of this mesentery. The tube thus formed, which is the equivalent of the "stone-canal" of other Echinoderms, has the same high epithelium as the rest of the hydrocele ring, and it retains this character throughout, instead of sharing in the changes which the main part of the hydrocele subsequently undergoes. After entering the body-wall it turns slightly towards the oral surface, and on about the tenth day opens into the parietal canal (anterior body-cavity) (fig. 30). The course of the communication thus established between the hydrocele and the exterior is somewhat complicated, but can be traced in figs. 32, 33, and 34, which are taken from a series of transverse sections of a larva of the twelfth day, starting from the oral surface. In fig. 32 the edge of the water-pore is cut, together with the commencement of the parietal canal and of the water-tube. Owing to a slight obliquity in the plane of section, the lower wall of the water-vascular ring is cut on one side of the water-tube; while on the other side (in the radius D) the section passes through the base of one of the tentacles. Several sections intervene between

this and fig. 33, in which the water-tube opens into the parietal canal; as will be seen, the whole of the former and part of the latter lie in the oral longitudinal mesentery, which separates the two ends of the oral body-cavity.

After two sections more we come to that represented in fig. 34, which shows the continuation of the parietal canal below the water-tube. On one side of the oral longitudinal mesentery the section passes so low that it exposes the aboral longitudinal mesentery, lying in the radius C; and between the two longitudinal mesenteries is an open communication between the oral and aboral body-cavities, where part of the transverse mesentery has already broken down. Towards the radius D the transverse mesentery is seen joining the oral longitudinal mesentery.

During the transition to the cystid stage the walls of the parietal canal share in the general histolysis; but in the earliest stage of the true cystid it has recovered from this, its lumen is quite distinct, and it is bounded by a cubical epithelium, which is, however, quite distinct from the epithelium of the water-tube (fig. 33). The epithelium of the pore does not at this stage materially differ from that of the parietal canal; but subsequently the epithelium of the latter flattens out, while that of the former remains cubical, and spreads somewhat further in from the surface.

The Alimentary Canal.—Late on the eighth day the alimentary canal, which is completely filled with cells, and whose true epithelium is with difficulty, if at all, distinguishable, is flattened or slightly concave towards the interradius CD. Almost immediately after its formation that part of the transverse mesentery which lies along this concave side of the alimentary canal, between the oral and aboral longitudinal mesenteries, breaks down, and so establishes the free communication between the oral and aboral body-cavities, which has already been mentioned in describing fig. 34. A remnant of this part of the mesentery is still seen in fig. 30. At the same time the concavity of the mesenteron increases greatly, so that it assumes a crescentic form. One horn of the crescent is blunt, and remains connected with the floor of the vestibule; but the other horn, which is more tapering, loses all direct connection with the vestibule, and runs in the transverse mesentery to join the body-wall in or near the radius C, the aboral mesentery joining its lower border; it acquires a columnar epithelium, and forms the rectum, but does not open to the exterior till a considerably later period.

The blunt horn of the crescent becomes hollowed out by a funnel-shaped depression, which grows down from the vestibule, and round which a high columnar epithelium is developed. This depression (marked "*stomodæum*" in figs. 32–34) is, as LUDWIG remarked (14), eccentric, being in the interradius CD; and this eccentricity becomes more and more marked as the disc increases in size.

The alimentary canal now consists of three distinct regions; (1) stomodæum, (2) stomach, (3) intestine. By about the fifteenth day the stomach has developed a cubical or low columnar epithelium, and its cavity, which has now nearly got rid of its cellular contents, communicates by means of the stomodæum with the vestibule.

The roof of the latter has by this time become very thin, and shortly afterwards splits into five lobes in the well-known way, and places the cavity of the alimentary canal in direct communication with the exterior.

The Body-wall and Stalk.—As already mentioned, the commencement of the cystid stage is marked by the transparency of the superficial tissues; and this is due to the recovery of these tissues from histolysis (fig. 29). Moreover, we noticed that all round the larva there was a narrow hyaline border, in which were imbedded the pyriform "yellow-cells," and in which more careful observation shows us, especially at a later stage and in the stalk, thin strands of granular protoplasm belonging to other cells, and set perpendicularly, or nearly so, to the surface of the body. We might naturally suppose that this hyaline border was the ectoderm; but sections show us that, so far from this being the case, this border only marks the average limit of the nuclei; and, though in many places there is a more or less marked row of cells sending processes through the hyaline border to the exterior, yet these cells are not everywhere present, and are never marked off distinctly from the subjacent mesoderm (fig. 29). In fact there is no distinct superficial layer which we can speak of as the ectoderm; and the term seems only applicable to the cells bounding the water-pore, and to the mass surrounding the vestibule; and even the latter in places usually passes insensibly into the mesoderm (fig. 29), and at a later stage (fig. 35) is largely replaced by mesoderm, so that no part of the vestibule except its floor has a distinct epithelial lining.

A detailed description of the histology of the stalk has been given by PERRIER (19, p. 133).

The Chambered Organ and Axial Organ.—While the mesoderm was undergoing histolysis the cavities of the chambered organ were no longer distinguishable, but now, with the recovery of the tissues from the histolysed condition, they reappear as before in open communication with the aboral body-cavity. We have already seen that the aboral longitudinal mesentery, where it joins the stem, lies in the interradius BC. The present arrangement therefore of the chambered organ is that represented in fig. 57, and this diagram will also serve to explain why in the free-swimming larva it was assumed that the ventral (now anterior) chamber arose from the body-cavity on the left-hand side (cp. fig. 56). Very shortly after the cystid stage is reached the chambered organ becomes completely shut off from the body-cavity by means of thin transverse partitions, whose origin I have not been able to trace satisfactorily. In fig. 29 one of the chambers is seen still opening to the body-cavity, but in fig. 35 they are completely closed, and appear to end blindly in the base of the longitudinal mesentery.

It has already been mentioned that the central core round which the chambers are grouped represents the rudiment of the axial organ. It had not indeed any distinct structure at the previous stage, but as soon as the cystid phase is reached it begins to grow up into the lower part of the longitudinal mesentery, where it forms a cord of

cells especially conspicuous in transverse sections. As it grows higher up towards the oral surface it leaves the mesentery and pushes its way under the peritoneal epithelium into the position seen in fig. 31. This change will be better understood by reference to figs. 36 and 37, where the transition is represented on a large scale, fig. 36 being at the same level as fig. 31. In what has generally been described under the name of axial organ, PERRIER rightly distinguishes two parts—(1), which he calls the "stolon génital," consisting of cells with large deeply-staining nuclei; and (2), the sheath of this organ. It is to the former that I have confined the term "axial organ," as the latter appears to me to be at first nothing more than the peritoneal covering; for, though in figs. 36 and 37 we see something of an additional sheath, this does not appear to me to take any part in the subsequent changes that PERRIER attributes to the sheath of the "stolon génital," but to remain closely connected with this stolon. The true axial organ ends off by the side of the œsophagus at about the level of the transverse mesentery, but its sheath, the cells of which are somewhat different from those of the rest of the peritoneum, is seen in longitudinal sections to run up as far as the floor of the vestibule. The axial organ itself appears to grow up from the stem, and therefore to be mesodermic; PERRIER speaks of it as "d'origine entodermique" (19, p. 163), but by this he appears to mean nothing more than that it is derived from the splanchnic peritoneum, which he believes to be continued into the stem.

We have now traced the organogeny of the cystid up to the time that the vestibule opens to the exterior. Many points in its anatomy have been correctly described by previous observers, and have only been introduced here for the sake of clearness; but in other points the preceding description differs considerably from those of previous writers; and to the discussion of these differences we must now turn our attention.

That the two longitudinal mesenteries have hitherto escaped notice is, I believe, due to the fact that neither GÖTTE, LUDWIG, nor PERRIER cut transverse sections. So far as these two mesenteries were seen by these observers, they appear to have been either confused with the axial organ, or explained in some other way. Thus PERRIER (19. p. 142) describes the oral body-cavity as pushing its way down in the angle of the alimentary canal, and so driving before it that part of the tranverse mesentery which I have described as breaking down. To him, therefore, the cavity into which the axial organ projects is part of the oral body-cavity, while to me it is part of the aboral cavity, freely open above to the oral cavity. But the process described by PERRIER should lead to the formation of *two* aboral longitudinal mesenteries, whereas transverse sections clearly show that only one is present (fig. 31).

Part of the oral longitudinal mesentery was undoubtedly seen by LUDWIG, who regarded it as an incomplete partition separating off that part of the body-cavity into which the water-tube opens (14, p. 38). To PERRIER is due the credit of correcting LUDWIG's statements with regard to the water-tube, and denying its connection with the oral body-cavity. But, though I fully agree with PERRIER in this point, I am compelled to differ from him in regard to details. He describes a single "tube

hydrophore" leading from the hydrocele ring to the water-pore, and having in the early cystid stages the same structure throughout its course, though at a later period the part within the body-wall (parietal canal) has a thinner epithelium than the "partie libre" (water-tube). To me there is from the first a distinct difference between these two parts, corresponding to their distinct origin: while the so-called "partie libre" lies throughout its course in the oral longitudinal mesentery. Moreover PERRIER describes this "tube hydrophore" as forming a simple U, and in Plate I., fig. 9, he figures its lumen as cut throughout its length in a single section. My researches do not lead me to regard such a section as possible. The course of the two cavities is shown in figs. 32, 33, and 34, and seems to me closely to correspond with LUDWIG's description of it (14, p. 38), except that there is a closed parietal canal in place of his cavity L′ opening to the oral body-cavity (cp. also 19, fig. 16).

The rest of PERRIER's description, especially the histological part, is extremely good; but I cannot accept his view that the axial organ is a tightly stretched cord, which forces the alimentary canal to assume a spiral arrangement. Not only is this view unintelligible phylogenetically, but transverse sections would have shown him that, in most of its course, the axial organ does not lie in the angle of the alimentary canal, and is therefore not in a position to produce the effect which he supposes.

To his description of the later stages of the cystid, subsequent to the rupture of the vestibular roof, I have little to add; but it may be as well to give a brief sketch of the principal changes which occur.

The whole floor of the vestibule, as well as the œsophagus, is lined by ciliated columnar epithelium. The walls of the stomach are formed by high columnar cells, the free ends of which are merged (in sections) in a structureless granular mass (fig. 39). PERRIER attributes this to the extreme delicacy of the cells, causing instant decomposition after death; but I am more inclined to regard this mass as a form of secretion from the cells than as due to bad preservation; and I may call attention to the fact that W. THOMSON (21, p. 525) described glandular folds in the stomach, of which he says, "the slightest touch, even of a hair, ruptures them and causes the effusion of a multitude of minute granules, some colourless and transparent, and others of a yellow or brownish hue." I regret to say that I made no observations with respect to this point on the living animal. It is also possible that these granules are the last traces of the histolysis: at a later period the margins of the cells are often quite easily seen, and are clothed with long cilia.

Very soon after the rupture of the roof of the vestibule the anus opens to the exterior, and the alimentary canal at once becomes filled with the siliceous skeletons of diatoms, &c., which render the cutting of thin sections almost impossible. LUDWIG, as the result of the examination of "mehr als hundert Larven" (14, p. 44), asserts that the anus opens, not in the same interradius as the water-tube, but, following the curvature of the alimentary canal, in the one before it, *i.e.*, on the nomenclature here adopted, in the interradius B C. This is a point of considerable importance, but I

cannot but think that LUDWIG is mistaken, and that here again transverse sections would have led him to a different conclusion. From longitudinal sections, or from whole larvæ made transparent, such as LUDWIG used, I have been totally unable to arrive at any certainty on this point; but in series of transverse sections the radii are clearly marked, and the relations of all the organs to them can be seen at a glance.

Not counting numbers of such series before the appearance of the anus, in all of which the rectum joins the body-wall, either in the radius C or in the interradius C D (figs. 30 and 34), I have series of transverse sections through more than twenty larvæ, in which, with a single exception, the anus and water-tube most certainly lie in one and the same interradius. Since the two are at different levels, this point is usually only seen by looking through a series of sections; but in fig. 38 a section is represented which, by a fortunate obliquity, shows both anus and water-tube at once. The exception above mentioned is interesting. In one of my larvæ the anus does lie in the interradius B C, but close to the radius C; and, if LUDWIG's suggestion be true, that the anal interradius is not homologous in all Echinoderms, but that the position of the anus has undergone a phylogenetic change, this exception may be looked upon as a case of reversion to a condition which is permanent in the Asterids. In any case this exception does not affect the conclusion that the anal interradius in *Antedon* is normally the same as that of the water-tube; while it justifies me in making the latter, rather than the former, the standpoint for the nomenclature of the radii.

PERRIER unfortunately throws no light upon this point; he simply describes the alimentary canal as making "un tour de spire complet" (19, p. 141), which seems to support my account; but he says nothing about the radii, and if he had been aware of Ludwig's error, he would surely have mentioned it.

The stomach, which in the previous stage was thick and extended almost to the centre of the body, is now much thinner, and the alimentary canal winds as a spiral round a well-developed axial cavity (fig. 39). The axial organ, however, still retains a central position, and to enable it to do this the peritoneal epithelium covering it is pushed into a mesentery, which, however, does not reach the body-wall.

The cells of the axial organ, at first grouped irregularly, now range themselves round a central cavity, but, up to the time of the formation of the arms, the organ does not usually undergo any further complication.

Late in this stage the mesenteries begin to break down; the aboral one is the first to go (fig. 39), but the transverse mesentery soon follows, though both continue for some time to be represented by fibrous bands running at intervals from the alimentary canals to the body-wall. Other similar bands are also developed independently of the mesenteries, especially between the floor of the vestibule and the œsophagus.

The water-vascular system really changes considerably just before the end of the last stage, but the description of these changes has, for convenience, been left till now.

The water-vascular ring closes completely, and about the same time a number of

muscular (?) threads appear, which traverse the lumen of the vessel. These threads appear to me to be nothing more than processes of the ordinary cells of the epithelium, which has now become extremely thin. At a later period the nucleus shifts into the middle of the thread, which then appears to be a single cell, with a protoplasmic core surrounded by a formed substance (fig. 41). LUDWIG, however, describes them (13, p. 17) as being composed of a central muscular thread, covered by a thin epithelial layer, derived from the epithelium of the water-vessel.

