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Studies on the Development of Larval Nephridia.

Part I. *Phoronis.*

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With Plates 31—33.

General introduction.

Some twenty years ago it was pointed out by R. S. Bergh (1) that the provisional larval nephridia of some Oligochaets, Mollusca and the head-kidney of the *Polygordius* larva, were probably one and the same structure, and homologous with the excretory system of Platyhelminths[1]. It consists, in these animals, of a simple or branched tube opening on the exterior, internally being closed by one or many peculiarly modified flame-cells. It lies not in the true coelom, but in the spaces of the mesodermic tissue or blastocoel outside the coelom. Since the adult nephridia, in distinction to the provisional nephridia, have always some relationship with the coelom, Bergh considered the two sets of organs distinct. The adult nephridia were to be homologised with the ducts of the germinal follicles of a Nemertine, while the cavities of these follicles themselves, were to be compared with the coelom of Annelids. It was soon pointed out, that Bergh's objection to the homology between larval and permanent nephridia, on the ground that the former do not lie in the true coelom, does not hold, when we consider that in the forms that Bergh studied, the Gnathobdellidae, the provisional

[1] I am aware that Bergh was by no means the first to express this homology of the larval excretory organs, in fact the whole of Bergh's theory was somewhat forestalled in the well known words of Hatschek, published some time previous: »Die secundäre Leibeshöhle verhält sich wie die Höhle der Geschlechtsdrüse der niedrigeren Formen.« (Stud. ü. Entwickel. der Anneliden. in: Arb. Z. Inst. Wien 3. Bd. 1878 p. 90).

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organs occur only in the anterior part of the larva, where no permanent organs develop, and where the coelom itself is frequently wanting. And also owing to the fact that the cells, the nephroblasts, which in the embryo give rise to both sets of organs, consist of cell rows, the provisional organs arising from the anterior, the permanent, from the posterior portions of these rows; these rows in turn have their origin in a continuous, not a discontinuous embryological basis. Moreover, recent investigation has shown, that the adult nephridia can be closed internally by flame-cells, in a manner similar to the provisional organs; so far as simple structure is concerned, they are essentially the same.

If we classify the Polychaeta according to the form of their nephridia, they are readily separable into two great groups. One of these, which includes most of the Phyllodocids, Glycerids and the Nephthyids (see 9), is furnished with nephridia which resemble the provisional organs of Oligochaets, the *Polygordius* larva, and the protonephridia of Platyhelminths, being closed internally by flame-cells. The other is provided with nephridia that open into the coelom. The structure of this opening, in turn, separates this last group into two subdivisions. In one of these the nephridium opens by means of a large funnel, which arises from the peritoneal epithelium of the coelom, only in the later stages of development joining the nephridium, thereby increasing the effectiveness of this organ as a collector of the products of the coelom. The nephridia of the second subdivision are provided with true coelomic openings, or nephrostomes, which are much smaller, and never develop into the great funnel-like openings of the previous group.

If we endeavour to determine which is the most primitive of these three types of nephridia, we select the flame-cell form of nephridium, from its resemblance to the excretory tubules of Platyhelminths. This opinion is supported by the fact, that this type of nephridium is found in larval forms, and also by the fact that in certain of these larvae, while the nephridia are at first of this form, as development proceeds, they gradually lose their flame-cells and acquire openings into the coelom.

I have examined the head-kidney in a number of Trochophore larvae[1], and I have never found this structure opening into the body-cavity (blastocoel). The whole organ is justly comparable to an

[1] *Eupomatus uncinatus*, *Hydroides pectinata* and *Pomatoceros triqueter*.

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enlarged flame-cell, the tube of the flame-cell answering to the canal of the head-kidney. Thus the head-kidney, the nephridium of the first segment of those Polychaeta that pass through a Trochophoral stage, never develops beyond the flame-cell condition.

Beyond this mere resemblance therefore, there are reasons for regarding the flame-cell type of nephridium as the most primitive, and as being derived phylogenetically from the flame-cells and protonephridia of lower forms.

