The Development of Asterina gibbosa.¹

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With Plates 18—29.

The investigations which form the subject of the present memoir were commenced with the object of seeking in Asterids the results which the author (14) had already obtained from the study of Ophiurids, viz. the development of the so-called heart and its accompanying sinuses.

A study of the literature soon led to the conclusion that our knowledge of the development of most organs in the Asterid body was very defective, and that a thorough revision of the whole embryonic and larval history would be most desirable. This work has occupied my attention for the last two years, and I am now in a position to give a fairly complete account of the whole organogeny; an account which will, I hope, place our knowledge of Asterid development on the same level as that to which our acquaintance with Crinoid ontogeny has been raised by the researches of Bury (1) and Seeliger (18); I have to express my warm thanks to Mr. Sedgwick not only for the suggestion of Asterina gibbosa as a proper type to investigate, but also for much assistance and advice in revising the proofs of this paper.

That there was an immense lacuna in our knowledge to be

¹ A preliminary account of the observations recorded in this paper was the subject of the successful essay in the competition for the Walsingham Medal of the University of Cambridge in 1893.
filled up will become evident when I state in the first place, that my researches have made it clear that the Crinoids are only very distantly related to the other classes of Echinoderms, and secondly, that our previous knowledge of the metamorphosis of Asterids and their allies was confined principally to the changes which take place in their external form.

It will be most convenient, I think, to give first a general account of the development, and then to point out how far the results of other workers have been confirmed, as by this means needless repetition will be avoided.

Methods adopted.

My material consisted of a large number of larvae of all stages including those which had just completed the metamorphosis, and of a considerable number of young adults varying from an age of about three weeks to several months from the metamorphosis. Of these the former, with the exception of two small collections made by myself in Plymouth, 1893, and Jersey, 1894, were collected for me and preserved according to my directions by the authorities of the Naples Zoological Station; the latter were obtained for me and preserved by myself during my stay in the Naples Station in 1892. I have to express my deep sense of my indebtedness to Prof. Dohrn for his kindness in meeting my wishes, and to Cav. Salv. Lo Bianco for the extreme care and attention with which he carried out my directions.

All the stages were preserved in osmic acid, followed by 14—24 hours in Müller’s fluid, as this method had yielded me the best results in the case of Ophiurids. It makes the specimens exceedingly brittle, but at the same time gives the most excellent preservation of the minute histology; preserved in this manner the various tissues are differentiated as to their staining capacities, so that the sections look almost like coloured diagrams.

On account of their brittleness, and in order to avoid shrinkage in the tissues, the larvae were embedded in celloidin, and the celloidin block subsequently embedded in paraffin.
They were then cut into series of sections in most cases 4½ μ thick—in the case of the adults 7 μ; these sections were mounted on hot water on the slide to flatten them, and stained in either Grenacher’s haematoxylin or Mayer’s carmalum. Two points of interest in connection with this process may be mentioned: first, I found that when the slide was transferred from turpentine to absolute alcohol some of the sections were sure to be lost, but that this could be avoided by placing the slide for a minute or so, after taking it out of turpentine, into oil of cloves, and thence into 90 per cent. alcohol; second, that the readiness with which sections, especially when overcharged with osmic acid, will take up either haematoxylin or carmalum is greatly increased by immersing them for twenty-four hours in borax-carmine, though they do not acquire a particle of stain from it.

In the youngest stages the osmic acid produces too great impenetrability for either celloidin or paraffin, and accordingly my best results were obtained from some specimens preserved for me by Sig. Lo Bianco in a mixture of three parts concentrated aqueous solution of corrosive sublimate, and one part glacial acetic acid. This method also gives most excellent preservation, though without that fine differentiation of the tissues yielded by osmic acid and Müller’s fluid; as during the stages in question however the larvae consist almost exclusively of epithelial cells, this is not a matter of any importance. This second method was recommended to me by Dr. Eisig.

The orientation of the specimens was one of the chief difficulties to be overcome. I found that the best results were given by horizontal sections perpendicular to the median sagittal plane of the larva, and sections parallel to the disc and perpendicular to the median axis of symmetry in the just metamorphosed star-fish. The planes, to which in these two cases the sections are cut parallel, viz. a median horizontal plane in the larva and the plane of the disc in the adult, make an angle of about 70° with each other; and hence it is difficult to correlate sections cut parallel to the one with those cut parallel to the other. I shall call these planes the “larval”
and "adult" planes respectively. A rudiment of the præoral lobe of the larva is retained, as we shall see, until the close of the metamorphosis, and by means of it I found it possible to determine the direction of the "larval" plane up till the adult form has been almost attained. Hence, by cutting sections parallel to the larval plane, one can follow the internal changes of the metamorphosis step by step; then when the metamorphosis is complete it is possible to correlate with less difficulty sections cut parallel to the two planes, and the further history may be followed viâ, so to speak, the adult plane. This was the course which I adopted; and I also penetrated back a considerable distance from the adult condition into the stages of the metamorphosis by sections parallel to the adult plane, and so confirmed results obtained by the other method. For the youngest stages of all, which are spherical, orientation is, of course, impossible, and one has to trust to chance to getting sections in the proper direction; but it is fairly easy to recognise from their appearance when this is so.

General Account of the Development.

The ontogenetic history of the *Asterina gibbosa* may be conveniently divided into three parts: first, the development of the bilaterally symmetrical larva from the egg; second, the metamorphosis of this larva into the young star-fish; and lastly, the gradual development of what we may term the young adult into the sexually mature form. I have made no observations on the segmentation of the egg, nor on the gastrulation; my work, properly speaking, commences with the completed gastrula, and my material was not suitable for observing the development of the calcareous plates. On all these points I intend, however, for the sake of completeness, to say a few words, and my authority will be Ludwig, who, in his classic research (12), has on these subjects left nothing to be desired in point of view of completeness. I may add also that the figures illustrating the changes in external form are copied from Ludwig's memoir. The three figures illustrating the relations
of the Asterid and Crinoid to their common ancestor were designed for me by my friend and colleague Mr. J. J. Lister, of St. John's: in their present form they were drawn for me by a lady friend.

The Development of the Larva.

The eggs are laid by the parent on the under surface of stones, to which they adhere by means of their vitelline membrane. I have never discovered a male, though Ludwig says that the male twists his arms round the female whilst she is depositing her ova, and then pours out his spermatozoa upon them; it is quite certain that in the English Channel, at any rate, isolated females will lay eggs which develop with perfect regularity up to the conclusion of the metamorphosis. Cuvénot (4) says that young females of a certain size develop spermatozoa in their ovaries—a statement I have not been able to verify. It may, indeed, be said that Ludwig's statement that a kind of sexual congress takes place, Cuvénot's observations, and the experience of the authorities of the Jersey Biological Station are irreconcilable, and that the whole subject demands renewed investigation.

The eggs are larger than those of most other Echinoderms; they are about .5 mm. in diameter. This is a result of the yolk which they contain, and which gives them their bright orange colour. This yolk is so uniformly distributed, however, that it does not alter the type of segmentation, which is total and regular. The blastomeres, in consequence of their larger size, are more closely packed than is usual amongst Echinoderms; they are wedged into the interspaces between their neighbours, and so the strict "radial" type of segmentation characteristic of the group is no longer maintained.

The result of segmentation is a hollow blastosphere or blastula, which on the second day of development becomes converted into a gastrula by embolic invagination. The embryo
is not quite spherical, its long axis exceeding very slightly its transverse axis, so that we can see that the blastopore is situated in the centre of what afterwards becomes the ventral surface. The gastrula has acquired a uniform covering of cilia, and the blastopore is a round opening with well-defined lips. This well-marked stage of development, which is easy to recognise, I have called Stage A (Pl. 18, fig. 1). The blastopore narrows in a peculiar manner, one of its lips becoming reflected over it (Pl. 18, fig. 2), and it is finally reduced to a minute pore (Pl. 18, fig. 3). This opening, which is identical with the larval anus, gradually travels back to near the posterior end of the embryo; this is effected by differences in the rate of growth of surrounding parts. During this time the embryo has been lengthening its long axis, and on the fourth day it ruptures the vitelline membrane and escapes. It then has the form shown in Pl. 18, figs. 4—6, and as this stage is also a well-marked one, I have called it Stage B.

The foregoing is Ludwig’s account; my material was not suitable for such observations, which ought to be made on the living embryos, and I had not the opportunity of observing these early stages alive. As far, however, as I could make out, Ludwig is perfectly correct in his statements. I was able to recognise Stage A, for instance, with ease.

Let us turn now to the internal changes which have gone on during this time. Pl. 19, figs. 20 and 21, are two sections of an embryo of Stage A, and they form the starting-point of the changes we shall have to consider; I may here say at once that all sections which illustrate the development of the larva and its metamorphosis are to be understood to have been cut parallel to the larval plane except the contrary is distinctly affirmed. Fig. 22 is a sagittal section of a slightly older embryo; here mesenchyme cells have appeared. The large size of the archenteron is a remarkable feature, the blastocèle or segmentation cavity, usually spacious in Echinoderms, being reduced to a mere slit. Fig. 23 shows us that the archenteron becomes differentiated into an anterior thinner-walled vesicle, the coelom, and a posterior thicker-walled gut;
and in fig. 24 we see that the coelom has grown back in the form of two tongues, \( \text{lpc, rpc} \), lying one at each side of the gut. Fig. 25 shows us a more ventral section passing through the blastopore of the same individual, and we see that in it these coelomic lobes are absent; they are therefore still confined to the dorsal side of the embryo.

It has been mentioned above that the larva, immediately on escaping from the egg-membrane, has the form of Stage B, and it will be observed that its anterior end has the appearance of being obliquely truncated, and that the anterior surface so constituted is surrounded by a thickened rim, which is covered with specially long cilia, and to which I give the name of larval organ. The changes of form involved in acquiring this shape are considerable, and are undergone whilst the larva is still enclosed in the egg-membrane, though superficially the ovoid shape is maintained, the larval organ and the neighbouring ectoderm being to a large extent developed as invaginations into the interior of the larva, exactly as the Taenia head is developed on the wall of the cyst.

The histology of the embryo is illustrated in Plate 26, figs. 124 and 125. The first is a portion of section of a larva of Stage A, the same specimen as that from which figs. 20 and 21 are taken. Both ectoderm and endoderm are seen to consist of long narrow cylindrical cells, and there is no mesenchyme. Recent researches have gone to show that this is exceptional. Field (5) has proved for Asterias, and it has been long known in the case of Echinids, that mesenchyme is formed by the wall of the blastula before any invagination has taken place. Fig. 125 is taken from a slightly older gastrula. It shows the formation of the mesenchymatous cells by the division of the endoderm cells. I found no indication that mesenchyme continued to be formed when Stage B is reached. The anterior wall of the coelom is the spot where its formation lasts longest, as in Antedon (18). The coelomic epithelium consists of small cubical cells (see Pl. 23, fig. 95).

We must now return to Stage B, up to which we have traced the development. A stomodæum is now developed just behind
the posterior wall and ventral edge of the larval organ. This is well shown in the sagittal section, fig. 31. The larva increases in size, and the præoral portion and larval organ alter their shape, the latter changing from a circular to an elongated elliptical form, whilst the præoral lobe extends in a vertical direction (Pl. 18, figs. 7 to 9). The whole larva has now the form which Ludwig calls slipper-shaped, but which would be more correctly termed boot-shaped, the dorsal lobe of the præoral lobe representing the toe and the ventral one the heel of the boot. In the centre of the larval organ appears an elevation (fix.). This structure, which Ludwig did not interpret, we shall find to have a most important function during the metamorphosis; it is, in fact, the disc by means of which the animal fixes itself. Possibly this disc also functions during free life for temporary attachment, though in a different manner; thus when the larval organ is applied to the substratum, the retraction of this disc would cause a cupping action which would be relieved by its again being protruded. It has been pointed out by Ludwig, and I have myself confirmed it again and again, that the larva is able to attach itself most strongly to the substratum. The mode of life of the larva Ludwig calls "creeping." This is not strictly correct; as far as I have seen, the larva swims by means of the cilia of the larval organ. The latter is directed downwards, and for this reason Ludwig calls what I have termed the anterior surface of the animal the ventral, and the posterior end becomes for him the dorsal end. I cannot agree with this orientation; the proper longitudinal axis of any bilaterally symmetrical animal is the oro-anal one, and it is by this that I discriminate between the dorsal and ventral, the anterior and posterior surfaces. That the posterior end is held upwards is no more reason for calling it dorsal than the fact that the Cephalopod directs the apex of its visceral hump backwards is reason for calling that posterior. I should mention that Ludwig calls the whole præoral portion of the body, the præoral lobe in fact, the larval organ. I wish to avoid this, since the præoral lobe has functions which Ludwig did not suspect, and hence I confine the term "larval organ" to the
thickened ridge with long cilia, which is the locomotor organ of the larva, and is the first thing to disappear in the metamorphosis.

Stage C is the point which we have now reached, and it is characterised by the appearance of this disc for fixation. Ludwig compares the larval organ to the non-ciliated processes of the Asterid larva, the Brachiolaria. This larva appears to be merely a further stage in the development of the well-known Bipinnaria, from which it differs in the development of three stalked papillae from the apex of the preoral lobe, which are presumably used for attachment. These papillae arise between the anterior dorsal and the anterior ventral arms of the Bipinnaria: one of them is median and more dorsally situated than the other two, and to this arrangement Ludwig compares the occasional bifurcation of the ventral lobe of the larval organ of Asterina. Now, however, that we know the function of the adhesive disc, it is, in all probability, this which is to be compared to the papillae of the Brachiolaria; and the larval organ with its long cilia (compare Pl. 27, figs. 133—135) in all probability represents some portion of the ciliated bands of the Bipinnaria. Garstang (6) has, in fact, recently described a Bipinnaria in which the dorsal arm of the preoral lobe executes muscular movements in the same way as Ludwig asserts for the Asterina larva. I repeat, however, that the latter can swim by ciliary action alone, without any muscular movement.

The internal changes which have occurred between Stages B and C are numerous and important. We have already referred to the appearance of the stomodæum or larval oesophagus. About the same time the primary madreporic pore is formed; it arises by a pocket of the coelom slightly to the left of the mid-dorsal line, meeting a thickening of the ectoderm (fig. 26, mp.) and a perforation taking place. The pocket of the coelom is called the "pore-canal" (pc., fig. 26), and is lined by cylindrical ciliated cells. By this time the two posterior

1 This position is not shown in fig. 26; the figure represents a section which was rather oblique.
lobes of the coelom have extended so as nearly to meet one another in the mid-ventral line; the mesentery formed by their apposition is seen in fig. 30, posterior to the gut. The opening of the gut into the coelom has become closed ventrally (figs. 29 and 30); dorsally, however, it remains open for some considerable time yet. On the left side the coelom becomes segmented into an anterior portion, _a_, into which the pore-canal opens, and a left posterior portion, _lpc_., which we may call the left posterior coelom (fig. 27); this second cavity includes a large part but not all of the left coelomic lobe mentioned above; part of this latter is, as is seen in the figure, included in the anterior coelom. The septum between the two cavities is first formed dorsally, and then extends in a ventral direction; fig. 28 shows it in process of formation.

At the same time one can notice the first indication of that predominance of the organs of the left side which is the key to the whole ontogeny of the star-fish. We see in fig. 30 that the septum between the right and left coelomic sacs is pushed over to the right, owing to the tendency of the left posterior coelom to extend over to the right on the ventral side. At no time, so far as I have seen, however, does this septum break down. Some curious trabeculae are in this stage stretched across the left coelom. They are easily distinguished from the septum between the two sacs, as they consist of solid strings of cells, whereas the septum has two layers of epithelium with a slit of blastocoele between in this stage. These trabeculae are very transitory; in figs. 28 and 29 (Stage B) we see them being formed, and in fig. 33 is the last trace of them (Stage C).

As development proceeds the gut becomes more completely separated from the coelom, the larval anus closes, and the short rectum (fig. 31) disappears. Shortly before this, however, the stomodaeum opens into the gut, the main portion of which constitutes the larval stomach (_l. stom._), the rectum being very short; but it is only for an extremely short time that the larva possesses both mouth and anus.