About the time of rupture of the vestibule the number of tentacles increases to twenty-five, which, however, are still arranged in five radial groups.

The epithelium of the parietal canal flattens out, and gradually fuses with the surrounding mesoderm, so as to be no longer recognisable. At the same time a very distinct epithelium grows inwards for a certain distance from the water-pore, but never reaches the expanded part of the parietal canal shown in fig. 33. We have now an arrangement which closely corresponds with that seen in other Echinoderms, *e.g.*, in Ophiurids (cp. 15, Plate 14, fig. 1); in both the water-vascular ring communicates with the exterior by means of the following structures :—(1) a water-tube, with a columnar epithelium; (2) a swollen part, with a flat epithelium, called the *parietal canal* in *Antedon*, and the *ampulla* in Ophiurids; (3) a pore-tube with columnar epithelium ; (4) a water-pore.

The two vessels, supra-intestinal and sub-intestinal, described by PERRIER (19, p. 143), are very conspicuous long before the end of the cystid stage, and can be traced into connection with one another at the base of the aboral mesentery, but they do not appear to have any connection yet with the chambered organ.

In the latest stages examined by me the nervous system was not yet clearly developed.

The peritoneal epithelium covering the alimentary canal remains distinct up to the end of the cystid stage, but the somatic peritoneum usually fuses with the body-wall at a very early period. The outer wall of the water-vascular ring, too, completely loses its epithelium, which, as was noticed by PERRIER (19, p. 150), fuses with the mesoderm of the body-wall (fig. 41).

The whole exterior, except the floor of the vestibule and the tentacles, remains entirely destitute of ectodermal covering, and this I believe to be equally true of the adult. The walls of the water-pore are probably ectodermic, and the ambulacral epithelium of the arms is certainly so, being directly derived from the floor of the vestibule, but elsewhere I can find no true ectoderm. PERRIER describes a flat epithelium in the adult (18, p. 50), though he cannot find it in the larva (19, p. 125); and VOGT and YUNG also speak of a flat epithelium (22, p. 532), but I do not feel sure that they are not simply following PERRIER.

That an epithelium appears in surface views to exist in some parts I willingly admit, but in section we see that the superficial cells are in no way marked off from the mesoderm ; and on the dorsal surface of the pinnules and arms no appearance of

an epithelium is visible, even in surface views, the cells being separated by considerable intervals, and the surface being formed by a strong non-cellular membrane (see PERRIER's excellent figure, 18, fig. 11). This conclusion is completely borne out by nitrate of silver preparations (HARMER's method) ; at first sight they sometimes appear to show an epithelium, but in most parts no silver lines mark out the limits of the cells, and in all cases careful focussing shows that the nuclei are at very different levels, so that the epithelium, even if present, is certainly not flat.

Two points remain to be described which were purposely omitted from the foregoing account of the cystid :—(1), the Sacculi ; (2), the Skeleton.

The Sacculi.—Before giving an account of the development of these bodies, it may be well to describe their structure in the adult, so far at least as it is known. The only good description and figures of them that I have been able to find are those of PERRIER (18), but his account does not seem to have received much attention. Each sacculus is a spherical body, bounded by a thin membrane, in which are imbedded a few flattened nuclei. The interior of the sphere is more or less filled with a number of pyriform sacs, each of which in its turn is filled with highly-refractive spherules, and is bounded by a membrane, continued at its inner end into a long thread, which joins the wall of the sacculus. One of these pyriform sacs, with its process, is seen in fig. 42(*c*). The refractive spherules, which usually take up colouring-matter with great avidity, have, at any rate in some cases, a definite arrangement round a central cavity. Two such sacs are shown in transverse section in fig. 43. The spherules, which are spherical when isolated, are evidently much compressed within the sacs. On the wall of each of these pyriform sacs PERRIER describes a small nucleus ; but this point I have not yet been able to confirm, though the peculiar optical properties of the spherules, and the readiness with which they stain, render the investigation of this point a matter of no ordinary difficulty, and make the negative evidence afforded by my observations of little importance.

The greater part of the sacculus is imbedded in the tissues, but at one point its cavity is only separated from the exterior by its limiting membrane, which at this point stains deeply, and does not exhibit any nuclei (see the diagram, fig. 44). During life the sacculus has a swollen appearance, and its free margin frequently bulges out towards the exterior ; this is due to the presence of a quantity of mucus between the pyriform sacs and the wall of the sacculus ; and, if a living pinnule be placed on a slide with a drop of water, this water becomes charged with mucus ; though whether this is due to a continuous secretion, or to injury to the pinnule, I am unable to say. Any rough treatment, however, of the pinnule leads to the escape not only of increased quantities of mucus, but also of many of the spherule-bearing sacs. In spite of this, it is rare to find in sections a sacculus freely open to the exterior, and I can only suppose that there is some means of rapidly mending the ruptured membrane.

Let us now turn to the development. The first rudiments of the sacculi appear

on about the tenth day, as five small bunches of cells situated at the radial angles of the water-vascular ring. In this position they were recognised at a later stage by W. THOMSON (21, Plate 26, fig. 1, &c.) and by LUDWIG (14, Plate 12, fig. 2), and it is, therefore, surprising to find PERRIER (19, p. 150) stating that they *alternate* with the groups of tentacles, especially as this is opposed to his own figures (19, Plate 2, fig. 16). Each of these groups of cells really has the form of an epithelium surrounding a small slit-like cavity. The side of the organ towards the water-vessel remains flattened, but the outer face soon becomes convex, and so increases the size of the central cavity. At the same time certain cells are pushed out into the central cavity from the flattened side (fig. 40). In sections these cells appear to lie quite freely in the cavity, but I have very little doubt, from what I have seen in later stages and in macerated specimens, that they really remain connected with the epithelium by a fine process; and, indeed, some indication is given of this in fig. 40.

At first the nuclei of the cells composing the epithelium are indistinguishable from those of the surrounding mesoderm, though those of the cells within the cavity are somewhat larger. Very soon, however, all the cells of the sacculus undergo considerable changes, so that by about the twelfth day their contents stain almost as readily and deeply as in the adult. Fig. 41 shows the appearance of a section through a sacculus on about the twentieth day. The spherule-bearing sacs are developed much as in the adult; though, in correspondence with the small size of the sacculus, they are much fewer in number and smaller in size; being for the most part cut obliquely, they show neither the central cavity nor the thread-like continuation at the base, but the latter can be seen in teased preparations (fig. 42, *b*). From their size it might be supposed that each spherule was derived from a single cell, and, perhaps, even from the nucleus of that cell, but a careful examination of the cells composing the wall of the sacculus makes this improbable. It will be seen (fig. 41) that the epithelium of this wall is already much flatter than in the previous stage, though by no means so thin as in the adult. Each cell of this epithelium contains several refractive spherules, similar in character to those in the central cavity, but smaller in size than most of them; and besides these each cell bears a nucleus, which is, however, much reduced in size and obscured by spherules. From the analogy of these cells I was led to believe that each spherule-bearing sac (not each spherule) represented a single cell, which had become greatly enlarged, and whose protoplasm had broken down into spherules of some formed matter. This conclusion is borne out by the examination of teased preparations of larvæ at various ages (fig. 42, *a* and *b*); but between the earliest stage of the refractive spherules (fig. 42 *a*) and the cells represented in fig. 40 I never succeeded in finding any intermediate form.

The cells of the central cavity alter in their chemical and optical properties before those of the epithelial wall: and it was probably this that led PERRIER to describe the sacculus in its earliest stage in the regenerating arms as consisting solely of a few refractive spherules, without any definite wall (18); it was hardly likely that he

would detect this wall without sections before it began to stain differently from the rest of the mesoderm.

My investigations on the subsequent changes undergone by the sacculi are still far from complete; but I have frequently noticed a few quite young spherule-bearing sacs in a fully developed sacculus of the adult; and I have some reason for thinking that these sacs break down and form the mucus which distends the sacculus.

Several suggestions have been from time to time made as to the possible function of these organs; but the most obvious one, that they are excretory, has generally been given up, because no external opening has been found. I have little doubt that one of their functions is to secrete mucus; though whether this mucus is simply protective, or whether any waste products are got rid of with it, I am unable to say: it is quite possible, however, that more than one function may be performed by them.

One suggestion, however, as to their nature cannot be passed over in silence. They have recently been described by VOGT and YUNG (22, p. 570) as collections of algoid zoospores; and the amœboid spores of these Algæ are supposed to enter the free-swimming larva in the form of "yellow-cells." Dr. P. H. CARPENTER has already discussed these statements (8), and has shown strong reasons for doubting them; and to his arguments I will now add others.

VOGT and YUNG's theory involves three distinct questions, which we shall do well to consider separately: (1) Are the "yellow-cells" amœboid spores of Algæ? (2) Are the sacculi zoospores of Algæ? (3) Have the yellow-cells and sacculi anything to do with one another?

(1.) The colour of these cells when seen by transmitted light is certainly suggestive of chlorophyll; but, of course, there are many other green colouring matters, and I unfortunately had no opportunity of applying the spectroscope to these cells. Their appearance in the free-swimming larva has already been described. In the later stages, and in the adult, they are, so far as I know, always superficial, and, when decolorised, indistinguishable from the cells surrounding them; indeed I am strongly disposed to agree with PERRIER that the ordinary connective-tissue cells and these yellow-cells "sont morphologiquement de même nature, que ces derniers ne diffèrent des autres que parce que la matière jaune a envahi tout l'intérieur de la cellule et distend ses parois" (18, p. 53). The objections, then, to regarding these cells as amœboid spores of Algæ may be summed up as follows:—

(*a*) They appear before the rupture of the vitelline membrane.

(*b*) They acquire their colour gradually.

(*c*) They closely resemble the surrounding cells in all points except colour.

(*d*) They are always superficial.

(*e*) They exhibit no amœboid movement.

As far as I am aware, the vague possibility that the colouring matter of these cells may be chlorophyll is the only point of support for this part of VOGT and YUNG's theory.

(2.) This part of the theory is to me even more incredible than the last. VOGT and YUNG state that certain "paquets de granules réunis ont, suivant M. PERRIER, des queues très longues et déliées ; ce sont donc de véritables zoospores" (22, p. 570). That certain "paquets de granules" do exist buried in the tissues of the adult I willingly admit, but they have no sort of resemblance to the true sacculi, and the account given above of the development of the latter is entirely opposed to the supposition that they are formed by collections of these granules. Moreover, the fine processes of the spherule-bearing sacs were described by PERRIER as joining the wall of the sacculus ; they exhibit no amœboid movement, and are not in the least suggestive of flagella.

But the strongest argument of all against this part of VOGT and YUNG's theory is the fact that during life the contents of the sacculi are *absolutely colourless*, which is entirely inconsistent with the statement that they are algoid zoospores. Yet this fact should have been well known, since it has been frequently mentioned (21, p. 527 ; 6, p. 127 ; 18, p. 67).

(3.) It is impossible absolutely to prove that the yellow-cells and sacculi have no connection with one another ; but their extremely different appearance in the living animal and the entire absence, so far at least as my observations go, of any intermediate structures between them render such a connection so highly improbable, that the onus of proof must rest with Messrs. VOGT and YUNG.

The Skeleton.—As already mentioned, the number of stem-joints in the free-swimming larva is variable, but by the time the larva fixes itself from thirteen to fifteen are usually present, and this number is maintained throughout the pentacrinoid stage. Very shortly after fixation all the stem-joints in succession, beginning with the most anterior one, form complete rings, the closure being of course in the radius C ; and at the same time longitudinal processes spring from them at a short distance from the inner margin, while the horizontal processes already noticed anastomose, so as to increase the diameter of the plate: such a plate with rudimentary longitudinal processes is seen in fig, 51. New longitudinal processes now arise from this network, which again anastomose freely with their fellows ; and in this way the structure of each stem-joint becomes very complicated. Each consists of a transverse plate, from each side of which arise a number of longitudinal rods, united among themselves by cross anastomoses ; and the transverse plate, which marks the middle of the joint, projects both externally and internally (*i.e.*, towards the hollow axis) slightly beyond the longitudinal rods (fig. 46). The origin of these longitudinal rods has been misunderstood by both THOMSON (21, p. 523) and GÖTTE (11, p. 495), who regard them as bundles of rods arising, not *from* the ring, but *within* it, or, in THOMSON's words, as "a hollow sheaf of parallel calcareous rods . . . as it were, *bound* in the centre by calcareous rings."

By the elongation of the stem-joints the dorsocentral plate is rapidly driven forwards into the disc of attachment, where it remains as a circular, and afterwards pentagonal, plate, which undergoes no important changes.

The oral and basal series of plates, which were oblique in the free-swimming

larva, now assume a transverse arrangement, in correspondence with the transverse position of the mesentery separating the oral and aboral body-cavities. At the same time they increase greatly in size, though not much in thickness (figs. 46 and 49), and soon fill up the wide gap which formerly existed in the radius C. One of the oral plates envelopes the water-pore.