The present work was undertaken in the hope of proving this on a basis of development. It has been my first aim to study the origin and growth of the flame-cells, the characteristic feature of the larval nephridium. For these cells GOODRICH (9 pag. 442) has recently proposed the name of "Solenocyte", by which it is best to designate them in future. If we compare them with the flame-cells of Nemertines as described by BÜRGER, the resemblance is remarkable. There is the same arrangement of the cell body at the end of a fine canal down which their cilia work, the cell body itself throwing out a number of processes. The comparison of some of the figures given in the following paper with the drawings of the excretory organs of *Drepanophorus* given by BÜRGER (2) brings ut I think a number of striking resemblances. (Compare figs. 5, 6, 7 of BÜRGER's paper with figs. 11, 16 and 25 of the present paper.)

At present it is perhaps premature to speculate regarding the amount of morphological importance to be attached to these solenocytes. Their wide distribution in the class of the Polychaeta, and their presence in such widely separated forms as *Amphioxus*, the *Polygordius* and the Actinotrocha larva, is significant in itself.

A review of a few of the facts, that have been brought to light on the development of the excretory organs, is sufficient I think to convince anyone, that up till now, we have been confusing under the name of nephridium two organs of very different character and origin. One distinctly coelomic, the genital duct and its funnel, the other the true nephridium, which is not necessarily coelomic but may be separated from the coelom altogether. It is true the nephridium may, and often does, come into relation with the coelom; this is a secondary modification and not the original condition. The first and most important function of the coelom has always been the development of the genital cells, the renal excretory function has been acquired later. It is only after this has taken place that the nephridia come into relation with it, when the two organs, genital duct and

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and nephridium, are found side by side. Once this exists, various modified conditions arise in which one of these organs replaces the other, or we get a partial fusion of the two structures. It is only on this theory that we can explain the complex organs of some Polychaets, consisting in a genital funnel grafted on the end of a nephridium. It is to be hoped therefore that the study of the development of the solenocytes will furnish fresh evidence against that theory which still regards the true nephridium as a modified but an essential part of the coelom.

Part I. *Phoronis.*

1. Literature.

The conflicting statements to which the study of the development of *Phoronis* has given rise, are gradually decreasing as new facts are brought to light in its life-history. As the result of much of this recent work, the tendency of opinion may now be said to regard the adult, rather than the Actinotrocha larva, as the most suitable place to look for what chordate features *Phoronis* ma possess. Recent work has shown how much Masterman (**17**, **18**) has been influenced by theoretical prejudices in his conception of the structure of this interesting animal. Yet the concurrent work of Ikeda, Goodrich, De Selys Longchamps and Cowles has nevertheless shown that there are at least three body-cavities in the larva, of which two are undoubtedly coelomic. This taken with the Trochophore characters possessed in the early stages, make it a curious puzzle. The more one considers these early stages up till the time the larva begins to assume the Actinotrochal stage, the more one is impressed by the Trochophoral characters it possesses; the more one examines it after this stage is reached, the more one is influenced by the many features it has in common with the Brachiopoda and the Hemichordata. Conklin (**5**, pag. 70) in a recent paper has gone even so far as to say that with the exception of the segmented coelom, there is no essential difference between the Actinotrocha larva and the Brachiopod larva, but Conklin's conclusion was based on the work of Masterman, who is mistaken in regarding the preoral coelom of *Phoronis* like that of Brachiopods a gut diverticulum. There are evidences in the structure of the adult *Phoronis* however to warrant the suggestion first put forward

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by CALDWELL (3) that this animal is related to Brachiopods, and in a minor degree to Sipunculids and possibly the Polyzoa.

It is beyond the scope of the present paper to enter into a discussion of the systematic position of *Phoronis*, especially as the subject has been so thoroughly reviewed in the recent papers of DE SELYS LONGCHAMPS (25 pag. 102) and HARMER (13 pag. 114).

In many important memoirs, the nephridia have been overlooked, or have received but scanty notice. While some find them opening into the body cavity, others find them closed, and others again have found no trace of them in the larva. Only within the last few years have they been the subject of careful examination. GOODRICH (11) was the first in 1903, to draw attention to the fact that the Actinotrocha larva possessed nephridia furnished with solenocytes similar to those of Polychaets. Since then several important papers have appeared.