Stage C is reached about the end of the fifth day, or the commencement of the sixth day. The division of the left
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posterior cælom from the cælom of the praæoral lobe, which we may now call the anterior cælom (a., figs. 32—35), is complete. On the right side the separation of the posterior part of the right cælomic lobe, the right posterior cælom, from the anterior cælom has just commenced dorsally (fig. 32). On the left side the rudiment of the water-vascular system, or, as it is convenient to term it, the left hydrocæle, has appeared (as will be related immediately a similar rudiment appears on the right side, but "hydrocæle" alone means left hydrocæle). It originates as an outgrowth from the hinder end of the anterior cælom; and whilst it is as yet but faintly marked off from this cavity, indications of its five primary lobes are seen. These are arranged in a curve open anteriorly, and throughout all the figures they are denoted by the Arabic numerals; the most dorsal being No. 1, the most posterior No. 3, and the most ventral No. 5 (see figs. 32—34). Their mutual relations are well shown in the sagittal section (Pl. 20, fig. 47), though this represents a somewhat later stage.

We have seen that the division of the right posterior cælom from the anterior cælom has begun in exactly the same manner as happened in the case of the left posterior cælom at an earlier stage. This division has not proceeded very far towards the ventral surface, when the anterior cælom buds off a vesicle from its right posterior extremity. This vesicle is homologous to the water-vascular rudiment on the left side, for which reason it will be termed the right hydrocæle; so we see that the cælom on the right side of the larva undergoes exactly the same changes as that on the left, only that they are retarded in their appearance. The first trace of the right hydrocæle is shown in Pl. 23, fig. 95; we see that it consists of a small vesicle of cubical cells arising as a thickening of the cælomic wall. Its lumen is, in this stage, a minute slit; other preparations show this slit in open communication with the anterior cælom. It is important to observe that it originates from the dorsal portion of the hinder end of the anterior cælom, which extends further back ventrally to it, as would be seen if a more ventral section than fig. 95 were shown.
Later stages of this organ are seen in figs. 35 and 36. In fig. 35 it is a conspicuous solid bud; in fig. 36 it has acquired a lumen, and is connected with the anterior coelom by a string of cells, which soon atrophies, and it is then left as an isolated vesicle in the midst of the mesenchyme. Bury (2), indeed, has seen it in this stage, and called it "a mesenchymatous vesicle;" and Field (5) has described what I believe to be an homologous structure in the larva of Asterias. The right hydrocoele persists in the adult as a closed sac just under the madreporite, and has been seen here by Cuenot (3), and Leipoldt (9) has described a similar sac in Echinids. It may seem rather a rash assumption to regard this organ as the fellow of the water-vascular system, but a complete proof that this is really its nature will be given when abnormal larvae are described.

Stage D, the summit of the development of the larva, is reached on the seventh day, according to Ludwig (Pl. 18, figs. 10 and 11). The præoral lobe and the larval organ have greatly increased in size, the former having acquired a large ventral as well as a dorsal lobe. The internal changes are more striking than the external. The separation of gut from coelom was practically complete in Stage C, the last trace of connection being shown in fig. 36. The right posterior coelom is entirely separated from the anterior coelom, but, strange to say, the septum between the left posterior coelom and the anterior coelom has become broken down in two places. This occurs by the two layers of epithelium of which it is composed fusing, and then thinning out to a film. Of these two secondary communications between the two sacs, one is situated dorsal to the left hydrocoele (Pl. 20, fig. 42), and the other ventral to it (Pl. 19, fig. 41). Figs. 42 and 43 belong to the same series; we see that the dorsal opening is formed before the separation of the right posterior coelom is complete; the ventral opening is formed at the same time. Not having had the opportunity when I wrote my preliminary account (15) of observing younger larvae than these, I imagined that the segmentation of the coelom of the left side was incomplete ab initio, a mistake which was the more excusable as both the breaches in the
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The septum dividing the two portions of the coelom from each other become again closed during the metamorphosis.

The left hydrocoele has become much more sharply separated from the anterior coelom than in the last stage, though in the region of the third lobe the hydrocoele still opens widely into the anterior coelom (Pl. 19, figs. 38—41; Pl. 20, figs. 44—46). We saw that the pore-canal in Stage B originated a little to the left of the middle line; now, however, owing to the increasing predominance of the left side, it is shifted to the right of the median plane (pc., fig. 44). The stone canal (stc., figs. 45 and 46) arises as a groove along the anterior face of the transverse septum forming the hinder wall of the anterior coelom. The central portion of this groove soon becomes closed to form a canal, opening at one end into the hydrocoele between lobes 1 and 2 (fig. 46), and at the other into the anterior coelom (fig. 45); and this opening is in this stage entirely independent of the opening of the pore-canal.

I have referred more than once to the predominance of the organs of the left side. This is strikingly shown in the stage we are considering by the narrowness of the right posterior coelom as compared with the left. Already in Stage B we have seen that the left posterior coelom has begun to sweep round to the right on the ventral side of the right posterior coelom; this occurs more and more, and in the stage we are considering in the most ventral sections (fig. 41) the right posterior coelom is entirely absent. The left not only passes under it, but to a certain extent interposes between its anterior portion and the gut (figs. 39 and 40), and here opens freely into the anterior coelom1 (fig. 40) by the secondary ventral communication described above. This portion of the left coelom we may call its right ventral horn; it plays a most important part in the metamorphosis, and it is marked 'p'c'. in all the figures.

Ludwig failed entirely to recognise the left posterior coelom.

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1 I may anticipate a little by informing the reader that the anterior coelom gives rise to the axial sinus of the adult; a space which opens to the exterior by the pore-canal and into the left hydrocoele (water-vascular ring) by the stone-canal.
as a sac separate from the anterior cælom; he states that the mesentery between the right and left cælomic lobes is absorbed ventrally. We have seen that only the posterior parts of the right and left cælomic lobes are employed in the formation of the right and left posterior cœloms respectively; the anterior parts of these lobes are continuous with the anterior cœlom, and the longitudinal mesentery between them breaks down, as Ludwig observed. Hence we see that the hinder part of the anterior cœlom in Asterina is at first a double structure; in the Bipinnaria larva the anterior cœlom is at first double throughout its whole extent.

At the dorsal anterior angle of the left cœlom (fig. 37) an invagination of its wall takes place, giving rise to a thick-walled vesicle (or. c.), which communicates by a narrow slit with the cœlom. This structure has been strangely misunderstood. Ludwig saw it, but not its origin, and supposed it to arise as a “schizocœle,” and regarded it as the rudiment of the oral blood-ring. In my preliminary account I recognised its true nature, but supposed that its upper end was the rudiment of the so-called heart,¹ with which, as a matter of fact, it has nothing to do. It is the rudiment of the oral cœlom, a space closely surrounding the adult oesophagus, the relations of which we shall study later.

**Histology of the Larva.**

The structure of the body-wall of the larva is shown in Pl. 27, fig. 138, and Pl. 28, fig. 144. In the first we see that the peritoneum of the left posterior cœlom consists of

¹ It will be observed that Bury, in his last paper (‘Q.J.M.S.,’ September, 1895), makes the same mistake. This work appeared after the present paper had been sent in for publication, and is therefore not referred to further here. The best answer to Bury’s criticisms on my observations as recorded in the preliminary account (15) is the publication of full details in the present paper. Bury’s observations contain much interesting matter, but also in my opinion many mistakes, which are due to the fact that the stages which he obtained in the development of most of the larvae he studied, did not form a series without gaps; the orientation which he adopted seems to me also not that which yields the best results.
small cubical cells; the ectoderm is made up of exceedingly long and narrow cells bearing flagella, and the wall of the hydrocoele of similar cells, but I could not make out any flagella there. Fig. 144 is taken from the posterior end of the animal on the right side; the form of the ectoderm cells is well seen, and one observes occasional goblet cells (gob.) amongst them. The section goes through a peculiar patch of peritoneum, where the cells are actively engaged in budding off the amœbocytes which float in the coelom. So far as I can make out, however, no cells are budded off at this stage into the blastocoele (i.e. the space between the ectoderm and the coelomic wall), and the mesenchyme cells are as yet entirely undifferentiated. The characters of gut cells are shown in Pl. 26, fig. 126. Although this is taken from a larva in which the metamorphosis has commenced, yet the characters of these cells do not vary till the very close of the metamorphosis. They have the same general form as the ectoderm cells, but the bases of the latter are often contracted, and leave chinks between them, whereas the endoderm cells are closely apposed to one another. Fig. 126 also shows another point of interest: here and there a small round amœbocyte may be seen applied to the basal end of the gut cells, and one discovers amongst the latter also one or two rounded cells, thus suggesting that these amœbocytes may be able to pass between the gut cells like the lymph cells in the Vertebrate intestine.

Plate 27, figs. 133—135, are three sections through the larval organ which have already been alluded to. It is to be noted that in this stage the adhesive disc has short cilia, just as Seeliger (18) has described for the adhesive disc of Antedon. Where I have put "nerv. larv." a thin strand of pale fibrous matter is observable with the highest powers. This is the only trace I can discover of a larval nervous system, and I am not perfectly satisfied about it, since it does not take the yellowish-brown tone with osmic acid so characteristic of the adult nervous system. Should my interpretation of it be correct, the larval nervous system would consist of a layer of "Punktsubstanz" underlying the larval organ.
Pl. 27, fig. 137, shows the character of the wall of the preoral lobe. The peritoneal cells have developed fine muscular tails (musc.larv.), and it is perfectly apparent to anyone looking at sections of a number of larvae that it is the peritoneum which is the active agent in contraction. The ectoderm is often wrinkled (fig. 38), but the peritoneum never, though its cells vary in shape from cylindrical to flattened according to the state of contraction; thus in some cases the peritoneal cells on the left side will be cylindrical, those on the right side flattened. The coelomic wall is in this case short and straight on the one side, and on the other bulged in to the lumen of the anterior coelom by a great accumulation of the fluid of the blastoccele, or rather (as we must conclude from observations which have been made on other Echinoderms) the blastocestic semi-fluid jelly. In fig. 137 we see some fine fibrils traversing the blastoccele; these, so far as I can make out, are not protoplasmic, but of skeletal nature—of the same nature, that is, as the adult fibrous tissue.

The Metamorphosis.

On the eighth day the larva fixes itself by the adhesive disc by means of a thin secretion of mucilage (see Pl. 27, fig. 136, which represents a much later stage), and remains fixed during the whole of the metamorphosis. I had the opportunity of observing this in Plymouth in 1893 and in Jersey in 1894, and it was most instructive to observe the difference between the larvae which had thus definitely become sessile and those which, being still able to move, had attached themselves by the cupping action of the muscles of the preoral lobe, the larval organ being applied to the substratum.

In the first case, that of truly sessile larvae, if one attempted to remove them with a pipette, one failed to move them unless very strong suction was applied or they were displaced by a needle; but once displaced they were perfectly helpless, those even which had to all appearance almost completed the metamorphosis being unable to use their tube-feet (which as yet were rudimentary); they could do nothing but feebly rotate by
the action of their general covering of cilia, and they had no power of re-attachment. In the case, however, of larvae which were attached by what we may call voluntary muscular action, if one brought the pipette cautiously near so as not to alarm them, it was very easy to remove them from a stone, just as it is easy to kick a limpet off a stone if it is taken unawares; but if they were irritated they were excessively difficult to remove, and when one finally succeeded in getting them up into the pipette, unless one promptly re-expelled them, they attached themselves to the glass, and it was almost impossible to detach them from it.

The metamorphosis of Echinoderms is probably the most remarkable ontogenetic change known in the animal kingdom; but our knowledge of its details has been up to the present most insufficient. We possess a completely satisfactory account of only one form, viz. Antedon, for which the credit is due to the researches of Bury (1), which have been amply confirmed by Seeliger (18). As I mentioned in the introduction, I hope the account I am about to give of the metamorphosis of Asterina will compare in completeness with those I have just mentioned; and as it is of the utmost importance for the comprehension of the meaning of the anatomical structure of the Asterid that its relation to the larva should be thoroughly grasped, I shall anticipate a little what I have to say in order to make the essence of the process perfectly clear. The metamorphosis of the Asterid, then, consists in the following processes, which go on simultaneously:

1. The constriction of the body into disc or body sensu stricto, and stalk, the latter being formed from the preoral lobe.

2. The sharp flexure of the disc on the stalk [the former is bent obliquely downwards and to the left. This is not well shown in any of the figures copied from Ludwig; it is better seen in the diagram, Pl. 29, fig. 158 (Dec. 1895)].

3. The preponderating growth of the organs of the left side, the left posterior coelom and the left hydrocoele both sending out dorsal and ventral horns, which meet so as to form complete
circles, whilst the right hydrocoele and the right posterior coelom remain small.

(4) The gradual atrophy of the stalk.
(5) The outgrowth of the adult oesophagus and the formation of the new mouth on the left side.

In the Crinoid the list would stand thus:

(1) The constriction of the animal into calyx and stalk.
(2) The displacement of the mouth and neighbouring organs, i.e. the hydrocoele, to the posterior end of the body by unequal growth.
(3) The mutual displacement of the right and left posterior coeloms, the left becoming posterior and the right anterior, both having a ring-shaped growth.
(4) The spiral growth of the intestine and formation of anus close to primary madreporic pore.

It will be seen that the Asterid metamorphosis is very different from that of the Crinoid, being much simpler: one great difference which strikes one at once being that in the former case the ends of the hydrocoele grow so as to embrace the stalk, which thus appears to spring from the oral surface; whereas in the latter case the hydrocoele is carried far away from the stalk to the posterior end of the body. Much diligent search has been made in the centre of the aboral surface of Asterids for traces of a stalk, but to anyone who has grasped the foregoing explanation it will be at once obvious how futile such search must prove. Pl. 29, figs. 158 and 159, though intended to indicate ancestral forms, illustrate the two metamorphoses outlined above very well.

The sections about to be described illustrating the metamorphosis are nearly all cut parallel to the larval plane, and as was the case with the sections of the larva, where two or three sections from the same series are figured the most dorsal is in every case placed first, and so one can clearly see their relation to corresponding sections of the larva. As one always thinks, however, of the organs of an Asterid as related to the plane of the disc or adult plane, it will be well to repeat the relation which these two planes bear to one another. The
adult plane makes an angle of about 70° or more with the larval plane; but without any very serious error, it may be regarded, for purposes of description, as at right angles to it: thus the direction right to left, according to the larval plane, becomes aboral to oral according to the adult plane, and dorsal to ventral according to the larval plane is nearly parallel to the adult plane. Here I may remark that the words "dorsal" and "ventral" will only be used with reference to the larval plane; in speaking of the adult plane the words "oral" and "aboral" will be used.

Pl. 18, figs. 12 and 13, show the appearance of a larva which has only been fixed for a short time. On the left side we see that the hydrocoele lobes have become visible externally, since they have raised the ectoderm into protrusions which, as we shall find, are the rudiments of sensory terminal tentacles of the radial water-vascular canals. Outside the curve of these rudiments is another set of protrusions, also arranged in an open curve. These are the rudiments of the arms: they are all, as we shall see, outgrowths of the left posterior coelom, and their primary function is to form supports for the lobes of the hydrocoele, to which they later become apposed. The constriction of the praenal lobe or stalk from the body proper is hardly as yet marked, but the rounded appearance of the dorsal and ventral outgrowths of the praenal lobe is to be noticed. This is due to the disappearance of the larval organ, the opposite sides of which become approximated to each other and wrinkled, and then broken up, portions of the organ becoming invaginated into the interior and destroyed by histolysis. The appearance of the remnants of it at this stage gave Ludwig the impression that one had to do with the outgrowth of a series of protrusions homologous to the adhesive disc. This is, of course, a mistake; the adhesive disc remains single and unaltered to the end of the metamorphosis. This well-marked phase of development we may call Stage E. Pl. 20, figs. 48 to 50, are taken from a larva of this age; fig. 48 is of course the most dorsal section (see explanation of plates). In fig. 50 we notice the great growth of the left hydrocoele, lobe 3 reaching nearly to the
posterior end of the body, and we can also make out an arm rudiment, which at this stage is a mere protrusion of ectoderm filled with mesenchyme cells; it forms the extreme posterior end of the section. The rudiment of the adult oesophagus is also seen, and we notice the relation of the oral coelom to it, and we may remark that the larval oesophagus is by this time disrupted from the gut. Fig. 49 shows that dorsally the hydro-cœle is completely shut off from the anterior coelom, and shows that the oral coelom dorsally opens into the left posterior coelom. Fig. 48 shows that the opening of the oral coelom is in close relation to a process of the left posterior coelom extending over to the right, dorsal to the gut. This is the right dorsal horn (see p. 351 for the ventral horn) of the left posterior coelom, and it is marked in all the figures. In later stages it extends ventrally for a short way, insinuating itself between the gut and the septum dividing the anterior coelom from the left posterior one (Pl. 21, fig. 61). The opening of the oral coelom is later shifted so as to be connected only with the right dorsal horn, and hence it came to pass that Ludwig regarded oral coelom and right dorsal horn of the left coelom as one structure, and described the oral coelom as the oral blood-ring and the dorsal horn as the "heart." In common with all other growing spaces in the larvae, this right dorsal horn has at its growing tip an epithelial thickening, and it was this which in my preliminary account I mistook for the rudiment of the "heart."