But by far the most interesting skeletal changes at this stage are connected with the three underbasals. The inner border of each of them soon becomes smooth and concave (fig. 50), and they then range themselves in a circle around the chambered organ, just above the top stem-joint. Two of them are seen in a cystid of the tenth day in fig. 46; but their relation to the radii is better seen in fig. 48; in this section the top stem-joint is seen lying immediately under the underbasals, and the closing point of this ring-like joint, still faintly indicated, marks the radius C, which, of course, can also be determined by following the series of sections. One of the previous sections is indicated by a dotted line, in order to make the positions of the radii more evident. We now see that the arrangement of these plates is still the same as in the earlier stage, the smallest plate being in the radius A. At a slightly later stage these three plates fuse with one another and with the top stem-joint, so as to form one large plate, which is represented as seen from the aboral side in fig. 52, and in side view in fig. 53. It will be seen that, though the sutures of the underbasals still persist, the plates themselves have grown out into five angles. These angles are radial in position, fitting in between the bases of the basal plates; and, while the underbasal of the radius A produces only one angle, each of the other two grows out into two angles: this fact strongly suggests that each of these larger underbasals represents a pair of coalesced plates, and that the primitive arrangement would be the possession of five radial underbasals. At a slightly later stage the sutures disappear, though the groove separating the underbasal series from the top stem-joint persists for some time. The whole large plate thus formed has always been regarded hitherto as a simple centrodorsal, whereas, in reality, the top stem-joint, forming only the lower half of this large plate, is the true centrodorsal. But, though agreeing in regarding this large plate (underbasals *plus* centrodorsal) as a simple centrodorsal, previous writers have differed somewhat as to its mode of origin. WYVILLE THOMSON described it as a modification of the top stem-joint, but suggested that it represented "a coalesced series of nodal stem-joints in the stalked Crinoids" (21, p. 536); and this view was adopted by W. B. CARPENTER (10, p. 737). GÖTTE, however, regards it as arising from the fusion of certain small plates (number not mentioned) developed in quite a different region from the youngest stem-joints, and surrounding the stem at some little distance from its growing point. In the deformed specimen which he figures (11, fig. 50) it is very probable that he actually saw one of the underbasals; but in his description and his fig. 13 he appears to refer to something quite different, possibly to broken pieces of the basals; for, as I have shown, the underbasals do not surround the stalk, but are developed close to its growing point,

and if any part of it is overlapped by the basals, the underbasals are overlapped by them too (fig. 45); moreover they are developed at a much deeper level than the basals, and one at least of them is radial.

Perhaps it will be well before proceeding further to give reasons for regarding the three plates which I have described as underbasals, and not as parts of the centrodorsal, as GÖTTE has done. Of course, if there had been five plates instead of three, and these plates had all been radial, there could be no question about the propriety of this nomenclature; and the facts above related are strongly in favour of regarding these three plates as representatives of five radial plates. But it is not on this alone that I have relied. Some of the dicyclic Palæocrinoids (*e.g.*, the Ichthyocrinidæ) have throughout life three instead of five underbasals, one of which is smaller than the others, and in some forms it is situated anteriorly, opposite to the anal interradius; so that these three plates have precisely the same symmetry as those in *Antedon*. Moreover, Dr. CARPENTER informs me that in the structure of the arms and rays the family Ichthyocrinidæ more nearly approaches the Comatulæ and Pentacrinidæ than do any of the other palæozoic Crinoids.

I cannot attempt to discuss in full the importance of this discovery of underbasals in *Antedon* on the classification of the Crinoidea, but attention must be called to the somewhat curious way in which it confirms the generalisations of WACHSMUTH and SPRINGER (23). As a result of their admirable researches among the Palæocrinoids, these observers find that the presence of underbasals is so invariably correlated with the existence of interradial angles in the stem that these angles may be taken as an indication of the existence of underbasals, even when the latter are invisible on the surface. They then state that, as regards the stem, the Neocrinoids are "built upon the plan of the dicyclic Crinoids" (23, Sect. I., p. 71), although hitherto they have been regarded as monocyclic; and, after pointing out that in all Comatulæ the angles of the centrodorsal are interradial, they add, "upon this mainly we base the opinion that perhaps also the Comatulæ in their early larvæ had rudimentary underbasals" (23, Sect. II., p. 222). Against these generalisations CARPENTER (9) raised what certainly appeared to be insuperable objections: firstly, that many of the Neocrinoids (*e.g.*, *Apiocrinus*) were not "built upon the plan of the dicyclic Crinoids," but had radial angles to the top stem-joint; and, secondly, that in the larval *Antedon* also the angles of this plate were at first radial, the interradial angles which it possesses in the adult being due to a secondary growth. Now, however, we learn that the underbasals are really present all the time, not, as WACHSMUTH and SPRINGER suppose, "hidden by the column" (23, Sect. I., p. 293), but actually visible in the larva of *Antedon*, as the radial angles of the so-called centrodorsal; and that the true centrodorsal (= top stem-joint), with which the underbasals are indistinguishably fused, either remains without angles, or by a later growth develops radial angles, and at the same time overlaps and conceals the underbasal angles.

The remaining changes in the skeleton are already so well-known from the works

of WYVILLE THOMSON (21) and W. B. CARPENTER (10) that no further description need be given here.

GENERAL MORPHOLOGY.

It is now time to justify the adoption of BARROIS's theory with regard to the orientation of the larva. In the first place, let us consider what are the grounds upon which the old orientation was based; they may be briefly summed up as follows :—

(1.) WYVILLE THOMSON, with peculiar theoretical opinions on the subject of larval forms, named the larval mouth the "pseudostome," and the præoral pit the "pseudoproct," and fancied he could distinguish an alimentary canal joining them. This view needs no comment.

(2.) The mouth, assumed to be anterior, ultimately appears at the pole opposite to that by which the animal fixes itself, and this is probably the main reason why the stalk has been regarded as posterior. We know, however, that many larvæ (Ascidians, Cirripedes, Polyzoa) fix themselves by the anterior end, and afterwards rotate the mouth round to the opposite pole.

(3.) GÖTTE described the œsophagus of the pentacrinoid as surrounded by the *left* body-cavity, as is the case in other Echinoderms; and this, if true, would form a strong objection to BARROIS's views. BARROIS, however, escapes from this difficulty by regarding the right and left body-cavities as retaining a lateral position; but this view involves a belief in a remarkable difference between the Crinoids and the other Echinoderms—an objection which BARROIS ignores. For my own part, as already stated, I am convinced that the two body-cavities do not remain simply right and left, but that, on the other hand, the shifting which they undergo is such as, on the old orientation, to bring the *right*, and not the *left*, cavity into an oral position in the cystid. Only by adopting the new orientation can we bring the Crinoids into correspondence with other Echinoderms on this point.

(4.) GÖTTE described the anus as appearing on what was originally the ventral side; it is true that it is not actually in the radius C, but it is so near it that it may be described as lying almost exactly between the mouth and what BARROIS has called the præoral lobe. Here then we encounter a really serious objection to BARROIS's theory, and one which, if his account of the body-cavities were accepted, seems to me absolutely insuperable. It would be interesting to know how BARROIS himself meets this difficulty, but unfortunately in his brief note he makes no mention of it at all.

But if the account of the body-cavities given in the preceding pages of this paper be accepted, the position of the anus does not seem to me to place any real difficulty in the way of regarding the fixed end of the larva as the præoral lobe. LUDWIG has already discussed the position of the anus in Echinoderms at considerable length, and with his usual ability (14); and he has come to the conclusion that, while the interradius of the water-tube is probably constant, that of the anus varies in the

different groups. Thus, if we make use of the nomenclature adopted in the preceding pages, and call the interradius of the water-tube CD, then the anal interradius will be in Holothurians and Echinids AB; in Asterids (but not in Crinoids, as LUDWIG thought) BC; and in Crinoids CD, showing a progressive shifting of its position up to the last group. The curvature in the course of the alimentary canal to which this shifting leads is, as LUDWIG pointed out, already shadowed forth in the bilaterally symmetrical larvæ of most Echinoderms in the curvature of the alimentary canal towards the ventral surface; and the shifting of the anus appears to take place along this ventral side, in the mesentery separating the right and left body-cavities.

Let us now see how this affects the case of the larva of *Antedon*. The analogy of other Echinoderms justifies us in supposing that the blastopore represents the anus; and, indeed, this assumption forms the main point of BARROIS's argument. We are not here directly concerned with the question whether the blastopore is terminal, or a little dorsal or ventral: it is enough for our present argument that both BARROIS and myself are convinced that it is somewhere near the pole which we have called posterior —nearer to it than is the larval mouth. This being so, let us imagine the anus shifting its position along the line of the mesentery separating the right and left body-cavities. If these cavities retained their lateral position, the anus would continue ventral, and could only move forward as far as the larval mouth. But these lateral positions are not retained; and, if at the time of shifting of the body-cavities the anus was on the ventral side, then the anus, with the ventral mesentery, would be shifted over on to the right side of the larva. I have not been able to represent this clearly by diagrams, but a little consideration will show that the mesentery represented in fig. 59 had originally a ventral position, and the anus may be imagined to lie in it. In this figure the mesentery is oblique, but after the rotation of the mouth to the posterior pole this oblique mesentery becomes transverse, and grows completely round the larva. There is nothing then that I can see to prevent the anus from continuing to migrate along the line of the mesentery, until it not only reached, but even passed, the radius C, in which the mouth formerly lay, so that, instead of stopping, as it does in Asterids, in the interradius BC, it might reach the interradius CD, in which we find it in the pentacrinoid stage of *Antedon*: and this view is to some extent supported not only by the exceptional case already mentioned, but also by the fact that the rectum, before the appearance of the anus, is attached either in the radius C, or at any rate nearer to it than the future anus is.

If once the possibility be admitted of the shifting of the anus along the mesentery, I do not see that any strong objections can be raised against the above hypothesis; but I confess that I should never have put this hypothesis forward if I had not been led to doubt the correctness of the old orientation by the fact that it necessitates a belief in very great differences between Crinoids and other Echinoderms.

Let us now for a while assume the correctness of the old orientation—let us suppose

that the larva swims backwards and fixes itself by its posterior end, and see what these differences are. They may be summed up as follows :—

(1.) The blastopore closes at or near the anterior end. In all other Echinoderms it either closes posteriorly or persists as the anus.

(2.) The first rudiment of the hydrocele appears at the posterior end of the right body-cavity (though not connected with it). In all other Echinoderms it is at the anterior end of the left body-cavity, from which it is usually derived.

(3.) The water-pore is on the right side, posterior to the right body-cavity. It is usually on the left of the middle dorsal line, anterior to the left body-cavity.

(4.) In the later stages the right body-cavity surrounds the œsophagus; in all other Echinoderms it is the left body-cavity which does this.

(5.) Looking at the animal from the side on which the right body-cavity lies, the alimentary canal winds round in the same direction as the hands of a watch; whereas, as LUDWIG has shown, the same direction for the winding of the alimentary canal is obtained in other Echinoderms, even in the bilaterally symmetrical larvæ, by looking at them from the left side.

These facts afford, I think, an almost overwhelming proof that the old orientation is wrong; but, as a final argument in favour of BARROIS's theory, I will show what a close comparison it enables us to make between the larva of *Antedon* and that of *Asterina gibbosa*, as described by LUDWIG (16). In doing this, however, I am compelled to differ somewhat from LUDWIG's nomenclature of the parts of the larva, which he gives on p. 143, since I regard the mouth as ventral, and the whole of the larval organ as anterior, representing the præoral lobe.

With regard to the external form not much can be said: but in both types the larval mouth lies in the middle of the ventral surface, and in both there is a large præoral lobe; and it is perhaps not extravagant to compare the large sucker of the præoral lobe in *Asterina* with the "præoral pit" by which the larval *Antedon* fixes itself.

In the internal anatomy the resemblance is more striking, as I have endeavoured to show in the two diagrams (figs. 61 and 62). In both these figures we are supposed to be looking at the larva from the side on which the hydrocele lies, which is already the oral side in one, and will be so later in the other.

In *Antedon*, at one stage at any rate, there are four separate cœlomic pouches; and, though in *Asterina* there is only one, yet this is partially divided into four, which closely correspond with those of *Antedon*. In the first place we have in both an anterior unpaired body-cavity, occupying the whole or part of the præoral lobe, and opening to the exterior by a pore on the left side: it is true that this pore is dorsal in *Asterina*, and lateral in *Antedon*; but then this pore has in later life a close connection with the hydrocele, with regard to which, as the diagrams show, its position is much the same in both larvæ; indeed, its position in *Antedon* is just that in which the change of position of the body-cavities would have left it, had it been originally dorsal. The

position of the first rudiment of the hydrocele is also strikingly similar, though this point is not fully shown in the diagrams. In both it appears on the left side, at the anterior end of the left body-cavity, in close connection with the anterior body-cavity; for, though in *Asterina* it is regarded as an offshoot of the left body-cavity, as it is in most other Echinoderms, yet it is clear from LUDWIG'S description and figures that it is really formed at the junction of this cavity with the anterior body-cavity, and belongs as much to one as to the other. In *Antedon*, where the connection between these two cavities never exists, the hydrocele at first opens into the anterior body-cavity, though later it becomes temporarily shut off from it.

In both larvæ the hydrocele grows as a ring round the œsophagus, and in both again it gives off five primary radial diverticula. Two points of difference, however, strike us in the diagrams with regard to the relations of the hydrocele. In the first place, the position of the water-tube with respect to the point of closure of the water-vascular ring appears to be different; but, in the present state of our knowledge of other Echinoderms, it would be unsafe to speculate on the meaning of this difference. In the second place, in *Antedon* a radius, and in *Asterina* an interradius, is directed forwards. This may be due to the shifting of the body-cavities in *Antedon*, or be connected with the peculiar twisting undergone by *Asterina*, by which the ambulacral and anti-ambulacral systems are made to close in different interradii; but here again we touch upon the question of which part, radial or interradial, of an Echinoderm is to be considered anterior, so that this point, too, must be left for more extended investigations upon Echinoderm embryology to settle.

Returning to the diagrams, we see that there is a considerable resemblance also in the course taken by the mesentery separating the right and left body-cavities. This mesentery runs along the opposite side of the body to that which we have been examining, and is hence represented in the diagrams only by dotted lines, the alimentary canal in *Antedon* having been omitted for this purpose. Since the mesentery is incomplete in *Asterina*, no very close comparison can be made, but it will be seen that in both it runs obliquely across the anti-ambulacral side, up to the water-pore. How far this resemblance is accidental I am unable to say, but I cannot believe that it is wholly so.

For a comparison of the skeleton in the two forms, so far as it can be made, I must refer to the works of previous writers (7 and 20), but I may point out that the series of interradial plates in *Asterina* developed round the right body-cavity at first forms a horseshoe-shaped curve, open towards the præoral lobe, just like the basals of *Antedon*, to which they correspond.

It might have been expected that the change in the orientation of the Crinoid larva would seriously affect the question of homologies of the plates of the Crinoidal calyx; but, as a matter of fact, owing to GÖTTE'S somewhat fortunate mistake, this is not the case, and P. H. CARPENTER'S arguments derived from the development of the basals and orals round the right and left body-cavities respectively remain unaltered (7).