It is now evident that these organs are limited to a single pair, situated in the third division or trunk region of the larva, and that they are closed, never opening into the body cavity or the primitive space of the blastocoel in which they develop. They are in fact typical larval nephridia, furnished with solenocytes similar in all respects to the solenocytes of *Glycera* and *Phyllodoce* among the Polychaets. They belong to the category of true nephridia and as such are quite different from the nephridia of *Peripatus*, Pulmonata, and some Chaetopods, which are differentiations of portions of coelom and so modified genital ducts. The existence of the solenocyte type of nephridium in the Actinotrocha is a fact of some morphological importance as it adds the Phoronidea to that class of animals possessing nephridia of this primitive type.

WAGENER (26) in 1847, was the first to describe the nephridia in the Actinotrocha larva though he misunderstood their nature. He figured the solenocytes on the ends of the nephridial canals as spermatozoon-like bodies, and considered the larva an adult form. His figures are remarkably good and all the main features of the larva are shown. He draws the retractor muscle strands running from the region of the oesophagus to the nephridia very clearly, structures which IKEDA has recently redescribed. For the observation of the nephridia, *Actinotrocha branchiata*, the form WAGENER studied, is very favourable. The nephridial canals are conspicuous and the solenocytes attached to their ends very numerous.

In 1883, thirty six years later, CALDWELL (3) was the first to

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give a description of these structures, as well as to follow in part, the development of the nephridia. His account remaining for many years the only one we possessed, it has become well known from text-books. Attached to the ends of the nephridial canals CALDWELL described a number of cells of peculiar form. "Each cell has a nucleus and a process similar to those of the ordinary mesoblast cells. By one of these the cell is attached to the end of the large canal. This process is larger than the fine process and has a cylindrical form. By the canal formed inside the cylinder, small brown concretions seen in the cell itself pass into the larger canal and so to the exterior. . . . At no time during the free-swimming life of the larva does the excretory canal system open into the body-cavity" (pag. 376). Regarding the origin of the nephridia, CALDWELL (**4**) in a paper published subsequently to the one just quoted, thought they arose in connection with the diverticula into which the anal pit divides. These open on the exterior in the middle line. "The closure of this opening proceeds in such a way that each pouch remains open to the exterior by a small pore on either side. . . . I believe — that each pore persists as the opening of the nephridium of its own side." The formation of the excretory cells which lie in the blastocoel and not in the body-cavity, — "I have independently traced from the mesodermic cells of the posterior pouches". Finally CALDWELL quoted HATSCHEK as believing that the whole organ arose from the mesoblast (pag. 19).

IKEDA (**14**) was the next to give a detailed description of the nephridia. He also ascribed their origin to CALDWELL's posterior pouches. The anal pit sinking in from the ectodermal surface forms two pouches which in time give rise to two blind tubes which project into the preseptal haemocoel, forming the nephridial canals; a certain number of mesenchyme cells attach themselves to the ends of these tubes and become later the solenocytes. He places these organs under the heading of mesoblast, although the nephridial canals are of ectodermal origin, "the organs as a whole bear intimate relations to the mesoblast". Of some interest is the discovery by IKEDA of a pair of retractor muscles running down from the oesophagus to the body wall in the region of the nephridia, which resemble the retractor muscles of the Trochophore larva.

DE SELYS LONGCHAMPS (**24**, **25**) has confirmed many of the points in CALDWELL's and IKEDA's description of the nephridia. First, that they never open into the body cavity, and secondly,

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they arise in intimate connection with the mesenchyme. Their canals are also according to his observations formed from the sinking in of the anal pit and its division into diverticula. Regarding the origin of the solenocytes he made no direct observations, but thinks that Ikeda has advanced no conclusive proof of their origin from mesenchyme cells.

It is to Goodrich (**11**) that we owe the most complete résumé and description of the nephridia and their relations to the body cavities. In the fully grown Actinotrocha larva the nephridia do not open into the body cavity. The excretory cells found at the ends of the nephridial canals are similar in all respects to the solenocytes found in connection with the nephridia of Polychaets. The nephridia open to the exterior ventrally behind the septum dividing the closed posterior trunk coelom from the anterior preseptal haemocoel, into which they project and end blindly. During metamorphosis the nephridia probably lose their solenocytes and acquire openings into the coelomic cavities by means of peritoneal funnels. This last however he did not determine by direct observation.

Cowles (**6**) in *A. architecta* has been able to confirm most of the points brought forward by Goodrich. The nephridia do not open into the collar cavity but end in thin walled bulbs to which the excretory cells are attached. These along with the canal of the nephridium are probably of ectodermal origin.