Figs. 51—53, taken from a slightly older larva, show the appearance of the rudiments of the perihæmal spaces. It may be useful to refresh our memory of the arrangement of these spaces in the adult; this the annexed woodcut is intended to do. They are usually described as consisting of a canal situated just aboral to each radial nerve, and divided by a longitudinal septum (Pl. 29, fig. 155). These radial canals open into a circular canal surrounding the mouth, inside which is another inner ring-canal. The longitudinal septa of the radial canals are inserted in the septum separating these two ring-canals. Into the inner of the circular canals a vertical canal opens
which is the axial sinus, embedded in the wall of which is the stone-canal (Pl. 25, figs. 110—118). This axial sinus was supposed to open at its upper end into an aboral perihæmal ring or pentagon, from which in each interradius two canals branched off to go to the genital organs. As is well known, these spaces were called "perihæmal" by Ludwig (10), because he imagined that he had discovered the true blood-system in the form of curious tracts of tissue embedded in the longitudinal septa of the radial canals, and in the septum separating the two circular canals. He further supposed that that curious
so-called heart, which projects along with the stone-canal into the axial sinus, was connected with this system, and that a string of tissue lying in the aboral ring and connected with the "heart" was also part of the vascular system. We shall, however, see later that these two latter structures ("heart" and aboral string) are of totally different nature from the oral ring, being composed of primitive germ-cells, and have, as a matter of fact, no connection with it. The radial tracts are absent in Asterina, but the oral circular tract is well represented, and we shall study its development later.

The woodcut shows us that the foregoing description is not quite correct. In the first place, we see that one can hardly speak of an outer perihemal ring, because this space is broken up into five compartments by the prolongations of the longitudinal septa of the radial canals; secondly, apart from the mistake we just pointed out in reference to the nature of the "heart" and aboral ring, we see that the axial sinus (a') does not open into the perihemal aboral ring; and, further, that to the upper end of the axial sinus is closely apposed a small closed sac, the right hydrocele.

Returning to figs. 51—53, we see that each of the five compartments of the outer oral perihemal ring arises separately as a wedge-shaped outgrowth of the coelom. I have numbered these rudiments according to the numbers of the lobes of the hydrocele between which they occur—ph. 1.2, ph. 2.3, ph. 3.4, ph. 4.5, and ph. 5.1; the last, however, arises later, and is not seen in these figures, and the first is an outgrowth of the anterior coelom (Pl. 20, fig. 51, Pl. 21, fig. 54): all the rest arise from the left posterior coelom. The shape and relations of these rudiments are well shown in the enlarged drawing given of one of them (Pl. 27, fig. 139); we see that the base of the wedge is directed outwards, and that its basal angles tend to insinuate themselves between the ectoderm and the hydrocele. As a matter of fact, each angle grows out till it meets the adjacent one of the next rudiment. The two then become apposed to each other, and their walls, which meet, form the longitudinal septum of the radial canal, and
both spaces grow out together underneath the growing lobe of
the hydrocole, and thus the radial perihæmal canal itself is
formed; we shall find later that the inner perihæmal ring arises
as an outgrowth from the oral end of the axial sinus or anterior
cœlom, and hence it is marked \( a' \) in the woodcut.

Fig. 53 shows us that the fourth and fifth lobes of the
hydrocole have extended over to the right; this being the
result of the tendency of the two ends of the hydrocole, which
have become entirely shut off from the anterior cœlom, to
approach one another. We also see from the obliquity of the
right posterior cœlom (compare figs. 44—46 with figs. 52 and 53)
that the lateral flexure of the body on the stalk has commenced.
The flexure in a downward direction cannot be well shown by
sections.

Pl. 29, figs. 54—57, are sections of a larva rather older than
Stage E. We see that the differentiation of the stalk from the
body has been initiated by the dorsal constriction of the neck
of the præoral lobe. In consequence of this the anterior cœlom
becomes divided into a stalk portion \( a \), and a body portion \( a' \),
the latter forming the axial sinus. We see, further, that the
ventral horn of the left posterior cœlom \( \ell'p'c' \) has pursued its
growth, extending obliquely to the right under the gut, and then
upwards in a dorsal and anterior direction, and on its course
the last of the five arm rudiments appears, viz. V. Fig. 57
shows the outgrowth of septa destined shortly to close the
ventral communication between this right horn of the left
posterior cœlom and the anterior cœlom. The primary lobes
of the hydrocole have each by this time given rise to two
lateral lobes, the rudiments of the first tube-feet, the primary
ones themselves being destined to form the terminal tentacles
of the water-vascular system.

Figs. 58 and 59 represent a larva about midway between
Stages E and F. We see the final division of the hydrocole
from the anterior cœlom, the last connection being in the
neighbourhood of lobe 3, and also the separation of the axial
sinus from the stalk cœlom. We see also the remains of the
larval òesophagus (\( t_< > \)), which already in Stage E has broken off
from connection with the gut; the relative position of the adult \emph{œsophagus} \((a.œ.)\) is also well shown. Fig. 60 is from a larva of about the same age; it shows the formation of the fifth perihæmal rudiment \((ph. 5.1)\) as an outgrowth of the ventral horn of the posterior cœlom: this lies beyond the fifth hydrocœle lobe, and will therefore come to lie between this and \textit{No. 1} lobe when the two ends of the hydrocœle meet. We also see the process of destruction of the stalk going on, the ectoderm of its anterior surface being invaginated in patches, and, as we shall see, each patch as it is invaginated becomes destroyed by histolysis. Fig. 61 is from a larva which has nearly attained Stage \(F\); it shows how the dorsal horn \((l” p” œ’)\) of the left posterior cœlom wedges itself in between the gut and the hinder wall of the anterior cœlom \((œ’)\). In this wall we see running from left to right (i.e. from oral to aboral sides of the disc) from the second lobe of the hydrocœle, the stone-canal. The ciliated cylindrical epithelium of this has now become continuous with that of the pore-canal, but only on one side; the conjoined tubes still open to the anterior cœlom, and this opening persists in the adult, a fact which Ludwig did not observe (to see this, a more dorsal section than fig. 61 would have to be shown). The reader will remember that the pore-canal is formed by a dorsally directed outgrowth of the anterior cœlom fusing with the ectoderm, and a perforation occurring at the point of contact, and that the stone-canal is at first a ciliated groove running along the posterior wall of the anterior cœlom. This groove we found became converted into a canal opening into the hydrocœle on one side, and the anterior cœlom on the other just below the inner opening of the pore-canal (woodcut 2).

We have now arrived at Stage \(F\), the external appearance of which is shown in Pl. 18, figs. 14—16. We notice that the prœoral lobe or stalk has become very much reduced, and that the two ends of both curves, that of the hydrocœle lobes (numbered in Arabic figures) and that of the arm rudiments (numbered in Roman numerals), have become very much approximated to each other.

At the same time we see that oral and aboral parts of the
future star-fish are decidedly oblique to one another, being closely apposed posteriorly, but anteriorly separated by the thick base of the stalk. We see also that a lateral shift of the arm rudiments has commenced, No. V having passed beyond the hydrocele lobe No. 5, and so also in the case of the others. A second pair of rudiments of tube-feet has grown out from each lobe of the hydrocele, so that they are now 5-partite.

Figs. 62—69, Pl. 21, are taken from a most instructive series of sections of a larva of this age, and are intended to give a clear conception of its internal anatomy. We are struck at once by the great reduction of the stalk, although ventrally (fig. 66) the stalk coelom still communicates with the axial sinus. In fig. 65 we see the last trace of the secondary ventral communication between the left posterior coelom (l'p'c') and the axial sinus a' (anterior coelom) just closing. The secondary dorsal opening persists much longer, but fig. 63 shows us that it also is beginning to be closed. Comparing figs. 64 and 65, we see that the adult oesophagus has acquired two lateral outgrowths, one directed anteriorly, the other posteriorly; there is also a third horn directed dorsally, which of course cannot be seen in the sections. Fig. 67 shows how the oral coelom (or.c.) now half encircles the adult oesophagus. As to the arm rudiments, the most interesting thing is to notice the wide separation of No. V from the hydrocele lobe No. 1. When the intervening tissue shrinks, a change which involves a reduction in size of the axial sinus (compare a', Pl. 22, figs. 75 and 76), the metamorphosis will be complete. The incipient shift of the other rudiments is seen, especially in the case of Nos. II and III, the latter falling between lobes 3 and 4.

By a continuation of the processes referred to above, viz. the constriction of the base of the stalk, the increasing flexure of the body on it, and the continued growth of the hydrocele and left posterior coelom, we soon reach Stage G, which is represented in Pl. 18, figs. 17 and 18. We notice the great reduction of the stalk (which is now usually directed downwards almost at right angles to the disc, though the extent of the angle between the two varies) and the completion
of the circle of arm rudiments, though No. I is not quite adjusted to hydrocoele lobe No. 2, and the hydrocoele ring is as yet incomplete. Here is a fitting place to give in a word or two the gist of Ludwig's observations on the calcareous plates. On the oral side (fig. 17) we notice ten small calcareous stars, two at the base of each primary hydrocoele lobe, situated on the inner side of the first pair of tube-feet rudiments. These are the beginnings of the first ambulacral ossicles (amb.). On the aboral side we notice eleven plates, one central (C.), five situated in the arm rudiments and destined to form the terminals (T.) (the plates which protect the terminal tentacles of the water vascular system), and five interradially situated, the basals (B.), one of which becomes the madreporite. The name "basal" is given on account of an imagined homology with the basals of Crinoids; the groundlessness of this assumption I shall point out later. All these plates make their first appearance simultaneously, rather earlier than Stage F. Fig. 19 shows the aboral surface of a young star-fish about sixteen days old. We see that the anus has been formed close to the central; that a plate has been interposed between each terminal and the central, the former maintaining its position in the tip of the growing arm, and that finally a pair of plates has appeared in each interradius, peripherally situated with regard to the basals, the latter retaining their position in the centre of the disc. These paired interradial plates are homologised by Ludwig with the interambulacral of Echinids.

Plate 22, figs. 70 and 71, are two sections of a larva of Stage G. As in all the figures the stalk is placed as nearly as possible in the same position, one can see at a glance the very great lateral flexure which the disc has undergone with reference to the stalk. We see the relation of the rudimentary larval oesophagus to the permanent one; we further see that the oral coelom is commencing ventrally to open into the left posterior one (this is of course a secondary communication, and I may say at once that the oral coelom does not give rise to a separate space in the adult, but merely forms the part of the coelom abutting on the inner side of the buccal membrane), and finally
we observe the incipient bifurcation of the posterior end of the pyloric sac (which is formed from the larval stomach) to form the pyloric cæca.

Fig. 79 is a section parallel to the adult plane of a slightly younger larva; it shows beautifully the mutual relations of the water-vascular ring (wvr), the axial sinus, and the oral cælom. If one compares this figure with Pl. IV, fig. 53, in Ludwig's paper, one sees at once that his supposed rudiment of the oral blood-ring is only the oral cælom. Figs. 75 and 76 show the completion of the metamorphosis by the apposition of arm rudiment No. V covering the tip of the ventral horn of the left cælom (\(l'p'c'\)) to hydrocoele lobe No. 1. As compared with the larva represented in Pl. 21, figs. 62—69, we notice the much smaller size of the axial sinus (\(a'\)). Fig. 75 shows also the bifurcation of the anterior end of the pyloric sac into two cæca. Comparing it with fig. 76, which is a more ventral section from a larva of the same age, we see also that the spaces between the pyloric cæca (\(py\)) and the aboral body-wall are continuations of the right posterior cælom.

Fig. 76 shows also the first trace of ovoid gland ("heart") (ov.g.) arising as a ridge of epithelium including blastocoelic jelly and fibres and amœbocytes, projecting into the axial sinus. By comparing this figure with Pl. 21., fig. 61, the shift of arm rudiment No. V can be clearly made out. Figs. 80 and 81 are sections parallel to the disc of a larva rather older than Stage G. Fig. 80 shows how the oral cælom almost surrounds the oesophagus, and also that the axial sinus is commencing to form the inner perihæmal ring by growth from its lower end (compare woodcut). In fig. 81 we see at the point marked * the closing of the water-vascular ring by outgrowths from the hydrocoele lobes Nos. 1 and 5 respectively. We also notice what we have already seen in fig. 76, that the septum between the oral cælom and the left posterior cælom is breaking down; and in fig. 82, which is from a young star-fish in which the metamorphosis is just complete, we see that from the remuants of this septum the retractor muscles of the oesophagus or "stomach" are formed. The remaining figures on the plate show the finishing touches
of the metamorphosis. In fig. 72 the adult mouth is formed, and the sessile mode of life has been given up, the stalk being reduced to a small solid rudiment. We see also the first trace of the eye as a small knob at the base of hydrocoele lobe No. 3. Fig. 78 shows the permanent anus; if we compare its position with that which the larval anus occupied, we find that they are by no means the same: the larval anus, if it had persisted, would be situated at the point $x$, though both occupy a position on the mesentery dividing the left from the right posterior cæloms. Fig. 77 from the same larva shows that the left posterior cælon now forms a complete ring by the breaking down of the partition between its right ventral and right dorsal horns ($l''p''c'$. and $l''p'c'$).

In fig. 73 a dorsal section, and in fig. 74 a ventral section, we see the incipient bifurcation of the right posterior cælon in order to form the outgrowths connected with the two dorsal and the ventral pyloric cæca respectively. We see, therefore, that of the five pyloric cæca, two are formed from the dorsal end of the pyloric sac or larval stomach, and two from its ventral end, and that their suspensory mesenteries are outgrowths from the mesentery separating right and left posterior cæloms. The fifth cæcum is directed dorsally and posteriorly. In Pl. 22, fig. 82, and Pl. 23, figs. 83, 84, we have three sections parallel to the adult plane of a specimen which had just completed the metamorphosis. Once the mouth is open, the trifid form of the adult oesophagus changes, we get the five slightly bifid lobes of the adult "stomach." In fig. 83 we see the first trace also of the bifurcation of the pyloric cæca; I remind the reader that in each arm of the adult there are two cæca; the characteristic appearance of the axial sinus, stone-canal, and right hydrocoele in a section parallel to the disc are also shown, the right hydrocoele having a crescentic form. Fig. 84 shows us the relation of the rectum and the rudiment of the rectal cæcum to the pyloric cæca; we see that the mesentery which binds the bases of the pyloric cæca together is only the original mesentery between the right and left posterior (oral and aboral cæloms); and, further, that the mesenteric band connecting the inter-
radius of the stone-canal with the stomach is a part of this same original mesentery, with which, however, is continuous a piece of the wall between dorsal and ventral horns of the left coelom, these two horns being still separated by this wall near their right sides (aboral surfaces).

**Histological Changes during the Metamorphosis.**

Up to Stage G the histology has little changed from that of the larva before metamorphosis. The most striking alterations are those connected with the destruction of the preoral lobe. Pl. 27, fig. 136, gives a specimen of them. This figure, which is taken from the larva represented in figs. 62—69, shows that the ectoderm becomes invaginated into pockets, and then these pockets completely closed, so that no breach in the continuity of the skin is made. The invaginated portion is then destroyed by amoebocytes as shown in the figure. The peritoneum lining the stalk coelom contracts violently, the cells becoming cylindrical instead of flattened, and the larval muscles very apparent. So far as I can make out, these cells are destroyed by amoebocytes of the coelom.