The only new piece of evidence which my observations afford on this point is the fact that at the time of its earliest development the water-pore has no connection with any of the skeletal plates; so that in this point too *Antedon* resembles other Echinoderms. In fact it seems probable that this and the other external openings (mouth and anus) of the Echinoderms opened primitively in or near the median line, along which ran the mesentery separating the right and left body-cavities; and that at the time the different groups of Echinoderms separated from one another the mouth alone had departed from this position, and had taken up a definite station in the centre of the left side. The water-pore, which may have been from the first slightly on the left side, subsequently worked its way, in some groups (Crinoids and Ophiurids) on to the oral, in others (Echinids and Asterids) on to the aboral, side; so that, although its interradius probably remains the same, its position with regard to the calcareous plates is secondary. The anus, on the other hand, had already commenced to shift its position along the line of the ventral mesentery, and in some groups it continued to do so without migrating either to the dorsal or ventral side, while in others such shifting of position was soon put a stop to by the migration of the anus on to the aboral surface. Thus in the Crinoids the anus retains a primitive position, in that it still lies in the mesentery separating the right and left body-cavities (at any rate as long as this mesentery is distinguishable); while, owing to this position, it has been able to continue its shifting past the different radii to a much greater extent than in any other Echinoderms, and in this respect its position is decidedly secondary. In the Echinids and Holothurians, on the other hand, the migration of the anus to the aboral surface must have taken place comparatively early, so that in these groups it is far nearer its primitive interradius than in the Crinoids. Finally, in Asterids we have an intermediate condition, the anus having advanced further by a whole radius than in Echinids and Holothurians, but having eventually migrated towards the aboral side before reaching the interradius to which it attains in the Crinoids.

Of course, in coupling the Echinids and Holothurians together I do not mean to assert that they branched off together from the primitive Echinoderm stock. Given a primitive form, such as I have imagined, with the mouth on the left side, and the anus and water-pore lying between the ambulacral and anti-ambulacral systems, there is no reason why an aboral position for the anus should not be arrived at independently in several different groups.

How far *Antedon* exhibits a primitive feature in having its right and left body-cavities separate from the anterior body-cavity I am unable to say. Hitherto the anterior body-cavity has only been distinctly recognised in *Asterina*; but the evidence afforded by *Antedon* and *Asterina* is strongly in favour of regarding the presence of an anterior body-cavity distinct from the hydrocele as a primitive feature in Echinoderm larvæ, and it is almost certain that such a cavity will be found in other forms. The hydrocele probably opened into this anterior body-cavity from the first (its early

separation in *Antedon* being probably secondary), but the water-pore appears to have belonged primarily to the body-cavity, and to have been only indirectly connected with the hydrocele.

That the completely formed free-swimming larva of *Antedon* is not primitive must be admitted, since its body-cavities have already undergone considerable changes of position; but in the possession of a distinct anterior body-cavity with a pore on the left side, followed by a pair of body-cavities which are at first lateral and approximately equal in size, it presents a closer resemblance to the larva of *Balanoglossus*, described by Bateson, in its internal anatomy than do any other Echinoderm larvæ hitherto described; and this resemblance is strengthened by its possible possession of a sense-organ at the anterior end; though, if this sense-organ is really absent in other Echinoderm larvæ, it is perhaps more probable that *Antedon* has developed it independently. In any case, the resemblance between these two larvæ, taken in connection with the well-known similarity between *Auricularia* and *Tornaria*, affords strong evidence of the common origin of the Echinodermata and Enteropneusta, already insisted upon by several writers (1, 2; 17).

Summary and Conclusion.

The following are a few of the more important points in the development of *Antedon*:—

The mesoblast is formed from the walls of the archenteron after invagination.

The blastopore closes early at or near the posterior pole.

The archenteron gives rise to four cœlomic pouches, (1) an anterior body-cavity, (2) the hydrocele, (3 and 4) the right and left body-cavities.

The hydrocele forms a ring on the ventral side of the alimentary canal, and subsequently opens by means of the water-tube into the anterior body-cavity, which communicates with the exterior by the water-pore.

The right and left body-cavities become anterior and posterior respectively, and afterwards aboral and oral. The former gives rise to the chambered organ.

After the fixation of the larva by means of the "præoral pit" the larval mouth invaginates to form the vestibule, which is rotated round to the posterior end.

The axial organ grows up from the stem in the axis of the body.

Besides the skeletal plates already known from previous descriptions, three "underbasals" are formed, which fuse with the top stem-joint. The anus opens in the same interradius as the primary water-tube (stone-canal).

In conclusion, I wish to express my most sincere thanks to my friend Dr. P. H. Carpenter for the ready kindness with which he has assisted and advised me throughout my work.

ADDENDUM.

(Received June 20, 1888.)

While this paper was in the press an account of the development of this animal appeared by M. JULES BARROIS,* which in most points very closely resembles mine. It will probably be found a convenience that I should give a brief list of such differences as still exist between the two accounts.

(1.) BARROIS's present account (*loc. cit.*, p. 557) of the separation of the right and left body-cavities from the gut, and the subsequent fate of the latter, appears to be somewhat different from that given in his previous note (see p. 263 of this paper). But it still differs from mine in that he does not find the gut forming a complete ring round the body-cavities, but thinks that only the dorsal of the two horns of the mesenteron, seen in my fig. 6, persists. This account is certainly simpler than mine, but I consider the latter so well established by my sections that it is easier to believe that this stage (a very transitory one) has been overlooked by BARROIS.

(2.) The cavity called by me "anterior body-cavity" is for BARROIS simply the "canal du sable" (= stone-canal = water-tube). The real water-tube I believe to be a distinct structure—an outgrowth of the hydrocele—absent, or at most rudimentary, in the free-swimming larva.

(3.) In describing the ciliated bands (*loc. cit.*, p. 562), BARROIS omits all mention of the anterior incomplete one; he seems (p. 574) to have seen something of it in sections.

(4.) He still denies the prolongation of the right body-cavity into the stem, seen by GÖTTE, PERRIER, and myself (see p. 268 of this paper).

(5.) On p. 280 I have alluded to PERRIER's belief that a portion of the oral body-cavity of the cystid assumes a vertical position in the axis of the body, forming the columellar cavity. BARROIS gives a similar account. To both of them that portion of the body-cavity which lies between the rectum and the parietal canal in figs. 30 and 34 of this paper is part of the oral body-cavity, while to me it is open equally to the oral and aboral cavities.

(6.) BARROIS (p. 636) attempts to show that the oral and basal plates are all developed round the right body-cavity, and he thinks that in this *Comatula* agrees with other Echinoderms (p. 634). I adhere to the old view, that the orals are formed round the left body-cavity, and the basals round the right; and shall in a future paper show that in Asterids and Ophiurids, too, some of the earliest plates to appear belong to the left side of the bilateral larva.

* "Recherches sur le Développement de la Comatule (*C. mediterranea*)." 'Recueil Zool. Suisse,' vol. 4, part 4, April 1888, p. 546.

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EXPLANATION OF PLATES 43–47.

Reference letters.

A, *B*, *C*, *D*, *E*, the different radii.
Ant. Anterior.
Dl. Dorsal.
L. Left.
Post. Posterior.
R. Right.
V. Ventral.

All the sections are magnified about 210 diameters, unless otherwise stated. Some of the transverse sections are seen from the anterior end, others from the posterior end, but, to avoid confusion, the right and left sides are always indicated.

Figs. 45 and 46 were drawn for me by Mr. H. A. CHAPMAN.

PLATE 43.

Fig. 1. Section of gastrula, early on second day. The vitelline membrane has shrunk considerably.

Fig. 2. Longitudinal vertical section of later gastrula (end of second day), showing formation of mesoblast.

Fig. 3. Longitudinal section of larva on third day, after the closure of the blastopore.

Fig. 4. Longitudinal section late on third day; the archenteron is dividing.

Figs. 5, 6, 7. From a series of longitudinal vertical sections early on the fourth day.

Fig. 5. Through the left side.

Fig. 6. Median.

Fig. 7. Through the right side.

Figs. 8, 9, 10. From a series of transverse (slightly oblique) sections late on the fourth day, fig. 8 being the most anterior. The mesenteron forms a ring.

Fig. 11. Transverse section early on the fifth day, at the level of the posterior end of the larval mouth. (Cp. fig. 13.)

Fig. 12. Section through the same larva near the posterior end.

PLATE 44.

Fig. 13. Surface view of larva of fifth day, still in vitelline membrane; showing yellow-cells. (× 190.)

Fig. 14. Surface view of free larva, sixth day, from the right side. Yellow-cells omitted. (× 190.)

Fig. 15. Surface view, seventh day, from left side. (× 190.)

Fig. 16. Surface view, early on eighth day, just after fixing; ventral view. Yellow-cells omitted. (× 190.)

Fig. 17. Longitudinal vertical section, seventh day; median plane.

Fig. 18. Oblique longitudinal section, seventh day.

Fig. 19. Part of transverse section, seventh day, about the level of the middle of the larval mouth. (× 960.)

Fig. 20. Longitudinal horizontal section near ventral side, early on the eighth day, just after fixing.

Fig. 21. Longitudinal horizontal section, seventh day, dorsal side.

Fig. 22. Longitudinal vertical section of præoral lobe, seventh day. Stained with GRENACHER's hæmatoxylin. (× 460.)

Fig. 23. Longitudinal horizontal section of anterior pole. GRENACHER's hæmatoxylin. (× 460.)

Fig. 24. Transverse section through anterior part of larval mouth, seventh day. Stained with borax carmine. (× 460.)

PLATE 45.

Fig. 25. Longitudinal vertical section, eighth day, a few hours after fixing.

Fig. 26. Transverse section through larval mouth, same stage as fig. 25. (× 460.)

Fig. 27. Transverse section through larval mouth, a few hours later than fig. 26. (× 460.)

Fig. 28. Longitudinal vertical section, about an hour later than fig. 27.

Fig. 29. Longitudinal vertical section of cystid, late on the eighth day.

Fig. 30. Transverse section, tenth day. (× 250.)

Fig. 31. Transverse section from same series as fig. 30, near the aboral end of the alimentary canal.

Figs. 32, 33, and 34. From a series of transverse sections, eleventh day, through the parietal canal and water-tube. (× 460.)

Fig. 35. Longitudinal section, eleventh day.

PLATE 46.

Fig. 36. Part of transverse section, tenth day, at same level as fig. 31; showing aboral mesentery and axial organ. (× 1800.)

Fig. 37. Part of transverse section from same series as fig. 36, but rather nearer the oral end. (× 1800.)

Fig. 38. Transverse section of cystid several weeks old, showing anus and water-tube (= stone-canal) in same interradius.

Fig. 39. Transverse section, near end of cystid stage, at a rather lower level than fig. 30.

Fig. 40. Part of transverse section, eleventh day, (cp. fig. 32); development of sacculus. (× 1520.)

Fig. 41. Part of transverse section through same region as fig. 40, about the twentieth day. (× 1520.)

Fig. 42. Pyriform sacs with refractive spherules from sacculi at different ages; (*a*) from cystid, about the twelfth day; (*b*) from cystid about the twentieth day; (*c*) from adult. (× 1520.)

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PLATE 47.

Fig. 47. Two plates from a larva of the seventh day; (*a*) an underbasal; this would equally well represent a basal some twenty-four hours earlier. (*b*) One of the uppermost stem-joints. (× 460.)

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Fig. 60. Similar diagram of left side.
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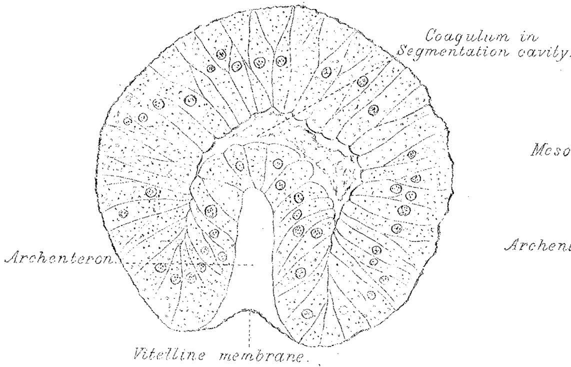

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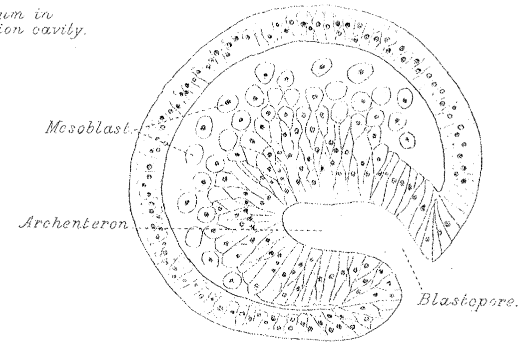

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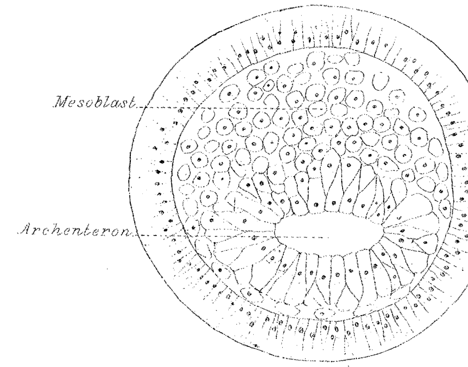

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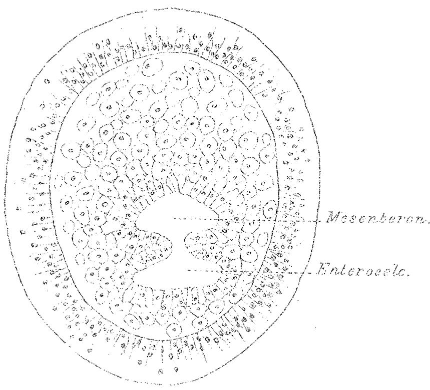

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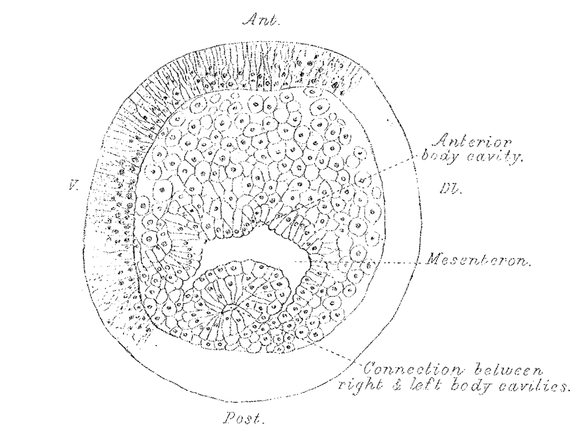

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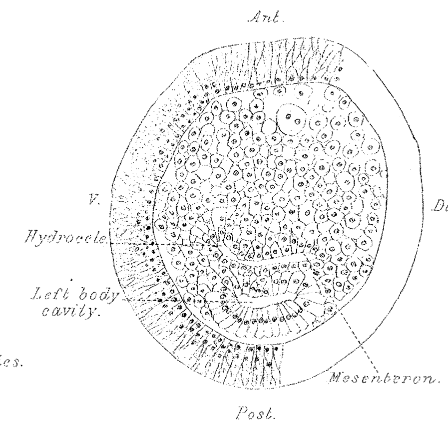

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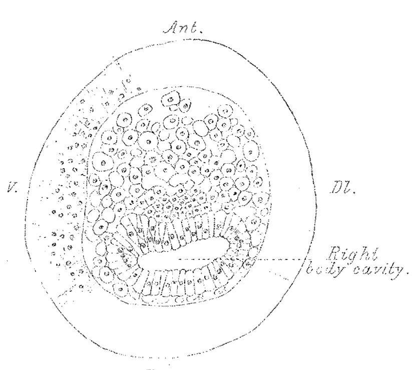

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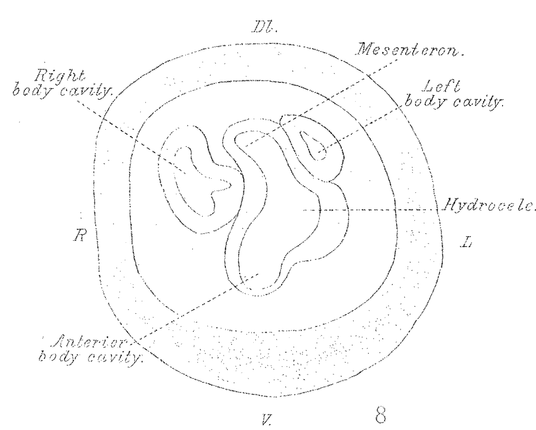

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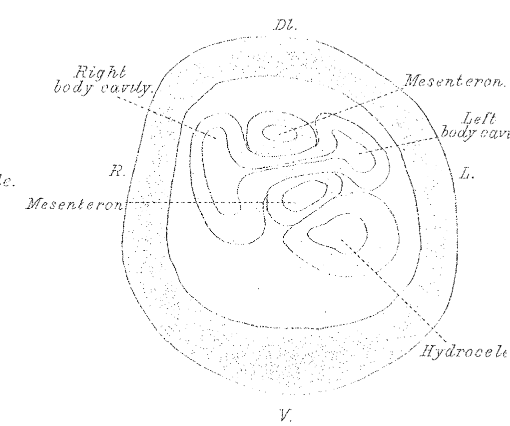

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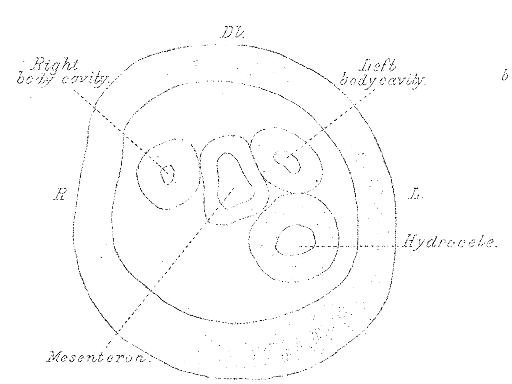

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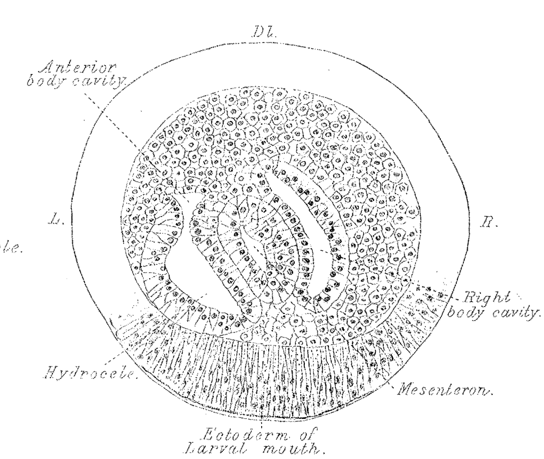

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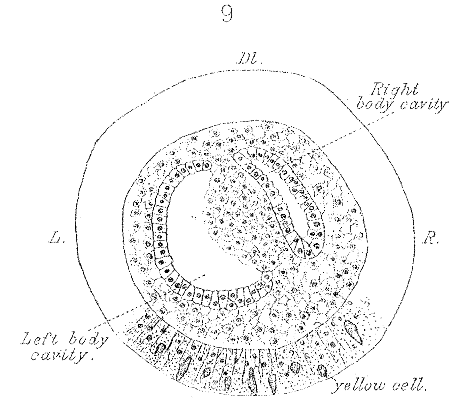

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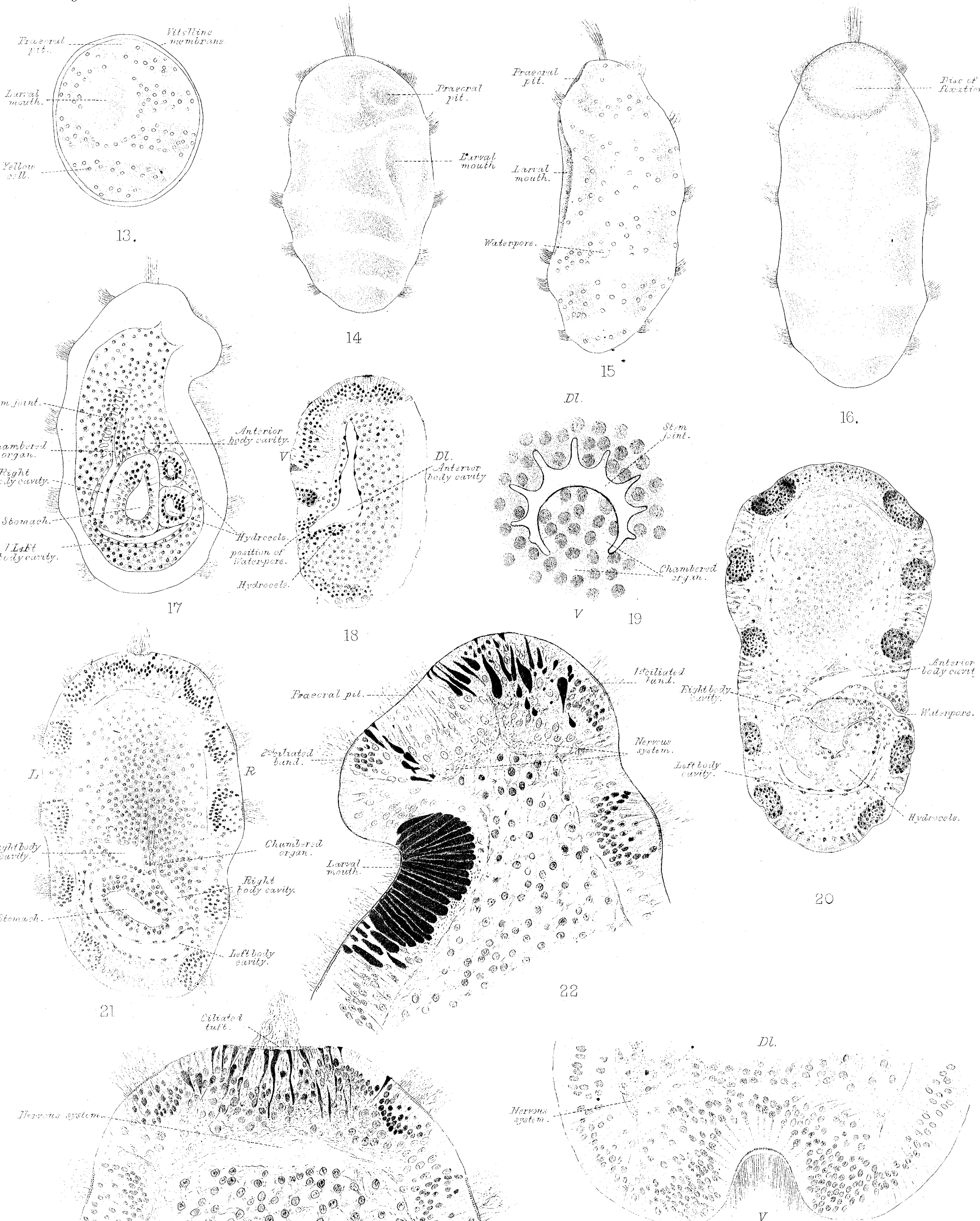
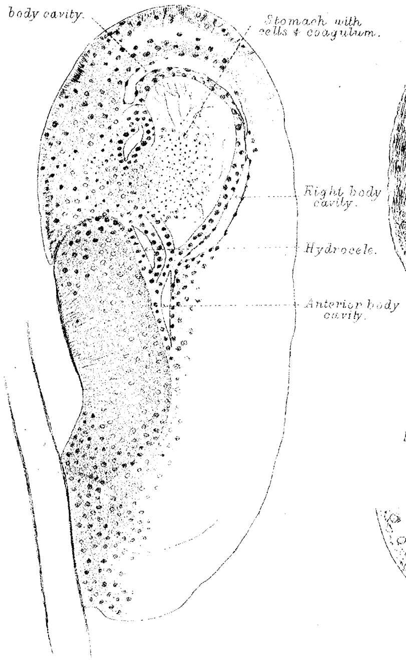

Praecral pit.
Vitelline membrane
Larval mouth.
Yellow cell.
13.
Praecral pit
Larval mouth
14
Praecral pit.
Larval mouth.
Waterpore.
15
Disc of fixation
16.
Stem joint.
Chambered organ.
Right body cavity.
Stomach.
Left body cavity.
Anterior body cavity.
Hydrocele.
position of Waterpore.
17
V
Dl.
Anterior body cavity
Hydrocele.
18
Dl.
Stem joint.
Chambered organ.
V
19
Anterior body cavity
Right body cavity.
Waterpore.
Left body cavity.
Hydrocele.
20
L
R
Right body cavity.
Chambered organ.
Right body cavity.
Stomach.
Left body cavity.
21
Praecral pit.
1st ciliated band.
2nd ciliated band.
Nervous system.
Larval mouth.
22
Ciliated tuft.
Nervous system.
23.
Dl.
Nervous system.
V.
24.



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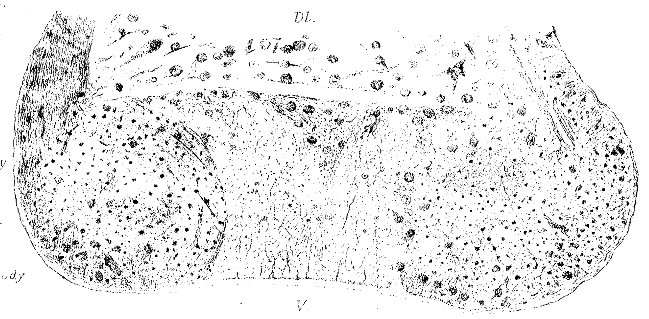

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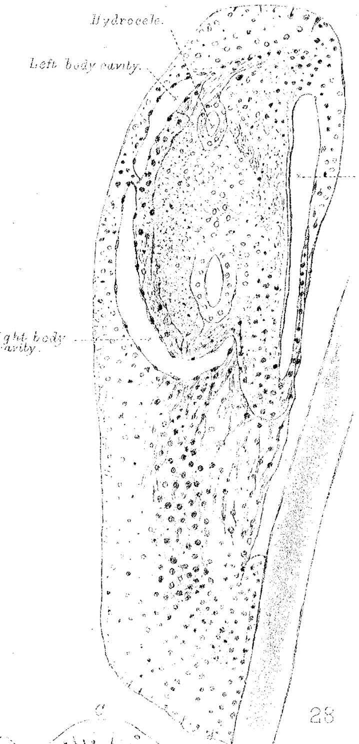

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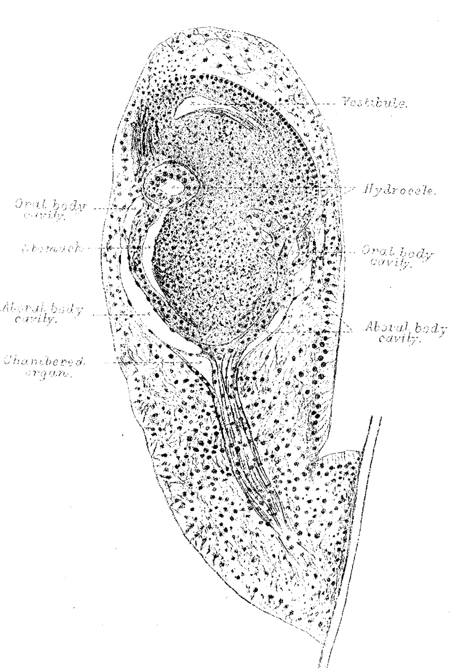