In the larva the whole hydrocele rudiment is lined by cylindrical cells (Pl. 27, fig. 138); but as metamorphosis proceeds, and the hydrocele increases in size, the cells are stretched so as to become flattened (Pl. 27, fig. 139); they retain their original character only in the rudiments of the tube-feet (Pl. 28, fig. 149) and terminal tentacles. The first trace of the adult nervous system appears in Stage F in the ectoderm covering the water-vascular ring,—that is, the portion of the hydrocele between the primary lobes. The ectodermal cells become long and filamentous, with their nuclei set at different levels, and amongst their bases (Pl. 28, fig. 140) appears a tangle of fine fibrils of excessive tenuity, so that the highest magnification is required to make them out; this is the first trace of the adult nervous system.

Ludwig talks of cells stretched parallel to the surface under the ectoderm, which he supposed to become the bipolar ganglion cells of the nerve-cord; but the cells in question, if I
rightly identify what he means, are only the epithelial lining of the perihemal spaces which at a later period become closely apposed to the ectoderm. The first trace of muscles in the body-wall appears much earlier. Pl. 28, fig. 145, shows the formation of a well-marked muscular band from the wall of the right posterior celom of a larva of Stage E. We see that it consists of indubitable myo-epithelial cells. I have traced this band into the oldest specimen I have examined for histology; and so far as I can see it appears to become a dilator of the anus. It is very strange that it should appear long before any other muscles of the body-wall; it forms quite a conspicuous feature in sections of all well-preserved metamorphosing larvæ. The same figure shows the first trace of histological differentiation in the mesenchyme; we see the first formation of that fibrous intra-cellular substance which gives firmness and tenacity to the adult body-wall.

The cells of the gut remain unchanged till the very end of the metamorphosis, but in Stage G we can trace some differentiation. Pl. 26, figs. 127, 128, show part of the lining of the adult oesophagus and of the pyloric sac of such a larva. The cells of the former are very long and narrow, and their outer portions take a clear yellow tone with osmic acid; those of the latter are ordinary cylindrical epithelium cells.

Abnormal Larvæ.

I mentioned above that the demonstrative proof that the sac I have termed the right hydrocele is of that nature is obtained from the study of abnormal larvæ. I suppose that about one in thirty of the larvæ I examined were abnormal, though in very different degrees. The commonest abnormality results from the unusually great development of the organs of the right side, and the consequent checking of the metamorphosis.¹ The larva of which the two sections are given in figs. 85 and 86 had about attained Stage D. The left hydrocele is perfectly normal, but the right, though not much larger than usual, is

¹ The reader will remember that in the analysis of the metamorphosis which I have given on p. 355, one of the main factors recognised is "the preponderating growth of the organs of the left side."
divided into distinct rounded lobes lined by cylindrical epithelium (rhy.), in all respects similar to those of the left, and the rudiment opens by a narrow but distinct slit into the anterior coelom. This larva also exhibits another very common abnormality, which I do not in the least understand; this consists of the breaking up of the gut epithelium into a mass of cells having the appearance of mesenchyme, which choke up the lumen, but leave the walls almost denuded of epithelium, consisting chiefly of the basement membrane. This curious change can take place at any stage from the commencement of the differentiation of the coelom, up to young adults a month old: in one such specimen it affected the pyloric caeca. As to what its meaning is, I confess I am entirely in the dark.

Figs. 87 and 88 represent a most remarkable larva. The development of the left posterior coelom would indicate that it had reached Stage E, but the left hydrocele consists only of four lobes, and is poorly developed. There are two rudiments of a hydrocele on the right side; the more ventral has three distinct lobes lined by cylindrical epithelium (r’hy’, fig. 88), and opens by a distinct opening into the anterior coelom; the more dorsal is perfectly normal (rhy., fig. 87); but, as if to emphasise the fact that, in spite of the presence of the other rudiment, it does in fact represent a hydrocele, we find in connection with it a second small stone-canal and pore-canal (p’c’. st’. c.). The relation of these to the right hydrocele may seem unusual; instead of the canal (conjoined stone and pore-canal) leading from the hydrocele to the anterior coelom and thence to the exterior, it appears to lead from the anterior coelom to the hydrocele and thence to the exterior. This apparent difference may be reconciled with the arrangement on the left side by observing the angle which stone-canal and pore-canal make with one another. Woodcut 3, p. 370, shows that this is an acute instead of an obtuse angle, and hence that stone-canal and pore-canal have coalesced laterally; Woodcut 2 shows for the sake of comparison the normal stone-canal and pore-canal and their relationship to the left hydrocele and the axial sinus or anterior coelom.
Fig. 89 is a section of a larva of Stage D; both hydrocoels are well developed—the right, in fact, better than the left; the right hydrocoel appears on the left side of the figure, since by an oversight the section was drawn from the wrong aspect. It took me some time in this larva to determine which side was which, but the right hydrocoel is rather more dorsally situated, and opens by only a narrow slit into the anterior coelom. It is also curved somewhat differently, the most posterior lobe being No. 4, not No. 3, as on the left side. Fig. 90 shows a most remarkable variation. We see a pore opening directly from the hydrocoel to the exterior. If, as I shall attempt to show later, the anterior coelom may be compared to the proboscis cavity of Balanoglossus, and the two hydrocoels to the collar cavities of that animal, we see that what we may term a collar-pore may arise as a variation. Figs. 91—94 are sections taken from a larva of Stage G. Its only abnormality is that in connection with the right hydrocoel, which is of normal character, a second pore-canal and stone-canal are developed. Fig. 92 should show the opening of the second stone-canal into the hydrocoel, but the lithographer has unfortunately not brought out the slit-like opening; fig. 93 the opening of conjoined pore-canal and stone-canal (compare woodcut 3) into the axial sinus. Fig. 91 shows that the two pore-canals unite, to open by a common median pore. The above are not by any means all the variations observed, but they are sufficiently typical to indicate their nature.
The History of the Young Star-fish.

The just metamorphosed Asterina gibbosa has a disc of about 6 millimetre in diameter; if we take R to denote the length from the tip of the arm to the centre of the disc, then R equals 36 millimetre. A larva such as that figured in figs. 51—53 may be 8 millimetre from the tip of the adhesive disc to the posterior end, and measured obliquely from the dorsal end of the preoral lobe may exceed a millimetre in length. There is, therefore, a considerable diminution in size during the metamorphosis, the reason of which is evident when we consider that no nutriment is taken during this time. A full-grown specimen may have a diameter one hundred times greater than that of the just metamorphosed star-fish,—that is, it may exceed the latter one million times in bulk. The young star-fish, however, rapidly increases in size, and by the time R equals 3.7 millimetres the ovaries are visible. This is the oldest stage I have examined; my account of the histology is, however, taken from smaller specimens, in which R equals 8 mm.

The changes we shall have to consider are (1) the formation of the primitive germ cells, the ovoid gland, genital rachis, and ovaries; (2) the dermal branchiae; and (3) general histological differentiation.

We have already in Fig. 76 seen the first trace of the ovoid gland. It there appears as a ridge projecting into the axial sinus; inside this ridge there is as yet to be found only amœbocytes, jelly and fibres, as is the case with the other blastocelic spaces in the larva. Later, a thickening of peritoneum takes place on the wall of the left posterior coelom opposite the aboral end of this ridge—and from this thickened patch a cord of cells grows into the ridge, gradually forcing its way in an oral direction; this is the characteristic core of the ovoid gland.

From this same thickening of peritoneum a cord of cells grows out in a direction parallel to the disc; this is the origin of the genital rachis. By the outgrowth of a flap of peritoneum it is enclosed in a space which is called the aboral sinus. The genital rachis and the space enclosing it both give off branches.
one at each side of each arm. Local thickenings of these branches of the rachis constitute the genital organs. The surrounding spaces, the genital sinus (ab gon, figs. 122 and 123), is shut off from the aboral sinus by the outgrowth of a septum.

Fig. 99 is the marginal portion of a section vertical to the disc of a larva of Stage G. We see the rudiment of the ovoid gland (ovg.) as a fold projecting into the axial sinus. Further up we notice a thickened patch of peritoneum, which is invaginated into the septum separating the axial sinus from the left posterior cælom (pr. germ. inv.). This is the rudiment from which, on the one hand, the genital rachis and, on the other, the core of the ovoid gland are derived. Figs. 100—103, similar sections to fig. 99, from a just metamorphosed star-fish, illustrate this. We see that from this rudiment a cord of primitive germ cells has grown out and filled the fold which is the rudiment of the ovoid gland. The last two sections cut a more oral portion of the fold, since they are slightly oblique; we see (figs. 102 and 103) that this core has not as yet penetrated to the oral end of the fold, and, further, that the fold is attached to the oral side of the inner perihæmal ring, or, in other words, that it traverses the lower end of the axial sinus, and is attached to its lower side. The original invagination to form the germ cells is situated at the very tip of the right dorsal horn of the left cælom, where it meets the right ventral horn, but at this level the two horns do not open into each other (see p. 367). Figs. 104—106, again representing sections vertical to the margin of the disc, are taken from a young star-fish, in which R equals '4 millimetre. Fig. 104 shows the cord of cells which arises from the peritoneal invagination and penetrates the dorsal organ, and the relation of this cord to the right hydrocœle and the axial sinus. We see that now this core of cells reaches to the oral end of the ovoid gland, and penetrates also a prolongation of the same, which is prolonged as a fold, hanging from the aboral wall of the inner perihæmal canal (figs. 105 and 106).

Pl. 25, fig. 110, which represents a similar section to figs. 99—106, shows practically the adult condition of the ovoid
THE DEVELOPMENT OF ASTERINA GIBBOSA.

We see that the madreporic pore has commenced to be divided into two by the ingrowth of a fold. It is not the case in Asterina, as far as I can make out, that the numerous pore-canals found in the fully grown adult are derived from fresh perforations, as Cuenot has stated (3). Rather the statement which he quotes from Perrier seems to give the actual method of their formation. We see that the openings of the stone-canal proper and the pore-canal into the axial sinus are still maintained. The ovoid gland with its core is seen to reach right down to the oral end of the axial sinus, and to be attached to its oral wall. Embedded in the septum dividing the inner perihemal ring-canal (lower end of the axial sinus—see woodcut 1) from the perihemal spaces proper is the so-called oral blood-ring (sang. circ.). This is a ring-shaped tract of peculiarly modified connective tissue; the section shows that it is of a different nature from the ovoid gland, and has no connection with it. In Asterias this ring gives off radial prolongations traversing the longitudinal septa of the radial perihemal canals, but these do not exist in Asterina. The development of this structure as far as its histology is concerned is shown in Pl. 24, figs. 107—109, which represent small portions of sections parallel to the disc. The first two sections are taken from the same specimen as figs. 82—84; in this specimen as we have already learned (see above, p. 366) the metamorphosis has just concluded. We see that the mesenchymatous tissue between the outer and the inner perihemal rings has undergone differentiation. Most of it has become converted into fibrous tissue, but at one level no fibres have been formed, the whole of the mesenchyme cells becoming amebocytes (sang. circ.); this part is the rudiment of the blood-ring. In fig. 109, taken from a specimen in which R equals 45 millimetre, we see that the ring is completely formed;

1 Durham, in a paper on "Wandering Cells in Echinoderms" (Quart. Journ. Micr. Sci., vol. xxxiii), has described the communication of the axial sinus and stone-canal in a young Cribrella. He also insists that we have no blood-vessels, but rather "hemal strands" in Echinoderms, but makes the common error of supposing the ovoid gland to belong to this category.
the intercellular jelly or plasma has acquired staining properties. To Leipoldt (9) is due the credit, in a careful paper on the anatomy of "the so-called excretory organ of the sea-urchin," of emphasising the fact that the ovoid gland and the oral blood-ring are of totally different nature; he describes branches from the blood-ring ramifying on the external surface of the ovoid gland.

The question arises, what is the true nature of this blood-ring? Cuvénot (3) answers that it is a lymphatic gland, or centre for the formation of amœobocytes; and there is a great deal to be said for this view. We must, however, remember that structures of similar nature are found accompanying the alimentary canal in Echinids and Holothurids. Ludwig (13) has given a splendid description of their arrangement in the last group. He brings out with great clearness that they are tracts of connective tissue in which the fibres are sparse. The close relation of these "vessels" to the alimentary canal suggests forcibly that we may have here the first attempt at forming blood-vessels. There is certainly no propulsive organ or proper circulation, but the staining properties of the plasma show that it has been chemically altered, and the idea is suggested of some secretion from the gut-cells propelling itself along these tracts by the vis a tergo force of secretion. In the Asterid no close connection with the gut is observable,—the oral cœlom, in fact, intervenes between the œsophagus and the ring, as we have seen (p. 365); but the altered character of the plasma suggests that perhaps here some substance is formed necessary for the well-being of the organism, which then diffuses out into the neighbouring cœlomic spaces. The blood-spaces of the higher animals are known in many cases to be remnants of the blastocœle or segmentation cavity of the embryo; this has been shown in the case of Balanoglossus with great clearness by Spengel (21). Strictly speaking, therefore, the blood and lymph spaces of other forms are represented in Echinodermata by all the spaces in the body-wall unoccupied by fibrous tissue and dermal ossicles, and traversed by amœobocytes; but the blood-ring, gut vessels, &c., may be a first attempt at specialisation.
Figs. 113—117 are intended to illustrate the formation of the genital rachis; and they all represent portions of sections cut parallel to the disc; those portions, in fact, which are transverse sections of one of the five interradial folds of the body-wall which in the star-fish project into the body-cavity. As we see in Pl. 23, fig. 83, the axial sinus, right hydrocoele, and the stone-canal, are embedded in one of these folds. It follows that the coelomic wall of this particular fold represents the larval septum between the anterior coelom and the posterior coeloms; and its interradial position in the star-fish becomes explained when we remember that the stalk with its contained anterior coelom lies opposite an interradius of the water-vascular ring; which interradius is constituted by the outgrowth of processes of the two lobes situated at the ends of the hydrocoele, which is as yet an imperfect ring. These outgrowths meet, so to speak, above the neck of the stalk. Figs. 113 and 114 are from the same specimen as fig. 109. We see the appearance of the rudiment of the germ cells in a section parallel to the adult plane, and notice the remains of the cavity of invagination (fig. 114, pr. germ. inv.). Fig. 113 shows us that one horn of the right hydrocoele has become embedded in the ovoid gland, and this is one reason why it is extremely difficult to trace the continuity of the primitive germ cells by sections taken parallel to the adult plane, since the cord of cells is in some spots so narrow, and is therefore difficult to distinguish from the epithelium lining the right hydrocoele. Longitudinal sections, such as fig. 104, show it much better. In figs. 115 and 116 (taken from a specimen in which R equals 7 millimetre) we see the formation of the genital rachis; this takes place by a lateral outgrowth from the primitive patch of invaginated peritoneum, from which we have seen the core of the ovoid gland originating as an orally directed outgrowth; the aboral sinus which surrounds it (ab.) is formed at the same time, it is a portion of the coelom shut off by the outgrowth of a fold of peritoneum. Fig. 117, taken from a much older specimen, shows the genital rachis in its complete form
in continuity with the original rudiment of the primitive germ cells.

It is, then, not quite correct to speak of the genital rachis as being an outgrowth from the ovoid gland, as Cuénot has done (3). This statement, nevertheless, marked a step in advance in our knowledge, for it gave a hint as to the meaning of the ovoid gland. Cuénot found specimens of Astropecten with the ovoid gland, but without the genital rachis, and noting the identity of the character of the cells in the two structures, stated that the rachis was an outgrowth from the gland, though he found no intermediate stages. These were first found by me (14) in the Ophiurid Amphipura squamata, and at the same time I demonstrated the epithelial origin of both gland and rachis. It is the genital rachis which of course was formerly known as the aboral blood-vessel; in most Asterids and Ophiurids it later undergoes partial degeneration, giving rise to cells containing violet pigment. Ludwig, however (11), and Haman (7) have pointed out that the central core remains unaltered; the latter was the first to point out that in all Echinoderms, except Holothurids, a genital rachis exists, of which the genital organs are local outgrowths. In Amphipura squamata, however, and in Asterina gibbosa, according to Cuénot (3), the whole genital rachis remains unaltered through life; this is only one of the many points in which Asterina shows itself to be one of the most primitive of Asterids. In the plans given in text-books of the blood system, two vessels are shown proceeding from the aboral ring in the interradius of the madreporite to the pyloric sac. These are two mesenteric bridles, remnants of the piece of septum left at this level between the two horns (right dorsal and right ventral) of the left cælom. At this spot the right (aboral) cælom breaks through into the left (oral) cælom, perforating the piece of tissue referred to, and leaving only the mesenteries. The peritoneum covering them seems to be peculiarly modified, and is possibly a place where the amoebocytes of the cælomic fluid are formed.