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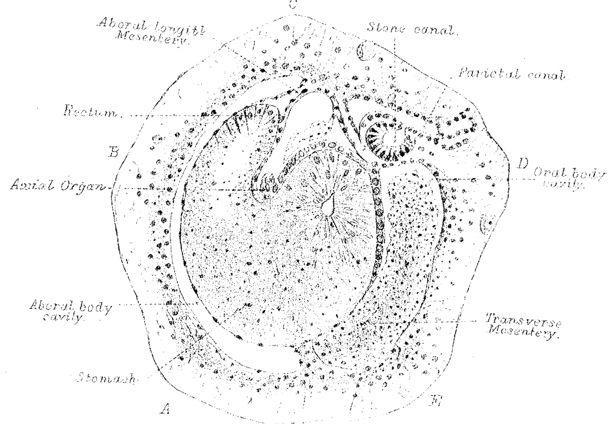

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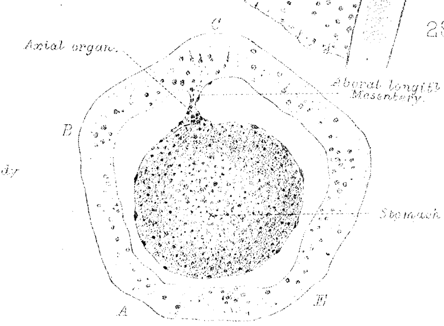

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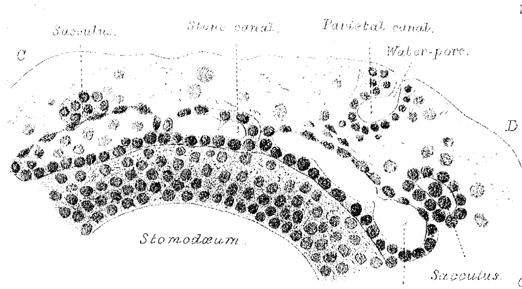

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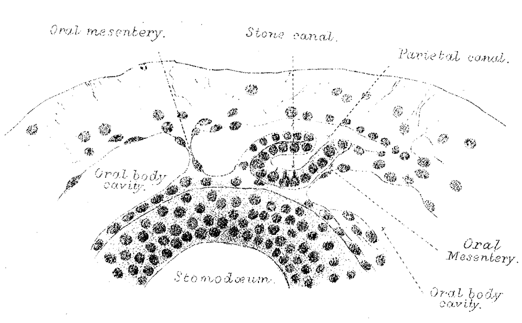

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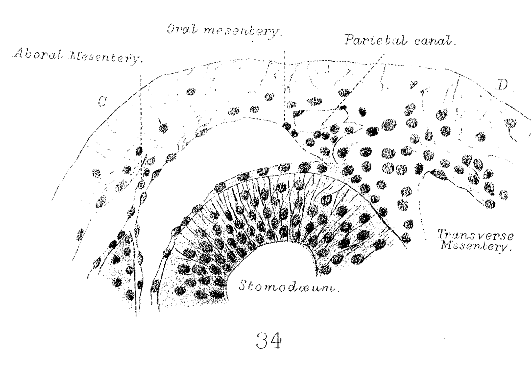

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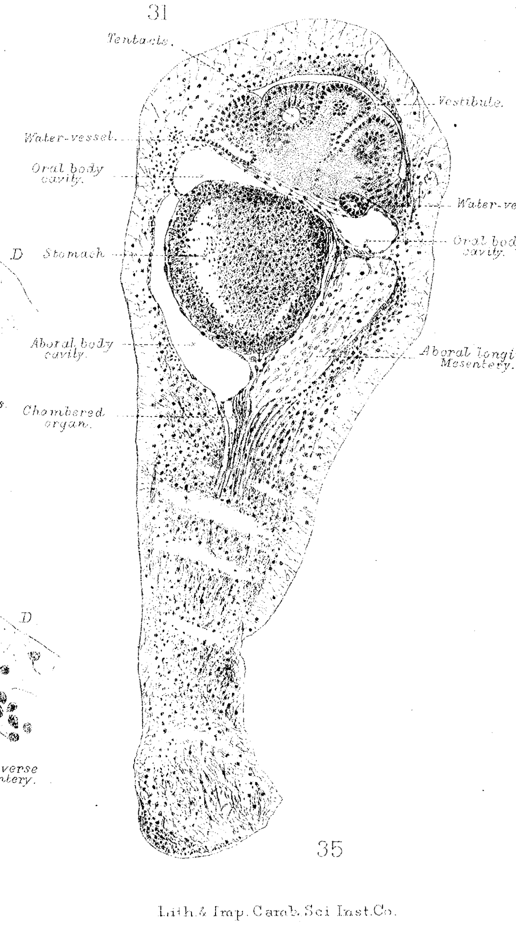

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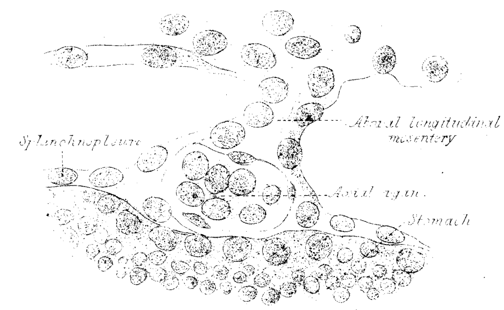

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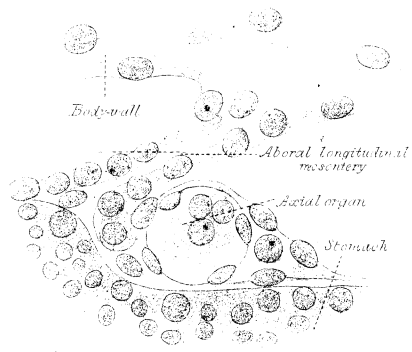

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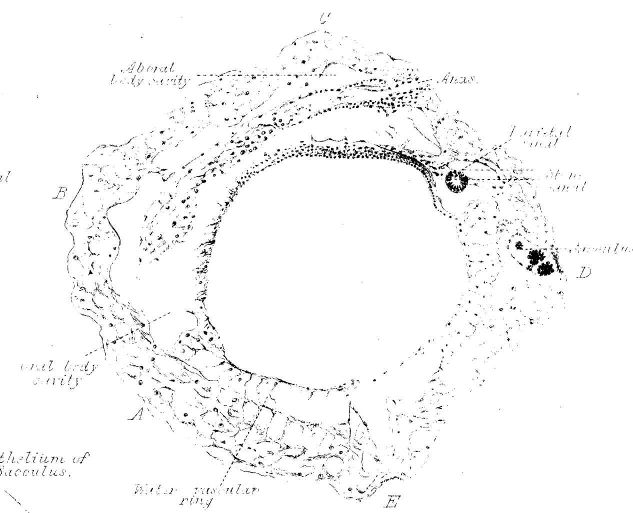

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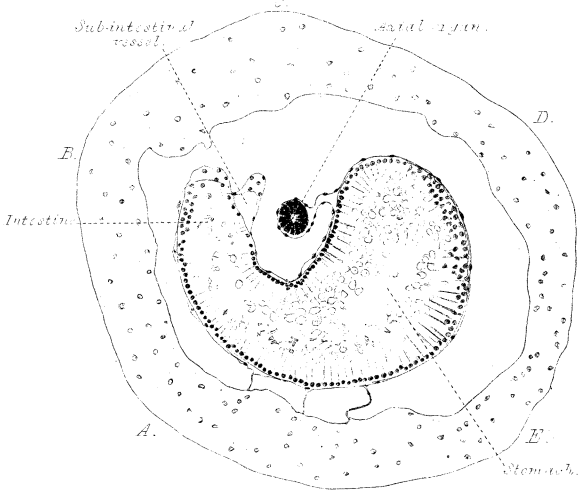

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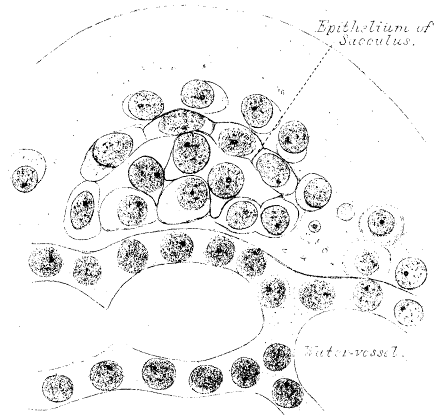

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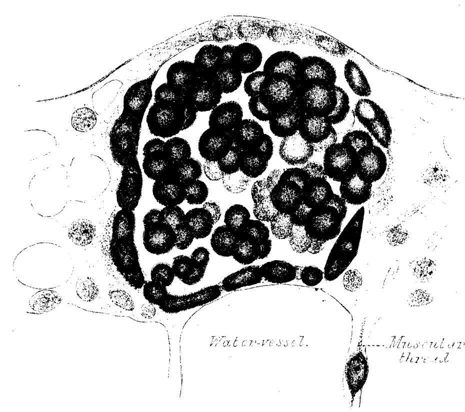

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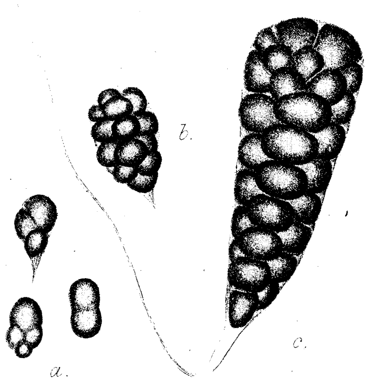

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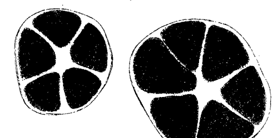

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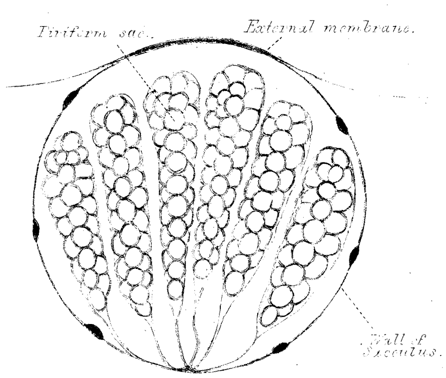

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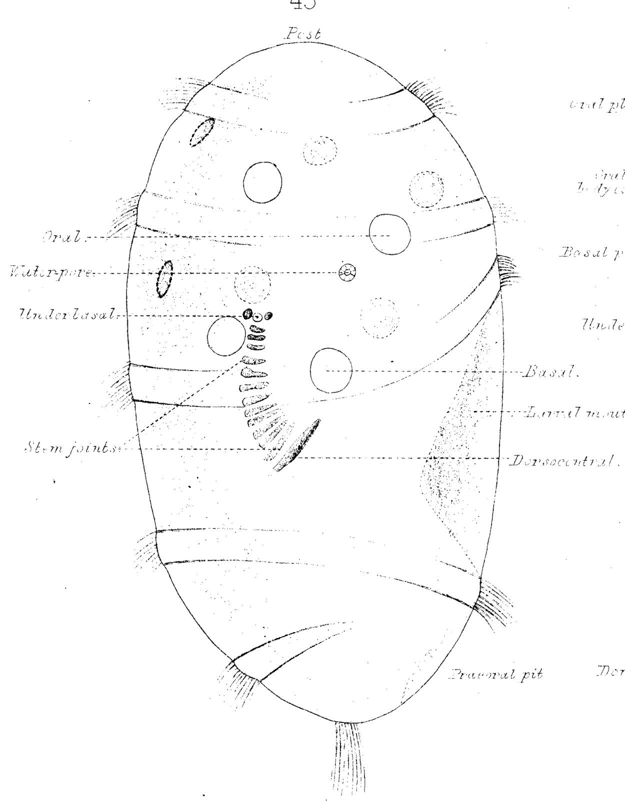

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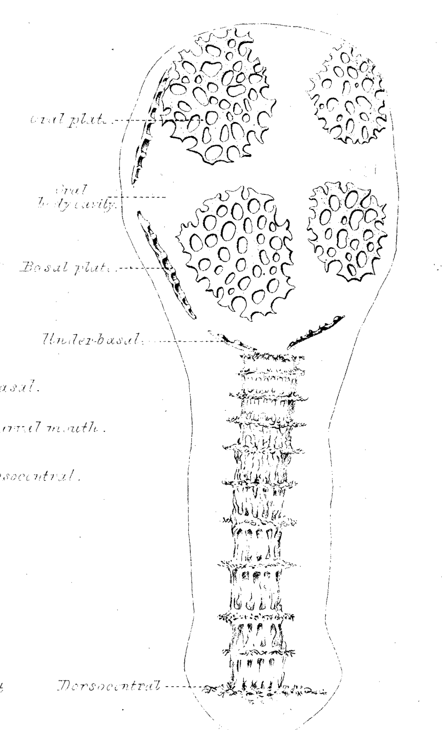