The genital rachis gives off, as it passes each interradius, two branches enclosed in corresponding branches of the aboral
sinus (gen. r., woodcut 1); one of these branches runs in an oral direction down each side of the interradial septum. This septum is an ingrowth of the body-wall, which has by this time become marked, though its first beginnings date back to the end of the metamorphosis (Pl. 23, fig. 84).

A section of one of these branches in an older specimen is given in Pl. 26, fig. 119). These genital branches are formed as the rachis reaches each interradial septum before it has formed a circle; in one specimen I have observed a rachis reaching only to the next interradius, and there giving off one genital branch. Figs. 120 and 121 (taken from the same specimen as fig. 119) show the first rudiments of the genital organs. The branch of the rachis ends in a swelling accompanied by a dilatation of the aboral sinus, and we see the beginning of a septum tending to shut off the main aboral sinus from this dilatation. This septum was first described by Cuenot (3), and in it the genital duct is formed. This is shown in fig. 123, taken from the oldest specimen I examined, in which R equals 3·7 millimetres. We see that the genital duct is formed by a core of primitive germ cells burrowing its way through the body-wall. Fig. 122, from the same specimen, shows the continuity of the rachis and the ovary. We notice also the formation of follicles from the indifferent germ cells.

We are now in a position to compare the arrangement of the ovoid gland and genital rachis and their accompanying spaces in Amphiura squamata with that found in Asterina gibbosa. In the former I described the genital rachis issuing from the oral end of the gland and accompanied by three spaces, which I named sinus a, sinus b, and sinus c (Pl. 25, fig. 112). This figure is a diagram of a section parallel to the long axis of the stone-canal. Fig. 111 is a diagram of a similar section of Asterina, but it is not quite accurate, since it shows both the ovoid gland and the stone-canal, and these two structures do not lie in the same radial plane in Asterina. In order to avoid obscuring the opening of the stone-canal into the axial sinus, it is necessary to indicate part of the ovoid gland by dotted lines.
Comparing figs. 111 and 112 we see that the axial sinus of Asterina is represented in Amphiura by sinus c, the so-called “ampulla.” The aboral sinus (ab, fig. 111, sinus a, fig. 112) is also obviously homologous in both.

[Since my paper (14) was published, and since the present work was sent in for publication, I have made a careful re-examination of my sections of Amphiura squamata, and have arrived at a more complete comprehension of the structure and development of the ovoid gland and the neighbouring spaces in that animal. The space marked sinus b' (fig. 112) is not, as I formerly supposed, a part of sinus b, but is quite distinct. Sinus b' probably represents the right hydroccele; it is already present in the youngest specimens I examined. Sinus b* is a portion of the coelom shut off by the outgrowth of a flap of peritoneum; from the inner wall of this sinus the cells which at the same time give rise to the ovoid gland and to the genital rachis take their origin; it is obviously homologous to the cavity of the invagination of the primitive germ cells (pr. germ inv., figs. 110 and 111), only in Asterina this space disappears.—December, 1895.]

We observe that the arrangement in Amphiura might be obtained from that in Asterina by rotating the stone-canal and accompanying structures outwards and downwards through an angle of 180°. That this is what has occurred in phylogeny is indicated, not only by the fact that in the young Amphiura the madreporite is near the edge of the disc and the stone-canal almost horizontal, whereas in the adult the madreporite is situated far in towards the mouth on the oral surface, but also by the curious undulating course of the genital rachis, which is aboral in the interradii and oral in the radii. This points to the conclusion that the aboral parts of the interradii

* In my paper on this subject (14) sinus b is referred to as the axial sinus—it was formerly supposed to be continuous with sinus c, though Ludwig knew this was not so. At that time the meaning of the axial sinus in Asterids which Bury first suggested (2) was not generally known, and his interpretations were not accepted, and hence two different spaces were called axial sinus, one in Asterids and the other in Ophiurids.
have greatly developed, and have grown in between the radii on to the oral surface, forcing the original oral plates to the extreme centre of the disc; and so the stone-canal has been swung round and the genital rachis pulled out of shape. Now in Asterina gibbosa there is a trace of this process; the rachis does not, as Hamann (7) has described in Asterias, lie in one plane, but pursues an undulating course, being much more aboral in the radii than the interradii. I am inclined to look upon this as the primitive condition from which the Asterid and Ophiurid arrangements have been derived. I may as well mention here some other facts which indicate the primitive nature of Asterina. Chief among them is, that in the family of which it is a member we meet with the most rudimentary form of those characteristic Asterid organs the pedicellariae. We have in Asterina the aboral surface covered with small spines, arranged in twos and threes, and acting on irritation like pedicellariae. It is true that some Asterids have no pedicellariae, but here the evidence from allied genera (cf. Luidia and Astropecten) suggests that they have been lost; Asterina, however, shows us pedicellariae in statu nascendi. The simple biserial tube-feet also constitute a primitive character.

Fig. 118 represents ovoid gland and stone-canal in the latest stage examined by me. The gland is attached by an exceedingly narrow pedicle to the wall of the axial sinus. Its surface is thrown into deep folds, and the peritoneal lining of the axial sinus, which forms its outer covering, is modified, consisting of cylindrical cells with projecting rounded ends. The interior of the gland is filled with a mass of primitive germ cells supported by fibres, doubtless of mesenchymatous origin. I was unable to find any trace of a tube lined by primitive germ cells, such as was discovered by Hamann in the young Asterias.

What, we may finally ask, is the function of this strange organ? Cuenot, as usual, maintains that it is a lymphatic organ. This I am disposed to doubt very strongly; the cells which it contains are of quite a different nature from the amœbocytes of the oral blood-ring, and the evidence that
Cuénot brings to show that they escape by diapedesis into the axial sinus is quite insufficient. The cells of outer epithelial lining are not flattened but cylindrical, and I strongly suspect that he has mistaken their freely projecting ends for escaping amoebocytes; and I may remark that this curious outer epithelium shows its distinctive character from the time the first rudiment of the ovoid gland appears. Whatever its function may be now, there is no doubt that the ovoid gland was primitively a part of the genital organ, and probably is a remnant of the arrangement of the reproductive cells before the radial symmetry was acquired. It is interesting to notice that it originates from the left posterior coelomic wall, whereas an analogous organ in Crinoids arises in the right or aboral coelom, so that they are not strictly homologous.

If Hamann is, as there is strong reason to suppose, right in stating that the primitive germ cells wander along the rachis into the genital organ, it seems very probable that, at any rate in the young adult, the ovoid gland is a centre of formation of the primitive germ cells; and its relation to the axial sinus may have to do with its aeration, for it must be remembered that the pore-canal opens into the axial sinus, and the current in this is, as we shall see, inwards. In the fully grown adult it no doubt undergoes, to some extent, the degenerative change noted above in the genital rachis of other genera. What the meaning of this change is, is very obscure. Observations on the histology of the gland at different seasons might elucidate its meaning.

Turning now to the stone-canal, we see, in fig. 118 (a section transverse to the axial sinus and stone-canal), the beginning of that curious T-shaped ingrowth which is so marked a feature of the stone-canals of Asterids, but which is much less developed in Asterina than in other genera. It is covered by short cilia, the rest of the epithelium bearing long flagella.

Cuénot asserted that the stone-canal was a functionless rudiment, the current being neither outwards nor inwards. Ludwig¹

subsequently showed that in the stone-canal of Holothurids and Echinids the direction of the current is inwards. He examined the stone-canal cut out of the living animal; I have confirmed his result by a somewhat more satisfactory method. I kept Amphiura squamata living for several days in sea water, carrying in one case carmine, and in another lamp-black in suspension; and on cutting sections I found these particles in the pore-canal, and in some cases apparently ingested by the cells lining it. In view of Ludwig’s researches Cuénot comes in a later paper (4) to what I believe to be the correct solution of the question of function. He there suggests that the flagella lining the stone-canal are always tending to produce an inward current, and that thus the turgidity of the whole water-vascular system is kept up. [This is practically the old view; except that he does not assert a continuous inward current.—December, 1895.]

It is obvious from the structure of the valves of the tube-feet that, in consequence of the ambulatory movements, there must be a slow loss of fluid. The ampulla and the tube-foot are shut off from the canal leading into the radial water-vascular canal by a pair of valves opening only inwards. Consequently during the contraction of either ampulla or tube-foot the two act together as a closed system, since no fluid can escape into the radial canal. The existence of the valves however shows clearly that fluid occasionally enters the tube-foot, and this can only be rendered possible by a slow loss of turgidity owing to the osmosis of the contained fluid when under pressure. This is confirmed by considering the case of Ophiurids, where, the tube-feet having lost their ambulatory function, the madreporite has only one or at most two pores, and the calibre of the stone-canal is exceedingly narrow.

The dermal branchiae arise when the star-fish has reached a diameter of about 1·5 millimetres (R equal 85 millimetre). We see that the branchia is only a very thin piece of the body-wall produced into a finger-like process (Pl. 23, fig. 98). Around the base of the branchia is a peribranchial space lined by flattened epithelium: this space, as Cuénot has rightly
observed, is the only one of the great "schizocœlic" spaces which Hamann (8) has described in the body-wall which has any real existence, the others being merely artefacts produced by the process of decalcification. I have found one specimen showing the first trace of a dermal branchia (figs. 96 and 97).

We see a slight thickening of the peritoneum, and above it the peribranchial space. Fig. 96 shows that the latter is a diverticulum of the cœlom. As I have only one section illustrating this I do not speak with absolute certainty on the point; but, with this possible though very improbable exception, there is no schizocœle whatsoever in Asterina gibbosa: all spaces lined by epithelium are of cœlomic origin.

Histological Differentiation.

The cells of the gut-wall have undergone some change since the close of the metamorphosis. Specimens of the epithelium from different regions are given in Pl. 26, figs. 129—132. These are all taken from a young adult in which \( R \) equals 85 millimetre. The cells of the lateral walls of the stomach (i.e. the adult œsophagus) have become exceedingly long and narrow; their outer ends are refracting and take a light yellow tone with osmic acid (fig. 129). The cells of the aboral wall, on the contrary, have developed numerous gland cells filled with globules; interspersed amongst them are some very narrow filamentous cells. Fig. 130 shows the spot marked \( \times \) where the stomach opens into the pyloric sac and the abrupt change in the character of the epithelium. The pyloric sac is lined by uniform columnar cells; the nucleus is generally near the base of the cell, and is never placed further up than the middle, and the protoplasm is uniformly granular (fig. 131). The cells lining the rectal cæcum (fig. 132) are similar in form but smaller, and the protoplasm is clearer, with the outer part more refringent. It is at least a plausible suggestion that the gland cells of the stomach secrete the poison which paralyses the prey, and that the cells of the pyloric sac give rise to a digestive ferment.

The differentiation of tissues which has gone on in the
body-wall is illustrated in Pl. 28, figs. 146 and 147. These sections are taken from young adults in which \( R \) equals \( 4 \) mm. and \( 86 \) mm. respectively, and they pass through the same region as fig. 145, which is from a larva in Stage E, and which we have already described. In fig. 146 we see that the muscular fibres of the muscle we may call the dilator ani are still connected with the peritoneal cells; but in fig. 147 they have become quite distinct, and the cells of the peritoneum have become quite flattened. The ectoderm has entirely changed its character, the numerous larval goblet cells have almost disappeared, and the cells in general have become shorter; many of them are inversely wedge-shaped, and are apparently about to become converted into gland cells, probably of the same histological character as those of the aboral wall of the stomach. Here and there is a narrow cell ending in a fine hair, one of the scattered sense-cells of the aboral surface; these are shown in fig. 148, a piece of ectoderm from another individual of the same age. All observers agree in maintaining that the ectoderm of the adult retains its ciliated covering; but though I have been able to make out easily the cilia, or rather flagella of the metamorphosing larva, I have not been able to do so with any certainty in the aboral wall of these young adults. Probably the cilia are very delicate and fragile. The tissues of the mesenchyme have undergone marked differentiation. So far as my researches have extended it seems that three fates are open to mesenchyme cells, all of which are illustrated in fig. 147. They may remain practically unchanged as amoebocytes or wandering cells (\textit{am\oeb.}), or they may become embedded in bundles of fibres so as to form connective-tissue cells (the fibres being intercellular, not outgrowths of cells); or, finally, they may fuse to form a syncytium having the form of a meshwork (\textit{calc.}). This is the skeletogenous tissue; lime is deposited in the interstices of the meshwork. There is a fourth fate, which is not reached by any as far as I have gone, but which obviously must be the lot of some, and that is to form the muscles moving the spines or rudimentary pedicellariae. The superficial position of these muscles renders it exceedingly
unlikely that their muscles are of peritoneal origin, and their position in other Asterids where, as in Asterias, for example, they occur on the skin covering the spines, growing even from their tips, makes such a supposition almost impossible. Therefore we must postulate some muscles of mesenchymatous origin for Asterina, although all those which I have examined are of epithelial origin.

The development of the nervous system has advanced greatly, and has reached, as soon as the metamorphosis is complete, its final form; this is shown in fig. 141, taken from the same specimen as fig. 146. The ectoderm cells have increased immensely in number, and become excessively filamentous, so that the nuclei are many layers deep; the fibrillar layer has increased very much in thickness. It is traversed by vertical fibres which sometimes branch and sometimes have small nuclei on them; these are in continuity with the ectoderm cells, but are probably of non-nervous character. Sections parallel to the disc show that numerous little bipolar cells are embedded in the mass of fibrils (Pl. 24, fig. 109, bip. gang.). Since these cells are not present in the just metamorphosed form, they must be ectoderm cells which have passed in, and occasionally one sees a cell just at the boundary of the fibres apparently in the act of passing in. The perihæmal spaces become closely apposed to the nerve-cord, no mesenchyme being left between (ph. fig. 141); the vertical fibres do not, however, arise in connection with the epithelium of these cavities, since they are present before this close apposition takes place. Cuenot states that all the ectoderm cells of the nerve-cord end in the vertical supporting fibres described above. This is a bold statement which it is quite impossible to prove by sections, and which is most improbable. As a matter of fact these vertical fibres are not present in nearly large enough number to account for all the ectoderm cells; and Hamann’s statement (8) is probably correct, that many of these end in fine processes which lose themselves in the mass of fibrils.

The sense-organs of Asterina are all developed in connection with the appendages of the water-vascular system. The eye
arises at the base of the terminal tentacle of the radial canal; two stages in its development are given in Pl. 28, figs. 142 and 143. In the first we see a simple ectodermic involution; in the second we see a pit surrounded by columnar cells, probably retinal, and filled up by closely fitting polygonal cells, which correspond to the layer of vitelligenous cells in an Arthropod eye. The existence of these cells has been vigorously denied by Cuenot (3), who maintains that we have only polygonal cuticular plates. My sections, however, remove all doubt on the subject; they show with perfect clearness that we have to do with cells, and their nuclei can be made out. This pit is the first only of the numerous pits which cover the "eye" of the adult, which is really essentially a small rounded swelling at the very tip of the radial nerve. The method of preservation employed seems to have dissolved the pigment.

The remaining sense-organs are the tips of the tube-feet and the terminal tentacle. A longitudinal section of a tube-foot is given in Pl. 28, fig. 150. This is taken from a specimen in which R equals 4 millimetre, but it holds true for specimens of a radius of a millimetre or more,—that is, for probably the first two months after the metamorphosis. Comparing it with fig. 149, a similar section taken from a larva in Stage F, we see that the ectoderm at the tip has become thickened, and underneath it we can make out on each side a mass of nerve-fibrils. A powerful nerve leaves the radial nerve-cord to supply each sense disc; it would be more correct to speak of these branches as actual prolongations of the nerve-cord with its cells and fibrils; they are, indeed, the only conspicuous branches which it gives off. Some of the ectoderm cells of the sense disc have a peculiar regular cylindrical form, which recalls that of the retinal cells.

The facts above related justify the view that the whole radial canal with its tube-feet is to be looked on as one large branched tentacle, the main function of which was probably originally prehensile and therefore also sensory; and since a plexus of nerve-fibrils is in the adult found under the ectoderm all over the body, the central nervous system may be said to be a local
concentration of this in the neighbourhood of a greatly developed sensory tentacle. The support of this tentacle by the arm is a secondary matter, as we have already learned—a fact which comes out still more clearly in Crinoid development. There the primary hydrocoele lobes develop into long free tentacles covered with sensory hairs. At a very late period (later than any which Seeliger observed) these primary tentacles, according to Perrier (17) become applied to five outgrowths of the body-wall; these latter immediately bifurcate to form the ten arms, and so the free tips of the tentacles are situated each in the angle between a pair of arms. Seeliger (18) adduces this last fact to show that the primary tentacles are not the same as the primary hydrocoele lobes of Asterids, forgetting that the point where a pair of arms diverge corresponds to the tip of the Asterid arm, since in Antedon there are ten arms which have arisen by dichotomy from five.

The epithelium of the water-vascular system in fig. 150 shows an interesting feature; the cells have developed muscular tails which are arranged longitudinally, and the important point is that these myo-epithelial cells persist as such for a considerable period of free life.

Pl. 29, figs. 151—154, show us that the aboral wall of the perihaeimat space also gives rise to muscles. These connect one ambulacral ossicle with its fellow of the opposite side, and serve, by approximating these to one another, to close the ambulacral groove. Figs. 151 and 152 show us that here again we have, in the first instance, to do with myo-epithelial cells. Muscles connecting one ossicle with its successor and predecessor are also present, but very much more feebly developed. In Ophiurids, however, as is well known, they are most powerful, and this point gives the key to nearly all the peculiarities of this group as compared with Asterids. Presuming, as we fairly may, that these muscles are developed from the perihaeial wall as in Asterids, we are brought face to face with a most interesting effect which this produces on the nervous system. Fig. 156 gives a section of the radial nerve-cord of an Ophiurid. We notice two great masses of cells and fibres on
the aboral side of the nerve-cord, and Hamaun (8) has shown that the nerves for the ambulacral muscles arise entirely from these.

Now it has been for a long time suspected, and Cuénot has finally proved it (4), that there is a similar but feeble development of what we may call "cœlomic nervous tissue" takes place in the Asterid. None of my specimens were old enough to show this, though one can see (fig. 141) that the perihæmal epithelium has come into intimate connection with the nervous matter. Pl. 29, fig. 155, represents a transverse section of the nerve-cord of a young Asterias; we see in it that this epithelium has become thickened on each side of the median septum; one requires, however, a section of the nerve of a fully grown adult to see the cœlomic nervous fibrils. So we may say that from their aboral wall the perihæmal spaces give rise to muscles, and from their oral wall to the corresponding nervous tissue. I ought to mention in this place that Cuénot describes a canal leading from the perihæmal space into the cœlom at the level of each ambulacral ossicle; also five pores leading from the outer perihæmal ring to the cœlom. If these communications exist, they are certainly secondary, as there is no trace of them in my specimens; but as Cuénot's results were founded on injection I am exceedingly sceptical as to the existence of such openings.

I have said above that the increasing importance of the ambulacral muscles is the explanation of the evolution of Ophiurids from Asterids. The Ophiurids have substituted the quick powerful movements of these muscles for the slow motions of the tube-feet. In correlation the nervous system has become better developed, the radial cords becoming gangliated, and the whole is removed from the exterior by invagination, and thus the subneural space is really a neural canal. The ambulacral ossicles have become firmly united, each to its fellow, to form a series of vertebrae, and thus the cavity of the arm is reduced, and this, with the simpler food, accounts for the disappearance of the pyloric cæca.

We have already pointed out that the lessened activity of
the tube-feet, consequent upon the loss of the locomotor function, explains the reduced stone-canal and madreporite, though probably their increased sensitiveness has helped in developing the nervous system.

Literature consulted.

An account of the earliest publications on Echinoderm development is not given here, since a résumé of them will be found in the papers I quote; and I hold it to be a waste of time to reiterate with each new paper the whole history of the growth of our knowledge ab initio. I mention here only those authors on whose results I have, so to speak, built, or from whom I have found it necessary to differ. Ludwig's work on the anatomy of Asterids (10) laid the foundation of our knowledge of the hæmal and perihæmal systems; though, as we have seen, many of his ideas about these structures were incorrect. Subsequently in treating of Ophiurids (11) he discovered the genital rachis: Hamann (7) extended this result, and pointed out the amoeboid nature of the primitive germ cells. Then we had Ludwig's great work on the development of Asterina gibbosa (12), the first account of the metamorphosis of any Echinoderm which had any pretence of completeness, and to which I have constant occasion to refer. His account of the changes in external form and of the development of the calcareous plates can hardly be improved upon. Owing, however, to the imperfect methods in vogue at that time he failed to penetrate with equal success into the course of the internal changes. He saw nothing of the segmentation of the cælom or of the ring-like growth of the left cælomic vesicle; he saw nothing also of the origin of genital organs, ovoid gland, or oral cælom. He did not observe the right hydrocele or find the origin of the perihæmal spaces. He missed the fixed stage, and he does not seem to have had any clear conception of the relation to each other of the larval and adult planes of symmetry. We owe to him, however, the clear distinction of pore-canal and stone-canal, and the recognition of the fact that the pore-canal is completely independent of the
hydrocoele. Bury (1) may be said to have introduced modern conceptions of Echinoderm development by his work on the development of Antedon; there he distinguished between anterior coelom and hydrocoele, and showed that the stalk was the preoral lobe. Then he made a series of observations on Echinoderm larvae (2), and showed that generally speaking the coelom on each side becomes segmented into two vesicles, an anterior and a posterior. He, however, regarded the hydrocoele as an essentially unpaired structure, an outgrowth from the anterior coelom, and was greatly distressed to find that it originated from the posterior vesicle in Ophiurids, and that in Asterina the stone-canal, which in other forms represented the original neck of communication between anterior coelom and hydrocoele, was apparently an independent perforation. The last difficulty has been answered by Ludwig; as to the former, the proof I have brought that the hydrocoele is paired shows that there are really three primary divisions of the coelom on each side, viz. the anterior coelom, single in Asterina, but primordially paired in Asterias; the right or left hydrocoele, and the posterior coelom (right or left as the case may be); the apparent formation therefore of the hydrocoele from the anterior or posterior vesicle is a mere question as to whether the septum between the posterior coelom and the hydrocoele or the septum between the hydrocoele and the anterior coelom is formed first.

In speaking of the Bipinnaria, Bury says that in a future paper he intends to prove that the anterior coelom becomes the axial sinus, but up till now he has published nothing further on the subject. He made a few observations on Asterina

1 Bury had not seen the stage of development when the stone-canal is an open groove.

2 Since the preliminary account (15) of the present paper was published, a paper on the "Organogeny of Stellerids," by M. Achille Russo, has appeared in the 'Atti della Accademia reale di Napoli' for 1894. In this work (to which I only obtained access some considerable time after the present paper was finished) M. Russo gives a description of the ontogeny and anatomy of the ovoid gland and axial sinus in Asterina gibbosa and an Ophiurid. He combats my statements about the origin of these structures in Amphiura squamata. The origin of the axial sinus in Asterina has been correctly described; it is about the only thing that is correctly described in the paper.
larvae of Stage D, and saw the completely closed coelomic vesicle on the right, and the imperfect transverse septum on the left side, and was at a loss how to interpret these appearances; the right hydrocoele he calls a mesenchymatous vesicle.

It is curious to see how unable many zoologists have been to grasp Bury's idea of the anterior coelom; thus Seeliger, who has confirmed his work on Antedon and amplified it till it may be said that we have an exhaustive knowledge of the subject, objects to consider the structure Bury named anterior coelom as such, on the supposition that Bury meant by that a fellow of the hydrocoele, which it obviously is not. Seeliger calls it the "parietal canal," but the structural facts he so accurately relates are convincingly in favour of Bury's interpretation. The weak point in Bury's observations on Plutei and other larvae was that in no case were any more than a few stages taken at random examined; but I hope the account I have given in this paper will provide a more solid basis for the idea of segmentation of the coelom in Echinoderms. Field (5) has published a short paper on the development of the Bipinnaria; he carries it up only to a stage corresponding to midway between Stages B and C of Asterina. The chief points of interest in the paper are that many of the larvae had two madreporic pores, and he suggests that this is a normal stage in the ontogeny; also that the two ciliated rings characteristic of the Bipinnaria are derived from one, and that there is a præoral sense-organ comparable to that in Antedon.

This paper does not contain the discovery that the water-vascular rudiment is paired; for, as a matter of fact, in the oldest larva examined no trace of the left hydrocoele was present. The "schizocoelic space," near the madreporic pore, may represent the rudiment of the right hydrocoele; needless to say, it was not recognised as such.

Theel (22) has recently succeeded in following the metamorphosis in Echinocystus pusillus so far as the external features are concerned. He finds that already in the blastula
a praëoral sense-organ is present; this subsequently becomes incorporated with the ciliated ring, and if this organ is homologous with that of the Bipinnaria, we may conclude that the ciliated band of the Pluteus corresponds only to the posterior of the two bands of the Bipinnaria, since in the Bipinnaria the sense-organ is situated between praëoral and post-oral ciliated bands, and this spot corresponds to a constriction in the original longitudinal ciliated ring, not to a position on its anterior edge.

Our knowledge of Echinoderm histology is largely due to Hamann (8) and Cuenot (3 and 4). The latter, as we have seen above, was the first to suggest that the ovoid gland gave rise to the genital rachis. The first account of the development of ovoid gland and rachis is given in my paper on Amphiura squamata (14), and I have there collected the fragmentary notices on this subject, which had till then appeared.

[I regret that when I sent in this paper for publication I did not mention the well-known paper of Metschnikoff ("Studien über die Entwicklung der Echinodermen und Nemertinen," 'Mémoires de l'Académie Impériale de St. Pétersbourg,' tome xiv, No. 8), in which he describes a right hydrocoele in Amphiura squamata. He there says that the right coelomic vesicle becomes divided into anterior and posterior portions just like the left; the anterior portion sometimes atrophies but sometimes develops into a regular five-lobed hydrocoele. It has been the fashion to ignore this work, since it was not accomplished by modern methods; but after my experience with Asterina I feel morally certain that Metschnikoff was right, though of course he did not distinguish between hydrocoæles and anterior coelom. Bury (2) seems to have missed the importance of this observation.—Dec., 1895.]

General Considerations.

On reviewing the developmental history recorded in this paper, two main questions present themselves: first, what light does it throw on the affinities of the Asterids with other Echinoderms? and second, does it suggest any direction in
which we may look to find the origin of the group Echino-

dermata as a whole?

In answer to the first question, we must observe that the
stalks of Asterina and Antedon are morphologically equivalent,\(^1\) both being formed from the præoral lobe, and, so far as one
might judge from the different shape of the latter in the two
cases, the adhesive discs by which they fix themselves are
situated in precisely the same position. Now no one doubts
that Antedon had a fixed ancestor; it is, in fact, one of the
very few Crinoids which do not remain fixed throughout their
whole life. If Asterids ever had an ancestor in common with
Crinoids which could be called an Echinoderm at all, it must
have been one represented by the fixed larva of Antedon before
it has fully acquired radial symmetry, since, as we have already
pointed out, the metamorphoses of Antedon and Asterina
pursue different courses. In the first case the mouth is shifted
backwards and upwards, and a precisely similar thing happens
to the larvæ of Entoproct Polyzoa, Ascidians, and Cirri-
pedes when they fix themselves. In the second case, how-
ever, the disc is flexed obliquely downwards on the stalk, so that
the left coelomic sac and the hydrocele both come to encircle
the base of the stalk; and as consequence the aboral poles in
the two cases are not homologous, for in the first case this pole
is the cicatrice left by the rupture of the stalk, whereas in the
second case the point where the stalk passes into the disc is
quite remote from the aboral pole. The apparent correspondence
of the calcareous plates of the calyx in Antedon and the so-
called calyx in Asterina is simply due, in my opinion, to the

\(^1\) Since the present paper was sent in for publication, my attention has been
called to some observations of Perrier's which I regret having overlooked. In
his account of the Echinoderms collected by the "Mission Scientifique du Cap
Horn," he describes the larvæ of Asterias spirabilis, which adhere to the
buccal membrane of the mother. They are attached by a pedicle which
Perrier compares to the stalk of the Antedon larva and to the præoral lobe of
the Asterina larva. He points out that both in the case of Asterias spirabi-
ilis and of Asterina gibbosa the pedicle arises from the oral surface, whereas
in Antedon it is aboral in its origin, but he offers no explanation of this dif-
ference in position.
fact that their arrangement is in both cases dominated by the prevailing pentameric symmetry of the adult.

The reason why the change in the position of the mouth takes place in Antedon is that this animal, like the others in which a similar change occurs, feeds on swimming or floating prey, and, so to speak, turns the mouth upwards to receive it. Asterids and their allies, on the other hand, find their food on the substratum, and therefore we must suppose that in the fixed ancestor of Asterids the body was flexed downwards so as to bring the substratum within reach of the tentacles. The difficulty suggests itself that a fixed form finding its food on the substratum might very soon devour all within its reach; and the suggestion may be made that perhaps the ancestor of Asterids never was fixed, but that the divergence from Crinoids took place when the common ancestor was a creeping form, since we may reasonably conclude that creeping habits formed the transition stage between a free-swimming and a fixed mode of life. In this case, however, the difficulty meets us of accounting for that radial symmetry which is so deeply impressed on the organisation of Asterids and other forms. It would be rash to say that fixed life is the direct cause of radial symmetry when we consider the case of Brachiopods, Cirripedes, &c., but this symmetry is only, so far as our knowledge goes, developed in connection with a fixed life.1

The proximate cause of the radial symmetry of Asterids is the immense preponderance of the organs of the left side, and it is difficult to see how this could have gone on to the extent it has done in an animal which moved about with a definite part directed forwards. The motion of the Asterid when metamorphosed is vague,—that is, any part is directed forwards; and it seems to me that a fixed stage must intervene between this and the mode of motion in which the head went first.

1 Some might object that Ctenophores and Medusae are radially symmetrical, but the first are not truly so; and as to the second, I hold very strongly the view that the Medusa is only a specialised bud, which has secondarily acquired locomotive powers in order to disperse the ova. Its radial symmetry has been inherited from fixed ancestors.
Therefore I feel that we are shut up to the supposition that Asterids had a fixed ancestor, and we must suppose that this form lived under conditions where enough food drifted along the bottom to meet its demands. Pl. 29, fig. 157, represents the characters which I consider the common ancestor of all Echinoderms possessed when it became fixed. Figs. 158 and 159 show how these characters became modified in the cases of the Asterid and Crinoid respectively.

It is probable that a fixed stage occurs in the life history of all Asterids. The larvae of Echinaster and Asterias Müller, which are carried in brood-pouches, certainly possess one, and the three papillae on the Brachiolaria larvae are generally interpreted as an apparatus for fixation.

The fixed stage has, however, been lost so far as we know in all other Echinoderms; and it is instructive to note in this connection that Asterids alone retain the great præoral lobe. This has completely atrophied in the Plutei both of Ophiurids and Echinids; and in the latter case, as I have indicated above, (page 391) there is some evidence to show that a præoral ciliated band has likewise disappeared. The Auricularia still retains a trace of the præoral lobe, and it has been regarded as an exceedingly primitive form because it retains the undivided longitudinal ciliated band, and because the larval mouth becomes the adult one. The internal anatomy of this larva shows that, except in these two points, it is the most modified of all; the anterior coelom so conspicuous in the Bipinnaria is represented, as Bury has shown (2), by a bud of cells which forms the secondary madreporite on the stone-canal, and the whole mode of segmentation of the coelom is most erratic.