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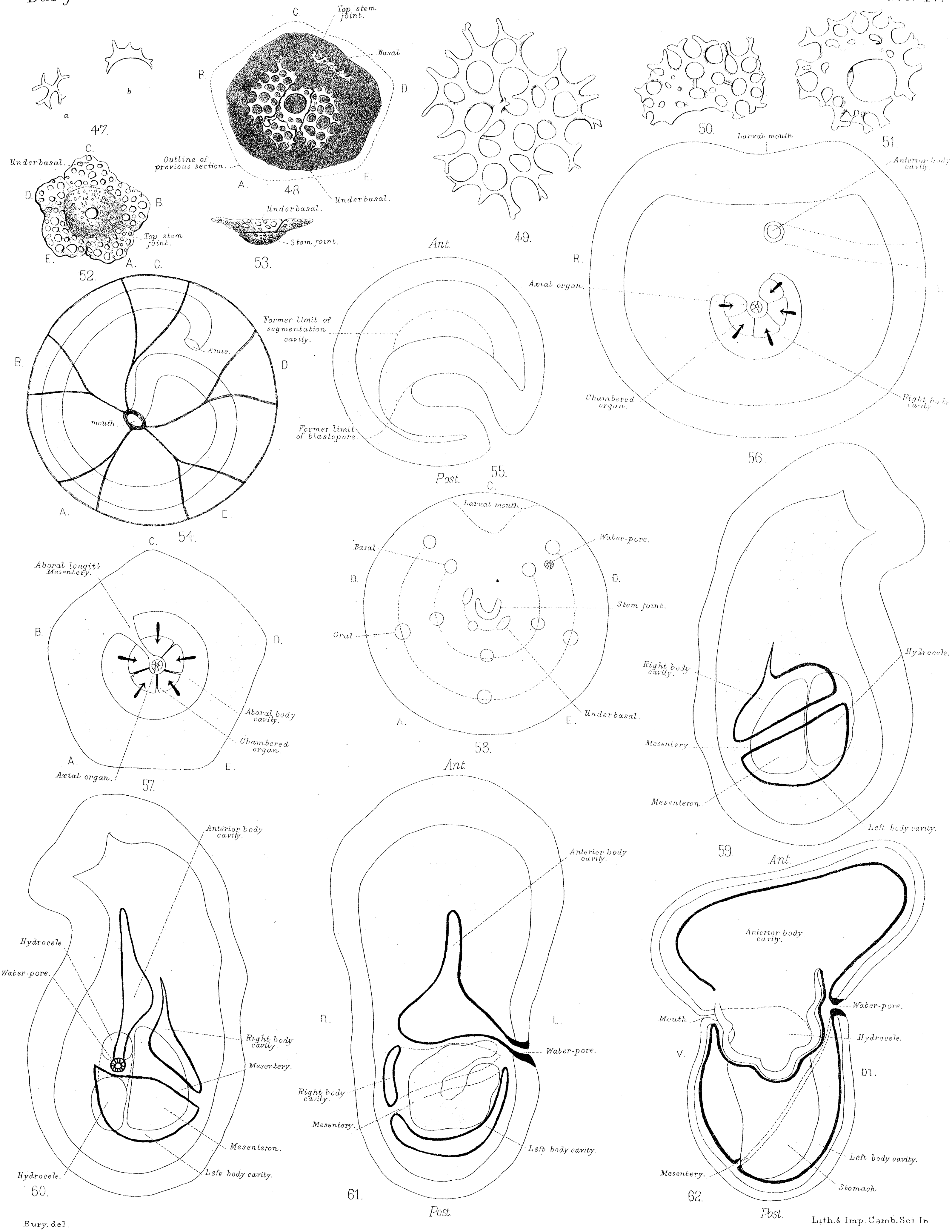
a
b
47.
C.
Top stem joint.
Basal.
B.
D.
Outline of previous section.
A.
48
E.
Underbasal.
49.
50.
51.
Underbasal.
C.
D.
B.
Top stem joint.
E.
A.
52.
Underbasal.
Stem joint.
53.
Larval mouth.
Anterior body cavity.
Ant.
R.
L.
Axial organ.
Chambered organ.
Right body cavity.
56.
C.
Anus.
B.
D.
mouth.
A.
E.
54.
Former limit of segmentation cavity.
Former limit of blastopore.
Post.
55.
C.
Larval mouth.
Water-pore.
Basal.
B.
D.
Stem joint.
Oral.
Underbasal.
A.
E.
58.
C.
Aboral longitl Mesentery.
B.
D.
Aboral body cavity.
Chambered organ.
A.
E.
Axial organ.
57.
Hydrocele.
Right body cavity.
Mesentery.
Mesenteron.
Left body cavity.
59.
Anterior body cavity.
Hydrocele.
Water-pore.
Right body cavity.
Mesentery.
Mesenteron.
Left body cavity.
Hydrocele.
60.
Ant.
Anterior body cavity.
R.
L.
Water-pore.
Right body cavity.
Mesentery.
Left body cavity.
61.
Post.
Ant.
Anterior body cavity.
Water-pore.
Mouth.
Hydrocele.
V.
Dl.
Left body cavity.
Mesentery.
Stomach.
62.
Post.

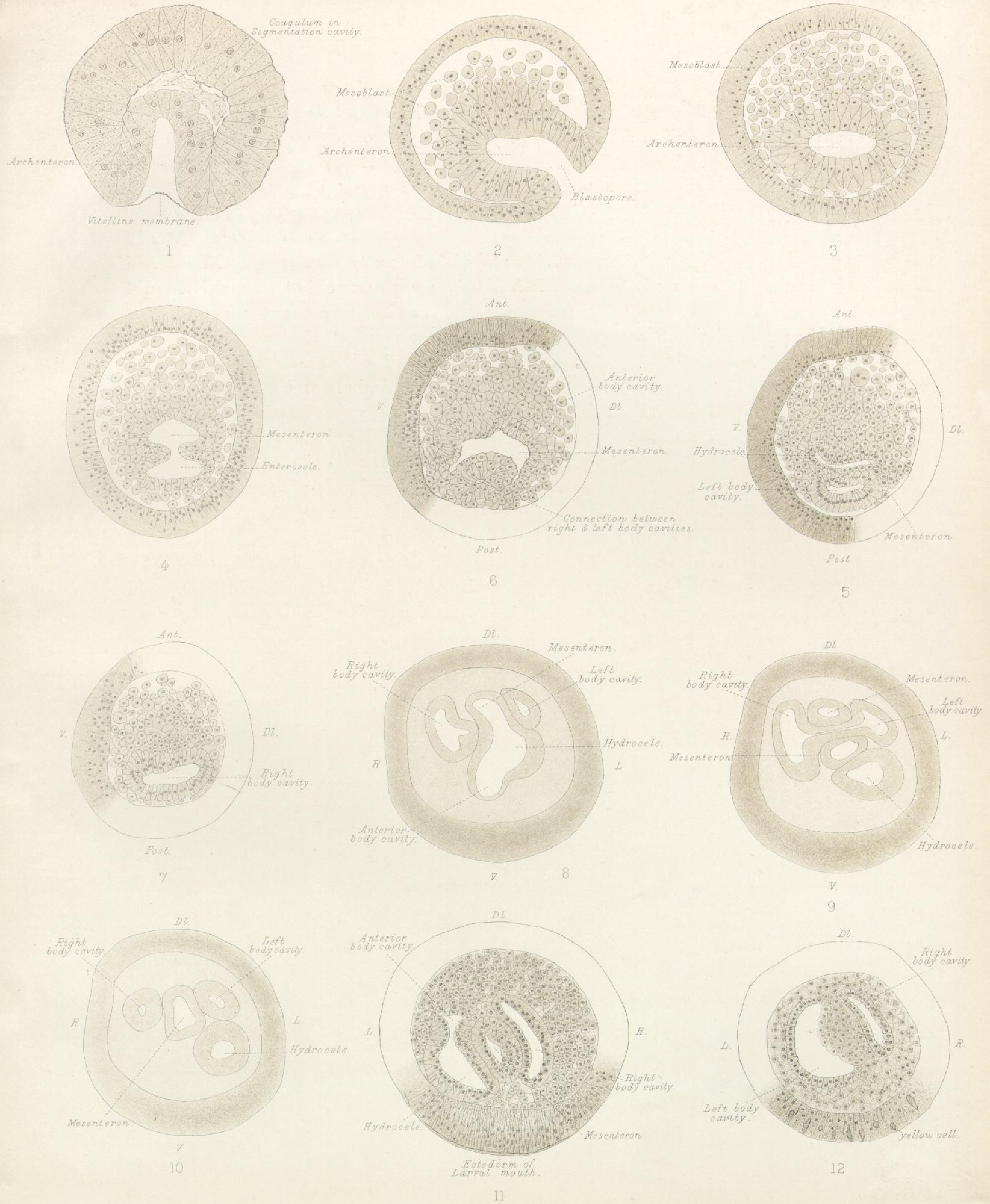

PLATE 43.

Fig. 1. Section of gastrula, early on second day. The vitelline membrane has shrunk considerably.

Fig. 2. Longitudinal vertical section of later gastrula (end of second day), showing formation of mesoblast.

Fig. 3. Longitudinal section of larva on third day, after the closure of the blastopore.

Fig. 4. Longitudinal section late on third day; the archenteron is dividing.

Figs. 5, 6, 7. From a series of longitudinal vertical sections early on the fourth day.

Fig. 5. Through the left side.

Fig. 6. Median.

Fig. 7. Through the right side.

Figs. 8, 9, 10. From a series of transverse (slightly oblique) sections late on the fourth day, fig. 8 being the most anterior. The mesenteron forms a ring.

Fig. 11. Transverse section early on the fifth day, at the level of the posterior end of the larval mouth. (Cp. fig. 13.)

Fig. 12. Section through the same larva near the posterior end.

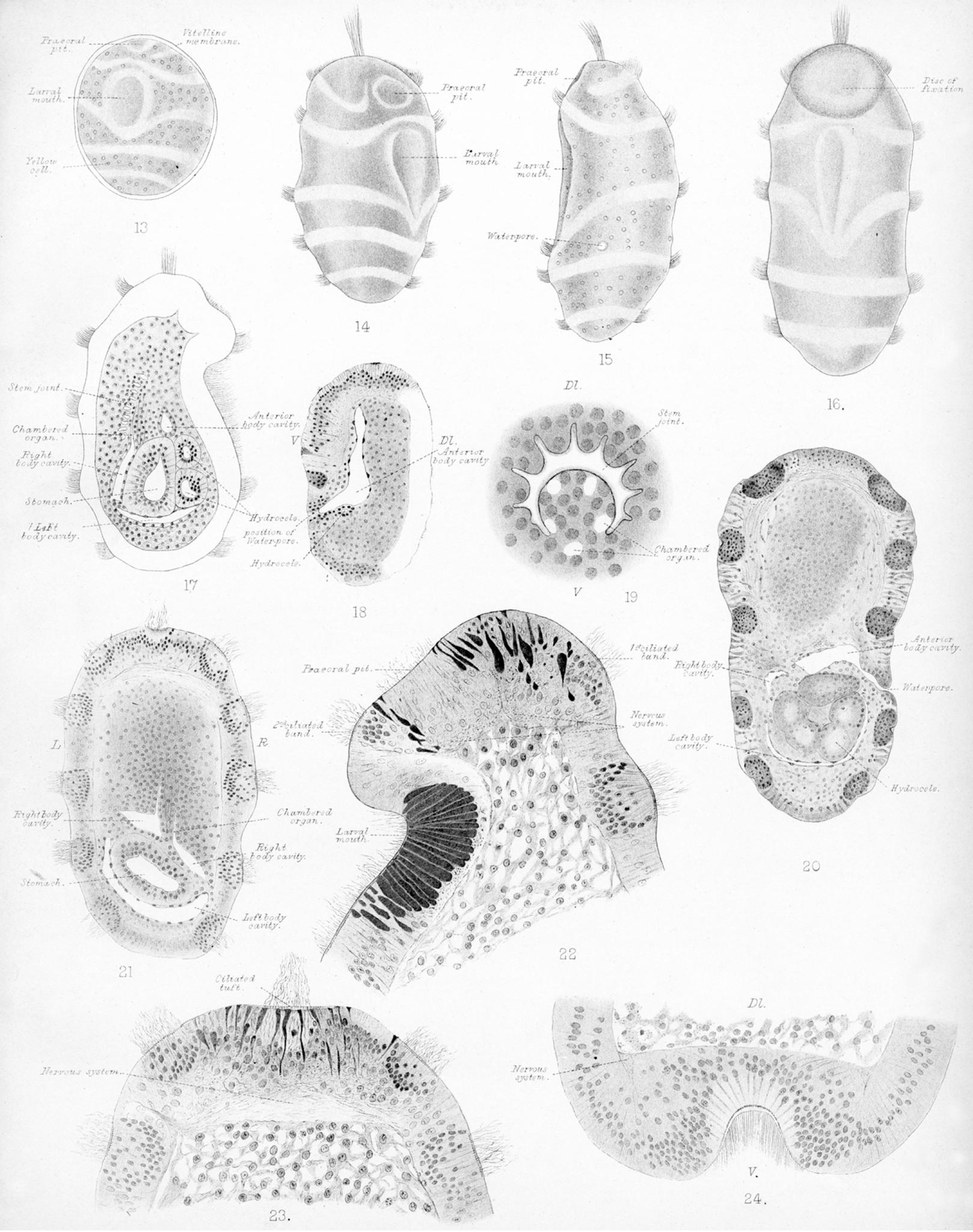

PLATE 44.

Fig. 13. Surface view of larva of fifth day, still in vitelline membrane; showing yellow-cells. (× 190.)

Fig. 14. Surface view of free larva, sixth day, from the right side. Yellow-cells omitted. (× 190.)

Fig. 15. Surface view, seventh day, from left side. (× 190.)

Fig. 16. Surface view, early on eighth day, just after fixing; ventral view. Yellow-cells omitted. (× 190.)

Fig. 17. Longitudinal vertical section, seventh day; median plane.

Fig. 18. Oblique longitudinal section, seventh day.

Fig. 19. Part of transverse section, seventh day, about the level of the middle of the larval mouth. (× 960.)

Fig. 20. Longitudinal horizontal section near ventral side, early on the eighth day, just after fixing.

Fig. 21. Longitudinal horizontal section, seventh day, dorsal side.

Fig. 22. Longitudinal vertical section of præoral lobe, seventh day. Stained with GRENACHER's hæmatoxylin. (× 460.)

Fig. 23. Longitudinal horizontal section of anterior pole. GRENACHER's hæmatoxylin. (× 460.)

Fig. 24. Transverse section through anterior part of larval mouth, seventh day. Stained with borax carmine. (× 460.)

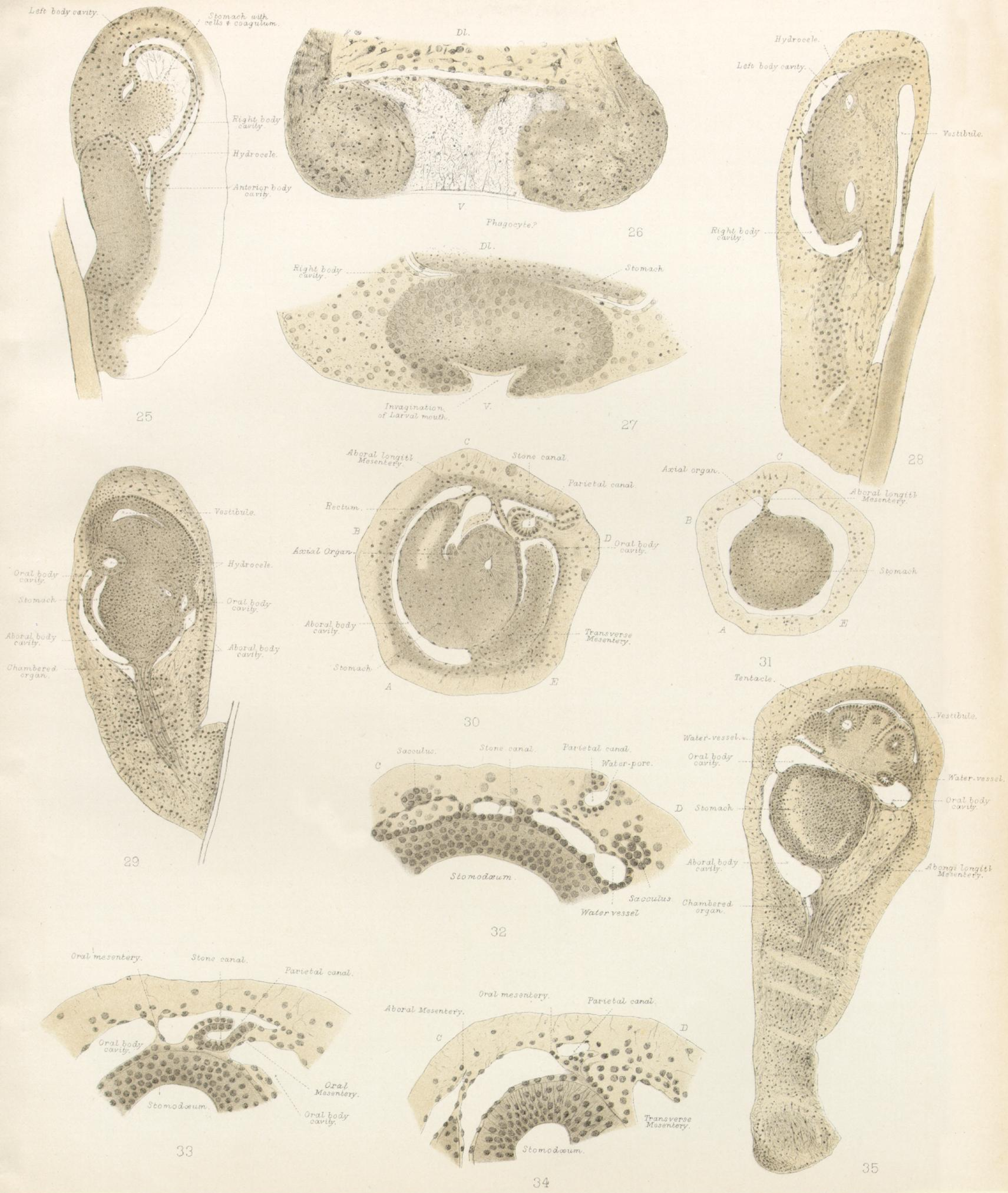

PLATE 45.

Fig. 25. Longitudinal vertical section, eighth day, a few hours after fixing.

Fig. 26. Transverse section through larval mouth, same stage as fig. 25. (× 460.)

Fig. 27. Transverse section through larval mouth, a few hours later than fig. 26. (× 460.)

Fig. 28. Longitudinal vertical section, about an hour later than fig. 27.

Fig. 29. Longitudinal vertical section of cystid, late on the eighth day.

Fig. 30. Transverse section, tenth day. (× 250.)

Fig. 31. Transverse section from same series as fig. 30, near the aboral end of the alimentary canal.

Figs. 32, 33, and 34. From a series of transverse sections, eleventh day, through the parietal canal and water-tube. (× 460.)

Fig. 35. Longitudinal section, eleventh day.

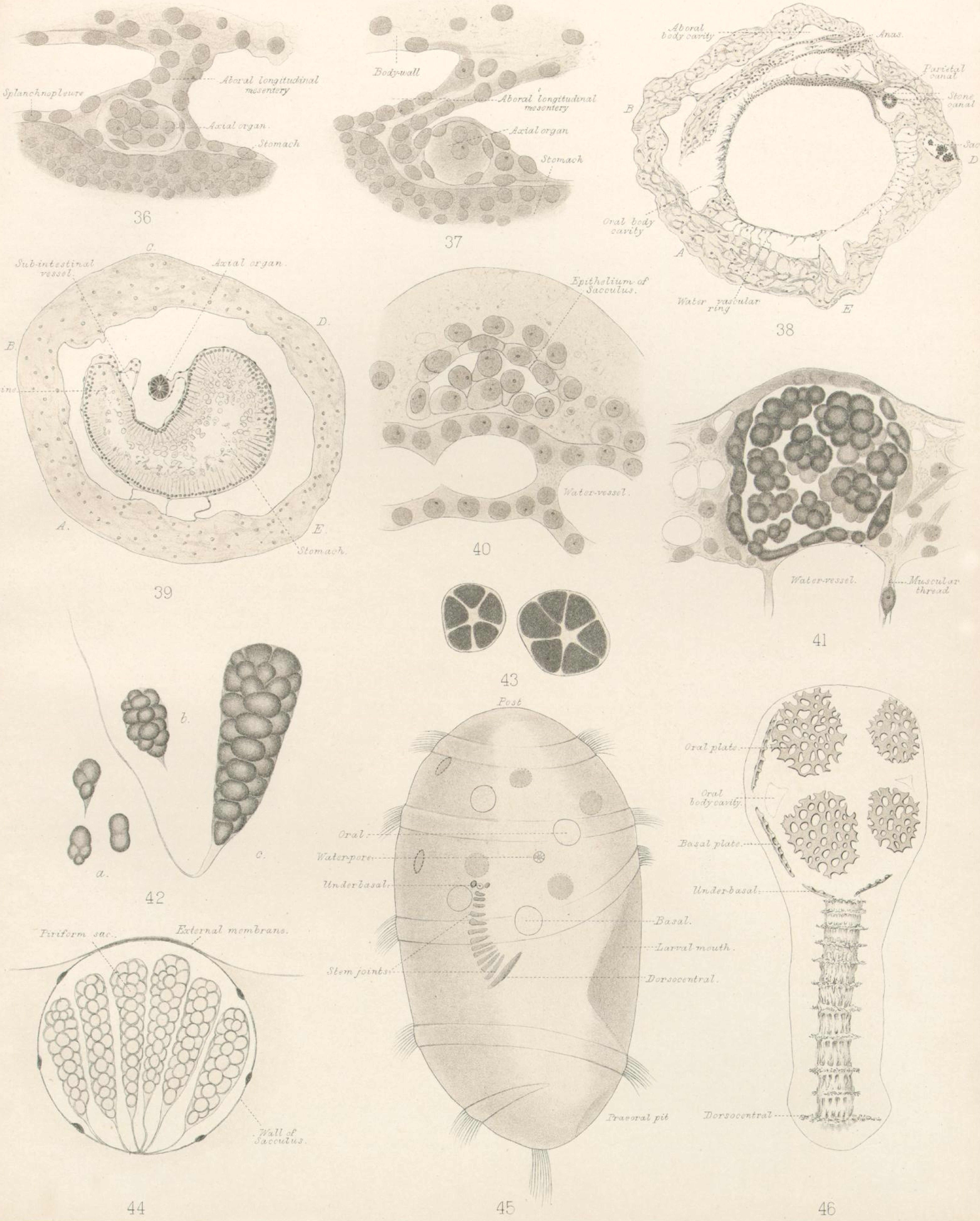

PLATE 46.

Fig. 36. Part of transverse section, tenth day, at same level as fig. 31; showing aboral mesentery and axial organ. (× 1800.)

Fig. 37. Part of transverse section from same series as fig. 36, but rather nearer the oral end. (× 1800.)

Fig. 38. Transverse section of cystid several weeks old, showing anus and water-tube (= stone-canal) in same interradius.

Fig. 39. Transverse section, near end of cystid stage, at a rather lower level than fig. 30.

Fig. 40. Part of transverse section, eleventh day, (cp. fig. 32); development of sacculus. (× 1520.)

Fig. 41. Part of transverse section through same region as fig. 40, about the twentieth day. (× 1520.)

Fig. 42. Pyriform sacs with refractive spherules from sacculi at different ages; (*a*) from cystid, about the twelfth day; (*b*) from cystid about the twentieth day; (*c*) from adult. (× 1520.)

Fig. 43. Transverse sections of two pyriform sacs from adult; deeply stained. (×1520.)

Fig. 44. Diagram of structure of adult sacculus.

Fig. 45. Diagram showing the arrangement of the skeletal plates in a larva of seventh day (cp. fig. 15). Drawn by Mr. H. A. Chapman.

Fig. 46. Larva of tenth day, seen as a transparent object: the plates on the far side of the body are, for the sake of clearness, omitted. (× 190.) Drawn by Mr. H. A. Chapman.

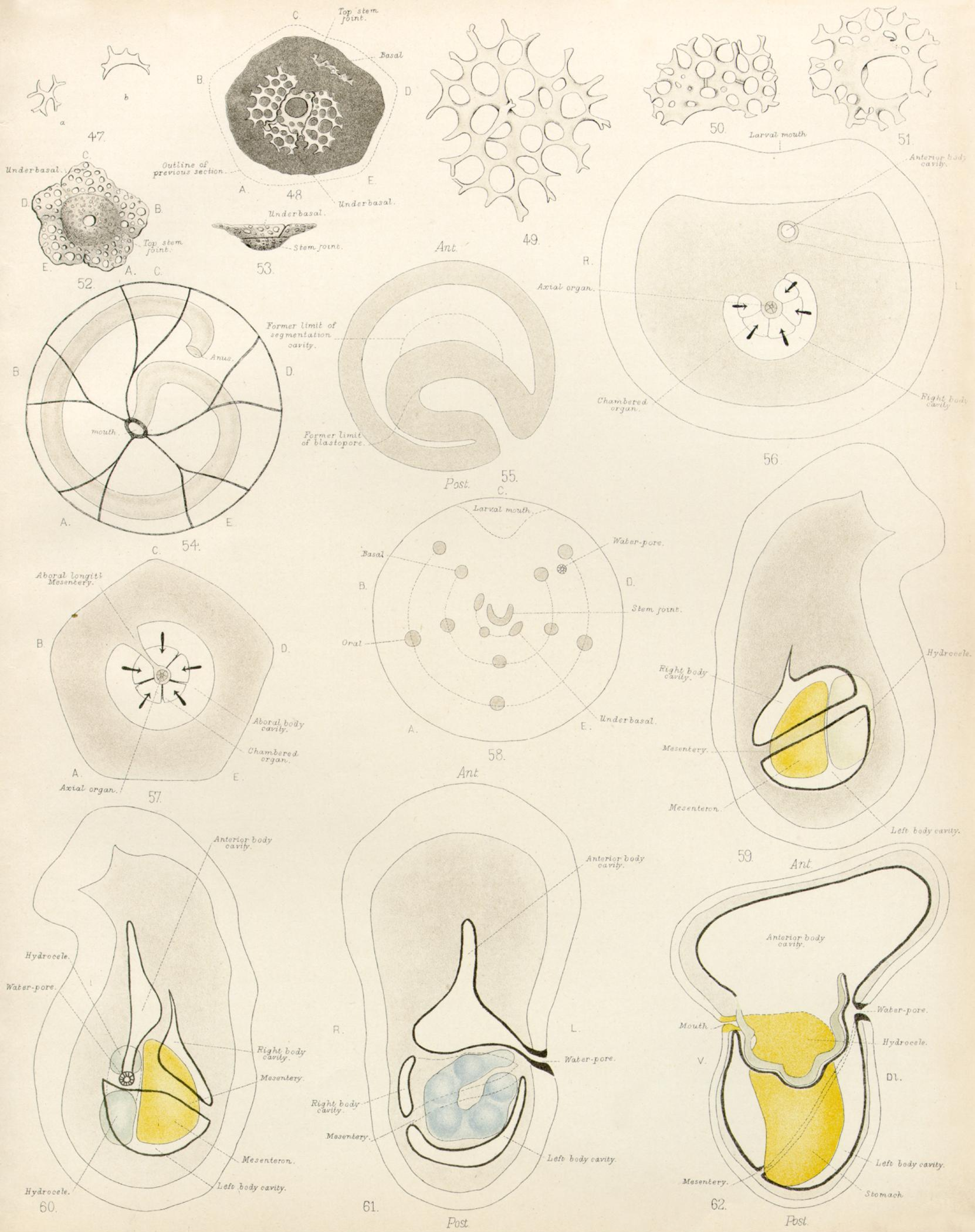

PLATE 47.

Fig. 47. Two plates from a larva of the seventh day ; (*a*) an underbasal ; this would equally well represent a basal some twenty-four hours earlier. (*b*) One of the uppermost stem-joints. (× 460.)

Fig. 48. Transverse section, tenth day, at level of the underbasals (cp. fig. 46). The dotted line shows the outline of a previous section nearer the oral pole. (× 270.)

Fig. 49. A basal plate, tenth day. (× 460.)

Fig. 50. An underbasal, tenth day. (× 460.)

Fig. 51. One of the uppermost stem-joints (tenth day) with rudimentary longitudinal processes. (× 460.)

Fig. 52. Underbasals and top stem-joint fusing into a single plate, aboral view. (× 170.)

Fig. 53. Same as fig. 52, lateral view.

Fig. 54. Diagram of oral surface of adult (from Carpenter).

Fig. 55. Diagram to illustrate the probable derivation of the stage represented in fig. 3 from a gastrula with long but narrow blastopore.

Fig. 56. Diagrammatic transverse section, seventh day, to illustrate the probable connection of the chambered organ with the right body-cavity.

Fig. 57. Similar diagram, ninth day.

Fig. 58. Diagrammatic view of skeletal plates (seventh day) from the posterior end. (The ventral radius should be wider).

Fig. 59. Diagrammatic view of right side of larva (seventh day), the ectoderm being removed ; showing course of mesentery.

Fig. 60. Similar diagram of left side.

Fig. 61. Similar diagram of ventral side. The mesenteron is omitted, and the course of the mesentery on the dorsal side shown by dotted lines.

Fig. 62. Similar diagram of left side of *Asterina gibbosa*, for comparison with Fig. 61. (Slightly altered from Ludwig.)