I have dwelt on this subject at some length because some have regarded the Holothurids as the primitive group of the Echinoderms, and Sémon (19) has even attempted to show that the primary hydrocoele lobes in them became the oral tentacles, whilst the so-called radial canals were really interradial outgrowths. Ludwig (13) has, however, shown the incorrectness of this; in the Synaptidae alone do the oral tentacles spring direct from the ring-canal, and it was the development of
Synapta on which Sémon based his theory. In all Holothurids the buccal tentacles spring like the buccal tube-feet of Echinids from the proximal portion of the radial canals. It is, however, difficult for me to see how anyone can doubt that the Asterids are the least modified group of the Echinoderms. I have already dealt with their relations to Ophiurids, and have also pointed out that the Asterid central nervous system is really a concentration of the diffuse nervous plexus in connection with what must be regarded as a great sensory tentacle,—that, in fact, the whole radial water-vascular canal is to be regarded as a pinnately branched tentacle for which the arm is a secondary support. Sémon himself has suggested this (20), and it comes out even more clearly in Crinoid development than in the case of Asterids. Now the long radial canals in Echinids, ending in degenerate sense tentacles, clearly at one time had arms to support them; but these supports have been drawn back into the body. The Holothurids have been probably derived from the primitive Echinids; their calcareous nodules are most likely plates and spines atrophied in order to allow of free muscular movement. The terminal sense tentacles of the radial canals have entirely disappeared, and the forward shift of the madreporite and genital opening is no more difficult to understand than the varying position of the anus in Echinids. In the Asterids alone is locomotion entirely dependent on the tube-feet, and in them only we have the nervous system exposed.

On the second question, viz. that of the affinities of the Echinodermata as a whole, much light is thrown by the development of Asterina gibbosa. It is of course well known that the Tornaria larva of Balanoglossus shows a strong resemblance to the Bipinnaria in the course of its ciliated bands, and in possessing a præoral cælom opening by a pore on the left. The adult Balanoglossus has five cælomic cavities, and Bateson has shown that these arise as separate pouches of the gut. The question arises whether it is legitimate to homologise with these the five cælomic cavities of the Asterina larva which arise by division of pouches already formed, but
which still persist in the adult as sharply separated cavities, only the most posterior pair, viz. the right and left posterior coeloms (oral and aboral) of the adult having partially fused with each other. The development of Antedon seems to answer this question in the affirmative. In its case the hydrocele is budded off quite independently of the posterior coelomic sacs.

Adopting, then, the view that the coelomic sacs of the Enteropneusta and Asterids correspond, we find that the hydrocele represents the collar cavity. Now in Cephalodiscus the collar cavities are produced into long pinnately branched tentacles, comparable to the radial water-vascular canals, and further a branch from the central nervous system accompanies each tentacle, just as the radial nerves accompany the radial canals in Echinoderms. Now, if we suppose that the two hydroceles of Asterina were equally developed and approximated in the mid-dorsal line, the fusion of the anterior portion of the two nerve "rings," which of course would in this case be only open curves (since a ring-form is attained through the preponderating growth of one side) would give rise to a mid-dorsal nervous system like that of Cephalodiscus. Nor is that all; Professor Spengel (21) has shown in his monograph of the Enteropneusta that the currents in the proboscis-pore and collar-pore are inwards, and that by this means the animal inflates the proboscis and collar so as to render them efficient locomotor organs. We have seen that the function of the stone-canal is a similar one.

We conclude, then, that the free-swimming ancestor of Echinoderms, for which we may adopt the name Dipleurula, and the Tornaria ancestor of Balanoglossus, were closely allied. This involves the assumption that they were allied to the Protochordata, for, as I have elsewhere stated (16), Professor Spengel's attempt to refute the Chordate affinities of Balanoglossus has been, in my opinion, futile. Although it may seem somewhat fanciful, I cannot help seeing hints of Vertebrate peculiarities in the anatomy of Echinoderms. Where else among all animals of higher grade than the Coelenterates do we find calcareous ossicles in the dermis? Where else
is the removal of the nervous system from the surface effected by invagination leading to the formation of a neural canal?

When we come to try and picture the characters which the Dipleurula possessed, we see at once that it must have been far more primitive than any existing form. In point of fact an Asterid is about the most undifferentiated animal above the level of Cœlenterates which exists. No proper blood-vessels, no specialised excretory organ, a central nervous system which is really a local concentration of a diffuse skin plexus, perfectly simple generative ducts, a most feebly developed muscular system, the fibres being for a considerable time simply myo-epithelial cells,—where is such a state of things to be found outside the Cœlenterata? When we further add that in the Crinoid the ambulacral nervous system nearly atrophies in the adult, and is replaced by a new system developed in a totally different position, we see that we are at about as low a level as one could well imagine, since the central nervous system in all higher forms is a most persistent structure.

Assuredly Platyhelminths, which have been usually regarded as the basal group in the Cœlomata, or better, Triptoblastica, are far more highly specialised. To say nothing of their cephalic ganglia, we have their highly developed muscular wall and their complicated excretory and genital organs to prove this.

We shall not, then, go far astray in assigning the Dipleurula and the Tornaria to a group, the Protocoelomata, which were not far removed from the Cœlenterates; the cœlom was divided into three parts on each side, but of these the most anterior were usually fused to form an unpaired vesicle. The Dipleurula differed from the Tornaria chiefly in possession of an aperture, the stone-canal, in the wall separating the proboscis cœlom from the collar cœlom. This may have been the primitive arrangement, or it may have been a secondary arrangement acquired in consequence of the Dipleurula having lost the collar-pores, one of which may, however, as we have seen, be developed as a variation in the Asterid larva. At the apex of the præoral lobe was a more or less developed sense-organ with associated
nervous tissue. The collar cavities were probably prolonged into tentacles with which nervous tissue was associated.

If this supposition is correct, the group Protocoelomata was a pelagic cosmopolitan one, and it is in accordance with what we know of wide ranging groups that some of its members should adopt changed habits and modified structure. The Echino-dermata, then, represent the earliest offshoot which took to a sessile life and acquired radial symmetry. A little later the Hemichordata branched off, a burrowing life being adopted and consequent degeneracy resulting. The main stem, however, remained pelagic and gave rise to the Chordata. The Ascidians were the next offshoot, and then came Amphioxus. We see, therefore, that the track of the great Chordata phylum through past ages is traced by examining those of its members who at very different periods of its history, and at different stages in its evolution, have forsaken their high vocation, and taken to a sessile or burrowing life, with the inevitable consequence—degeneracy.

The following diagram may represent these relationships a little more clearly:

```
Protocoelomata
  | Dipleurula
  |     | Hemichordata (Tornaria).
  |     | Balanoglossus, Cephalodiscus.
  | Fixed ancestor of Echinoderms.
     | Crinoids.
     | Protochordata.
     | Asterids.
     | Protocelids.
     | Ophiurids.
     | Ascidians.
     | Amphioxus.
     | Echinids.
     | Holothurids.
     | Vertebrata.
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I hope in a future paper to be able to show that the Trochophore larva is also related, though much more distantly, to the Dipleurula.

March 8th, 1895.

Zoological Laboratory,
Cambridge.

List of Works referred to in this Memoir.

400 E. W. MACBRIDE.

17. PERRIER.—'Mémoire sur l'organisation et le développement de la Comataula de la Méditerranée,' Paris, 1886.

EXPLANATION OF PLATES 18—29,
Illustrating Mr. E. W. MacBride's paper on "The Development of Asterina gibbosa."
(The outlines of all the sections figured were drawn with the camera lucida.)

List of Abbreviations used.

THE DEVELOPMENT OF ASTERINA GIBBOSA. 401


PLATE 18.

All the figures are reproduced, though in a somewhat simplified form, from Ludwig’s memoir on the development of Asterina gibbosa. The various figures have, however, been enlarged or reduced as the case demanded so as to bring them to one uniform scale of magnification, viz. 85 diameters.

Fig. 1.—A gastrula with wide blastopore. Stage A. This stage is reached on the second day.

Fig. 2.—A slightly older gastrula. The blastopore is commencing to be narrowed, and one of its lips is reflected over it.

Fig. 3.—A still older gastrula.

Fig. 4.—Lateral view of larva three days old which has just escaped from the egg membrane. The “larval organ” (l. o.) or preoral ridge of ectoderm with long cilia has appeared. Stage B.

Fig. 5.—Ventral view of the same larva.

Fig. 6.—Dorsal view of the same larva.

Fig. 7.—Lateral view of larva of six days. The disc for adhesion (fix.) has appeared in the centre of the larval organ. Stage C.

Fig. 8.—Antero-lateral view of the same larva of six days.

Fig. 9.—Anterior view of the same larva of six days.

Fig. 10.—Left view of fully developed larva of seven days. Stage D.

Fig. 11.—The same drawn in the position it assumes in life.

Fig. 12.—Left view of larva in which metamorphosis has commenced, and which has fixed itself. The Arabic figures denote the primary lobes of the water-vascular system or hydrocele, the Roman figures the rudiments of the arms. The larval organ has disappeared. Stage E.
Fig. 13.—Right view of the same larva.

Fig. 14.—Ventral view of larva of about nine days. The arm rudiments form a nearly complete circle. The lobes of the water-vascular system have developed two pairs of accessory lobes each. Stage F.

Fig. 15.—Right view of the same larva of about nine days.

Fig. 16.—Left view of the same larva of about nine days.

Fig. 17.—Oral view of just metamorphosed star-fish about ten days old. am. Ambulacral ossicles. Stage G.

Fig. 18.—Aboral view of another specimen of the same age. C. Central plate. B. Basal. T. Terminal. The curve of the arm rudiments has become a circle, No. V coming to be apposed to the lobe No. 1 of the water-vascular system. mp. Madreporic pore. Stage G.

Fig. 19.—Aboral view of a young star-fish sixteen days old. Notice the anus, the additional calcareous plates, and the spines.

PLATE 19.

All the sections represented in this plate are magnified 80 diameters, and, except where otherwise stated, they have been cut parallel to the “larval plane,” i.e. they are horizontal longitudinal sections. Where several sections from the same series are figured, the most dorsal is in every case put first. The darkest shade represents the epithelium of the gut; the intermediate shade represents ectodermic and coelomic epithelium, including the lining of the derivatives of the coelom; the lightest shade represents the cavity of the blastoccele with all its contained structures, jelly, fibres, cells, &c., and also the muscular tails of the epithelial cells lining the water-vascular system. In Fig. 27, however, a portion of the gut opening into the coelom, and in Figs. 30, 31, 34, 39, 40, and 41 the larval oesophagus, have been printed (through oversight) in the intermediate tint.

Figs. 20 and 21.—Two sections of a gastrula a little older than Stage A. No mesenchyme has as yet appeared.

Fig. 22.—Sagittal section of a gastrula about the same stage as Fig. 3. mes. Mesenchyme cells.

Fig. 23.—Section of an embryo older than that shown in Fig. 3. It shows the differentiation of the archenteron into gut and coelom.

Figs. 24 and 25.—Two sections of an embryo somewhat younger than Stage B, and still enclosed in the vitelline membrane. The coelom has grown back at each side of the gut, forming two posterior lobes, lpc., rpc. Fig. 25 shows, however, that these lobes do not as yet extend ventral to the gut.

Fig. 26.—Section of larva rather older than Stage B, to show the formation of the madreporic pore. pc. Pore-canal ending blindly in contact with the ectoderm. l. stom. Larval stomach. mp. Thickening of ectoderm where the primary madreporic pore will be formed.
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Figs. 27—29.—Three sections of a larva slightly older than the preceding. Fig. 27 shows that on the left side the coelom is divided into an anterior coelom \(a\), and a left posterior coelom \(ipc\). Fig. 28 shows that this division only extends about halfway to the ventral side. Fig. 29 shows that the separation of the coelom from the archenteron commences ventrally, since here the coelom is shut off from the gut. \(tr\). First trabecula.

Fig. 30.—Section of a larva rather older than that shown in Figs. 27—29. \(la\). Larval oesophagus. \(tr\). Trabeculae cords of cells spanning the left posterior coelom.

Fig. 31.—Sagittal section of larva about Stage B, to show the formation of the larval oesophagus. It is clearly seen that this is a stomodeum which has not as yet joined the gut.

Figs. 32—34.—Three sections of a larva younger than Stage C. The segmentation of the coelom on the left side is complete; on the right side it has begun dorsally (Fig. 32). The left water-vascular rudiment or hydrocele \((lhy.)\) has appeared as an outgrowth of the anterior coelom, its lobes numbered as in Pl. 18. Fig. 32 shows Nos. 1 and 2; Fig. 33, No. 3; and Fig. 34, Nos. 4 and 5.

Fig. 35.—Section of a larva of Stage C. The first trace of the right hydrocele \((rhy.)\) has appeared.

Fig. 36.—Section of a slightly older larva than preceding. The development of the right hydrocele is more advanced.

Figs. 37—41.—Five sections of a larva of Stage D, or slightly younger. In Fig. 37 we see a section of the pore-canal \((pc.)\) and the origin of the rudiment of the oral coelom \((or. c.)\). In Fig. 38 the fully developed form of the right hydrocele \((rhy.)\) is shown. In Figs. 39 and 40 we see the left posterior coelom extending obliquely beneath the right posterior coelom \((rpc.)\); this is the right ventral horn \((r'p')\) of the left posterior coelom. In Fig. 41 we see it opening into the anterior coelom.

PLATE 20.

The same remarks apply to this as to Plate 19, but in addition it is to be remarked that the epithelium of the pore-canal and of the stone-canal is distinguished by a cross-striation.

Figs. 42 and 43.—Two sections of a larva rather younger than Stage D. \(ste\). Rudiment of the stone-canal. Fig. 42 shows the septum between the anterior coelom and the left posterior coelom broken down dorsally; and Fig. 43 shows that the septum between the anterior coelom and the right posterior coelom is still incomplete ventrally.

Figs. 44—46.—Three sections of a larva of Stage D. Fig. 44 shows the opening of the pore-canal into anterior coelom; Fig. 45, opening of the stone-canal into the same; and Fig. 46, the opening of the stone-canal into the

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hydrocoele. It shows also that the hydrocoele has a wide opening into the anterior coelom independent of the stone-canal.

Fig. 47.—Sagittal section of a larva of Stage D, to show the relations of the lobes of the left hydrocoele to each other.

Figs. 48—50.—Three sections of a larva of Stage E. The larva has suffered an injury, a piece of ectoderm in the præoral lobe indicated by the dotted line being missing. Fig. 48 shows relation of rudiment of oral coelom (or. c.) to the right dorsal horn of left posterior coelom (d'p'/c'). Fig. 50 shows the great growth of the left hydrocoele (compare Fig. 40). a. a. Adult oesophagus; rudiment of the "stomach" of the adult. In Fig. 49 the o of or. c. has failed to print.

Figs. 51—53.—Three sections of a larva slightly older than the preceding, to show rudiments of the perihemal spaces (ph.). These are numbered according to the lobes of the hydrocoele between which they occur: ph. 1.2, ph. 2.3, ph. 3.4, and ph. 4.5. ph. 1.2 arises from the anterior coelom, the rest from the left posterior coelom. The lobes of the hydrocoele are commencing to be trifid.

PLATE 21.

The same remarks apply to this plate as to the two foregoing.

Figs. 54—57.—Four sections of a larva about midway between Stages E and F. Fig. 54 shows the incipient dorsal constriction of the anterior coelom into a stalk portion (a.) and a body portion or axial sinus (a'); also the origin of the perihemal rudiment (ph. 1.2) from the anterior coelom. Fig. 55 shows the growing tip of the right ventral horn of the left posterior coelom, and over it the arm rudiment No. V; it shows also the stone-canal opening into the hydrocoele and the perihemal rudiment insinuating itself between the hydrocoele and the ectoderm. Fig. 56 shows the axial sinus and the stalk coelom continuous with each other, and also the anterior coelom opening into the right ventral horn of the left posterior coelom. Fig. 57 shows that this right ventral horn is commencing to be again divided from the anterior coelom ventrally by the outgrowth of a septum.

Figs. 58 and 59.—Two sections of a larva slightly older than the preceding, to show the separation of the axial sinus ventrally on the one hand from the stalk coelom, and on the other hand from the hydrocoele. Py. Rudiment of the pyloric sac of adult. la. Last trace of the larval oesophagus.

Fig. 60.—Section of larva about the same age as preceding, to show the fifth perihemal rudiment (ph. 51) which intervenes between lobes 5 and 1, as yet widely separated.

Fig. 61.—Section of larva about Stage F, to show the mutual relations of the stone-canal, the axial sinus (a'), the right dorsal horn of the left posterior coelom (d''p'/c''), and the right hydrocoele (rhy.).
Figs. 62—69.—Eight sections of a larva slightly older than Stage F, to show the relation of the arm rudiments to the lobes of the hydrocoele. Fig. 63 shows the incipient healing of the breach in the septum between the anterior coelom (axial sinus) and the left posterior coelom. Figs. 64 and 65 show that arm rudiment No. V is still widely separated from hydrocoele lobe 1 by the base of the stalk, and also that the right ventral horn (fpd') of the left posterior coelom is not completely separated from the axial sinus (a'). Fig. 65 also shows the complete separation of the hydrocoele from the axial sinus. Figs. 66 and 67 show relation of the oral coelom (or. c.) to the adult oesophagus (a. e.). Fig. 69 shows the adhesive disc of the stalk (fix.) attached to a piece of Alga (x), and the rest of the ectoderm of the preoral lobe being invaginated (hist.) to undergo destruction. It also shows that each primary lobe of the hydrocoele has developed two pairs of secondary lobes.

PLATE 22.

The same remarks apply to Figs. 70—78 as to the contents of the three foregoing plates. Figs. 79—82 are sections cut parallel to the disc of the star-fish or "adult plane," the magnification being the same, viz. 80 diameters.

Figs. 70 and 71.—Two sections of a larva of Stage G. Fig. 70 shows the relationship which the adult and the larval oesophagus occupy with regard to one another, the latter being a mere rudiment unconnected with the gut; it also shows the outgrowths from the adult oesophagus. Fig. 71 shows the oral coelom opening into left posterior coelom ventrally by breaking down of partition between them; also the first trace of the pyloric ceca as outgrowths from the pyloric sac.

Fig. 72.—Section of larva rather older than Stage G. The adult mouth is formed, and the oral coelom opens widely into the left posterior coelom. The stalk has become a small solid rudiment. The dotted line shows the boundary between the pyloric sac and the adult "oesophagus" or "stomach."

Fig. 73.—Section of a larva of the same age as the preceding; it shows the two dorsal pyloric ceca already formed, also the so-called heart or "ovoid gland" (ovg.), as a fold projecting into the axial sinus (a').

Fig. 74.—Another section from the same series as Fig. 72. Shows the two ventral pyloric ceca; it is seen also that their suspensory mesenteries are derived from the mesentery separating the right posterior coelom from the left (compare Fig. 75). Note also that the tube-feet have acquired their suckers. The animal has broken loose from its attachment, which accounts for the rudimentary condition of the stalk.

Fig. 75.—A section of a larva of Stage G. Shows the dorsal pyloric ceca and their suspensory mesenteries.

Fig. 76.—A section of another larva of Stage G. Compare with Pl. IV, fig. 61, and note that the arm rudiment No. V (not marked in the figure) has
now become applied to the lobe No. 1 of the hydrocele. The stone-canal is seen opening into lobe No. 2, and the perihemal rudiment 1.2 has grown out into a canal insinuating itself between the ectoderm and the hydrocele.

**Figs. 77 and 78.**—Two sections of a rather older larva. Fig. 77 shows that the right ventral and right dorsal horns ("p'c'. and "p"r c") of the left posterior coelom have coalesced, and that the left posterior coelom has thus acquired a ring-like form. Fig. 78 shows the formation of the anus of the adult.

**Fig. 79.—**Section parallel to the adult plane of a larva of Stage F. Shows the relationships of the axial sinus, oral coelom, and water-vascular ring (wvr.), the last being still incomplete; also four perihemal rudiments alternating with the five hydrocele lobes.

**Figs. 80 and 81.**—Two sections in same plane as Fig. 79 of a larva of Stage G. Fig. 80 shows the axial sinus ("a'") in process of growth to form the inner perihemal canal. Fig. 81 shows the completion of the water-vascular ring at the spot marked by the asterisk between the hydrocele lobes Nos. 1 and 5; it also shows the trifid form of the adult esophagus before the mouth is formed, and the oral coelom opening into the left posterior coelom.

**Fig. 82.**—Similar section of older larva in which mouth is formed. The five interradial lobes of the "stomach" are present, the trifid shape having disappeared; and the retractor muscles of these lobes are formed from remnants of septum between oral and left posterior coelom. The distance (R) from tip of arm to centre of disc 36 millimetre.

**PLATE 23.**

**Figs. 83 and 84.**—Two more sections from the same series as Fig. 82. Fig. 83 shows the pyloric sac with its five cæca just beginning to be bifid, and the mutual relations of the right hydrocele and axial sinus; also the stone-canal opening into the latter. Fig. 84 shows the point of origin of the rectum and the rudiment of rectal cæcum and the relation of right posterior coelom to the pyloric cæca. In Fig. 83 (pr. germ. inv.) is the involution of peritoneum from which the primitive germ cells are formed.

**Figs. 85—94 represent sections of abnormal larvae.** These sections are cut parallel to the larval plane, except Fig. 90, which is rather oblique to that plane. Magnification the same as before.

**Figs. 85 and 86.**—Two sections of a larva of Stage D, or slightly younger. "hy. Right hydrocele developed into two distinct lobes lined with cubical epithelium.

**Figs. 87 and 88.** Two sections of a larva between Stages D and E. "p'd', st'd'. Pore-canal and stone-canal of right side in connection with normal right hydrocele, r. hy. Their openings into this are in another section. r'hy'. A second, more ventrally situated hydro-
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coele rudiment on the right side, with a distinct opening into coelom. The left hydrocoele is feebly developed for the stage which the larva has reached, and has only four lobes.

Fig. 89. Section of a larva of Stage D, in which the right hydrocoele has five lobes, and is larger than the left. This section is drawn from the ventral aspect, and hence appears reversed.

Fig. 90. Section of a larva of Stage G, showing a “collar pore” opening from the left hydrocoele between lobes 2 and 3, directly to the exterior.

Figs. 91—94. Four sections of an almost normal larva of Stage F, or somewhat older. p. c. Normal pore-canal, opening into axial sinus, the septum between the latter and the left posterior coelom being still incomplete dorsally. p’. c’. Pore-canal, st’. c’, and stone-canal in connection with the right hydrocoele. Fig. 93 shows the opening of the second pore-canal into the axial sinus. Fig. 92 ought to show the opening of the second stone-canal into the right hydrocoele, but the slit-like opening has not come out in the figure. Fig. 91 shows the two pore-canals uniting to open by a common pore. (Compare Woodcut 3.)

Fig. 95.—Section parallel to the larval plane from larva of Stage C, showing the first trace of right hydrocoele. (Compare Plate 19, fig. 35.) Note its relationship to the anterior coelom, which extends obliquely beyond it posteriorly, passing under it and to the right of it. Magnification 1000 diameters; Leitz’s immersion \( \lambda_\mu \).

Figs. 96 and 97.—Two sections of body-wall of young star-fish, cut perpendicular to disc, in which R equals 8 millimetre. Fig. 97 shows first trace of “papula” or dermal branchia (branch). Fig. 96, origin of its peribranchial space, p.br. Magnification 400 diameters.

Fig. 98.—Section of body-wall of young star-fish, in which R equals 88 millimetre, showing dermal branchia and its peribranchial space. Magnification about 400 diameters.

PLATE 24.

Figs. 99—106 illustrate the development of the so-called heart or “ovoid gland.” The sections represented are perpendicular, or nearly so, to the disc of the star-fish, and the magnification is 350 diameters.

Fig. 99. Section of larva of Stage G. ov.g. Fold projecting into the axial sinus, the rudiment of the ovoid gland. pr. germ. inv. Invagination of peritoneum, whence the primitive germ cells are formed. Calc. Calcigenous tissue in the body wall.

Figs. 100—103. Four sections of a specimen older than preceding. Fig. 101 shows the growth of the primitive germ cells into the rudiment of the ovoid gland. Figs. 102 and 103 show that they do not yet extend through its whole extent. Fig. 103 shows that the ovoid gland
rudiment is at one point attached to the oral wall of the axial sinus.  
(Compare Plate 25, fig. 110.)

Figs. 104—106. Three sections of a young star-fish, in which R equals 4 millimetre. Fig. 104 shows the primitive germ cells arising from the involution of the peritoneum. Figs. 105 and 106 show that they now extend throughout the whole extent of the ovoid gland; these figures also show the relation of the oral end of the axial sinus to the perihumal spaces.

Figs. 107 and 108.—Two sections from same series as Figs. 82—84, magnified 350 diameters. They show the development of the oral "blood ring, sang. circ., as a modification of the mesenchymatous tissue of the blastoccele. fibr. Fibrous tissue.

Fig. 109.—Similar section of a young star-fish, in which R equals 45 millimetre. Same magnification. The blood-ring is fully formed. Notice also the minute cells amongst the nerve-fibres (bip. gang.).

PLATE 25.

Fig. 110.—Longitudinal section of the stone-canal of young star-fish, in which R equals 8 millimetre. sang. circ. Oral "blood" ring. wnr. Water-vascular ring-canal. muse. amb. Muscles of ambulaeral ossicles. Notice the incipient division of madreporic pore into two, and entire independence of ovoid gland and blood-ring. Magnified 350 diameters.

Fig. 111.—Diagram showing the relative positions of the ovoid gland, stone-canal, and various sinuses in proximity. gen. r. Genital rachis. ab. Aboral sinus (or sinus a.). pr. germ. inv. Primary peritoneal involution to form germ cells. The cavity of this is probably the same as sinus b in next figure. The axial sinus a' is sinus c. The dotted lines show the continuity of two parts of the ovoid gland in a different plane to that of the stone-canal.

Fig. 112.—Similar diagram of Amphiuara squamata. Accompanying spaces, sinus a, sinus b, and sinus c, as in the author's paper (14).

Figs. 113—118 illustrate the development of the ovoid gland and genital rachis. They are all taken from sections cut parallel to the disc; they are, in fact, transverse sections of the interradial septum in which the axial sinus is embedded.

Figs. 113 and 114. Two sections from a star-fish, in which R equals 45 millimetre. Fig. 113 shows the manner in which the right hydrocoele is enclosed in the upper part of ovoid gland; Fig. 114, the primitive peritoneal involution, the pore-canal, and the crescentic form of right hydrocoele. Magnification 350 diameters.

Figs. 115 and 116. Two sections from star-fish, in which R equals 7 millimetre. ab. Aboral sinus containing the rudiment of genital rachis. Fig. 115 shows that the sinus is a portion of the coelom shut off by the outgrowth of a flap from the body-wall.
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Fig. 117. Section from star-fish, in which R equals 2.2 millimetres, showing the continuity of rachis and ovoid gland, and that the rachis now extends in both directions. Magnified 150 diameters.

Fig. 118. Section from star-fish, in which R equals 3 millimetres, showing fully developed ovoid gland and changed form of stone-canal. Magnified 350 diameters.

PLATE 26.

Figs. 119—121.—Portions of three sections from the same series as Fig. 118. Fig. 119 shows the genital rachis enclosed in the branch from the aboral sinus, ab. Fig. 120 shows the passage of the genital rachis into the rudimentary genital organ, and the outgrowth of septum which cuts off the perivillar space surrounding this rudiment from the "genital vessel." ab. A branch of the aboral ring. Fig. 121 shows the development of the cavity of the genital organ. Magnification 350 diameters.

Figs. 122 and 123.—Two sections of young ovaries, from a specimen in which R equals 3.7 millimetres. Fig. 122 shows the continuity of the ovary and rachis, Fig. 123 the outgrowth of germ cells to form the genital duct.

Fig. 124.—Portion of body-wall of gastrula figured in Plate 19, fig. 21. Notice the absence of mesenchyme. end. Endoderm. Magnification 600 diameters.

Fig. 125.—Similar view of the body-wall of slightly older embryo, to show the formation of mesenchyme. Same magnification.

Fig. 126.—Portion of the gut epithelium of larva figured in Plate 20, figs. 51—53. Same magnification.

Fig. 127.—Epithelium of the adult oesophagus of the larva shown in Plate 22, fig. 76, Stage G. Magnified 480 diameters.

Fig. 128.—Epithelium of the pyloric sac (larval stomach), from the same section as foregoing.

Fig. 129.—Epithelium of the lateral wall of the stomach of a star-fish, in which R equals 8 millimetre. Magnified 480 diameters.

Fig. 130.—Epithelium of aboral wall of the stomach from the same section as foregoing. At x it passes into the epithelium of the pyloric sac.

Figs. 131 and 132.—Epithelium of the pyloric sac and of the rectal caecum respectively. From the same section as fig. 130.

PLATE 27.

Figs. 133—135.—Three sections of the ectoderm of the anterior surface of præoral lobe of larva of Stage D. Fis. Disc for fixation. l. o. Larva organ. nerv. larv. Larval nervous tissue. Fig. 133 is through the dorsal part of præoral lobe; Fig. 135 through its ventral tip. Magnified 480 diameters.
Fig. 136.—Section of the adhesive disc of larva shown in Plate 21, figs. 62—69. A small piece of alga, to which it adheres by a secretion of mucus. Involution of neighbouring portions of ectoderm to undergo destruction by amoebocytes, amoeb.; by this means the preoral lobe is reduced in size. Magnified 480 diameters.

Fig. 137.—Section of the lateral wall of preoral lobe of larva of Stage D. Larval muscles derived from the peritoneal cells. Magnified 1000 diameters.

Fig. 138.—Section through the ectoderm and hydrocoele wall of a larva of Stage D, to show the characters of the various larval epithelia. Magnified 1000 diameters.

Fig. 139.—Similar section from a larva between Stages E and F. A perihemal rudiment is shown. Magnified 1000 diameters.

PLATE 28.

Figs. 143, 149, and 150 are magnified 600 diameters, the rest 1000 diameters (Leitz’s immersion $\frac{1}{4}$).

Fig. 140.—Similar section from a larva of Stage F (that shown in Figs. 62—69). Nerv. The incipient nervous tissue developing as a fine plexus amidst the bases of the ectoderm cells.

Fig. 141.—Similar section from a young star-fish, in which R equals 1.4 millimetre. Nerv. circ. Nervous ring. calc. Calcigenous tissue. fibr. Fibrous tissue. retr. muse. Retractor muscles of stomach.

Fig. 142.—Developing eye of same star-fish. A simple ectodermic pit is seen.

Fig. 143.—Eye of star-fish from which Figs. 129—132 are taken. ret. Visual cells. vit. Cells functioning as “Glaskörper.”

Figs. 144—148 illustrate the differentiation of tissues in the body-wall.

Fig. 144. From the right side of a larva of Stage D. At * a cell is seen in the act of dividing, to form one of the amoebocytes of the coelom.

Fig. 145. From larva of Stage E (that shown in Figs 51—53). gob. Goblet cells. muse. Developing muscles; as yet they are simply tails of the coelomic epithelium. fibr. First rudiment of fibrous tissue.

Fig. 146. From the young star-fish from which Fig. 141 is taken calc. Small portion of calcigenous tissue.

Fig. 147. From the young star-fish from which Fig. 143 is taken, and also Figs. 129—132.

Fig. 148. Ectoderm of another specimen of same age, to show the sense-cells.

Fig. 149.—Tube-foot of the larva shown in Figs. 62—69.

Fig. 150.—Tube-foot of the star-fish from which Figs. 141 and 146 are

**PLATE 29.**

Figs. 151—154 show the development of the transverse muscles, which extend from one ambulacral ossicle to its fellow of the opposite side.

Figs. 151 and 152.—Two sections perpendicular to the disc from a starfish, in which R equals 4 millimetre. *sang. circ.* Oral "blood" ring. *musc. amb.* Ambulacral muscles; the reference line (in Fig. 151) is too long. *ph.* Periheemal space; the reference line (in Fig. 151) is too short. Magnified 350 diameters.

Fig. 153. Similar section from starfish in which R equals 63 millimetre.

Fig. 154. Similar section from starfish of the same size as the preceding, but more advanced in the development.

Fig. 155.—Transverse section of the radial nerve-cord of a young Asterias, to show the feeble development of celomic nervous system.

Fig. 156.—Similar section of nerve-cord of an Ophiurid, to show the great ganglia of the celomic nervous system.

Fig. 157.—Diagram of the hypothetical ancestor of Asterids and Crinoids. The hydrocoele is a paired structure.

Fig. 158.—Diagram of a stage in the evolution of Asterids from this ancestor. Notice the growth of both left hydrocoele and left posterior celom to form rings. The hydrocoele encircles the base of the stalk. This drawing does not properly represent the oblique position which the disc assumes in reference to the stalk. The mouth ought to be half turned towards the observer.

Fig. 159.—Diagram of stage in evolution of Crinoids. Notice that the hydrocoele is carried entirely away from the stalk.

These last two diagrams are only hypothetical, in so far as they represent as co-existing structures which succeed one another in ontogeny; otherwise they represent the actual fixed stage in both Asterid and Crinoid ontogeny.

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