Thus there is a more or less unanimous agreement that the nephridia arise in some way from the posterior pouches, that they do not open into the body cavity, are furnished with solenocytes, which may or may not be derived from the mesoderm, and that the funnel openings of the adult nephridia into the body cavity are a secondarily acquired feature, possibly of peritoneal origin. As regards the body cavities there is still considerable diversity of opinion and much remains to be done in elucidating their relationships.

2. The early origin of the mesoderm.

As the first appearance of the larval nephridia is essentially connected with the early origin of the mesoderm and the development of the body cavities, I have followed the process of gastrulation and the first appearance of the mesoderm with some care. Both the species[1] which I have studied agree with one another in all

[1] For material and methods see end of paper.

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essential respects. Except in several minor features I can corroborate most of the recent accounts of the origin of the mesoderm.

I have been unable to find any trace of the blastocoelic pore mentioned by IKEDA as present at the end of segmentation. I have also been unable to find the mesoderm arising from lateral archenteric folds. According to IKEDA (**14**) this is one of the principal sources of the origin of the mesoderm in the Japanese species.

The blastulae are frequently very irregular in shape from mutual pressure in the tentacles of the adult, individual cells being pushed out of place. Till the end of invagination no cells are to be distinguished in the segmentation cavity. On this point the majority of modern workers seem to agree, while earlier workers, dependent on optical sections alone, usually figure mesenchyme cells in the segmentation cavity during and after invagination. As invagination takes place over the entire ventral surface of the blastula the segmentation cavity is completely obliterated by the folding up of the ventral upon the dorsal surface (pl. 31 figs. 1—4). Shortly after this bilateral symmetry makes its appearance by the elongation of the gastrula in one axis (fig. 6). The lips of the blastopore close up rapidly from behind forwards meeting in the median line. Along this line of closure, over a short area where the lips of the blastopore are meeting, is a region said to give rise to mesoderm (fig. 5). I have examined this area repeatedly by means of sections without being able to see the actual formation of mesoderm cells. I believe that the active cell proliferation of this region has to do solely with the closure of the blastopore and not with the origin of mesoblast. Later however, there is an active formation of mesoderm on either side of the line along which the blastopore has closed. This takes place by individual cells being pressed into the segmentation cavity between the two layers from the endoderm (fig. 7). Towards the end of invagination a certain number of mesoderm cells have made their appearance from the ends of the invaginating endoderm cells. These are especially numerous over that region of the endoderm which will be later the pre-oral region. In the larvae from Faro these cells at this stage form what seems a closed sac (figs. 26 and 27). This is similar to the sac described by COWLES in *A. architecta* (**6**). This sac grows larger with the growth of the pre-oral region, so that it comes to have a horse-shoe shaped form, the two horns of the shoe extending back into the trunk region, where they are formed of the mesoderm cells derived from division from the lateral walls

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of the closed primitive streak, as mentioned above. I do not think that this structure is a true sac, in many larvae it is very imperfect, in some larvae being represented by a few scattered cells[1]. It cannot be compared for a moment to the sac that later gives rise to the large trunk coelom. It is perhaps almost unnecessary for me to add that it is not a diverticulum of the gut, being formed strictly by the irregular proliferation of cells from the anterior wall of the archenteron. The body walls of the larva at this stage become much thicker, and there is a rapid increase in size. The terminal portion of the primitive streak ends at the pointed end of the larva in a slight depression which is the "anal pit" (fig. 27).

On the external surface the primitive streak soon disappears from the rapid growth of the ectoblastic elements. The anal pit alone remains to mark its former posterior point. In transverse sections of the larva through the blastopore one finds a slight depression just inside the blastopore on either side. These I take to represent the anterior diverticula of Caldwell. They do not seem to develop beyond the stage of very shallow depressions, and never give rise to diverticula as in the Japanese species. I cannot find that they take any part in the formation of mesoderm. In the Faro larva, they reach about the stage represented in Caldwell's (4) fig. 8, after which they disappear. Soon the pre-oral lobe bends down ventrally, as shown in figs. 8, 9 and 26, the anal pit at the posterior end of the larva becoming deeper and more marked. I consider the anal pit to mark the former terminal point of the primitive streak, although this has been much debated, the actual pit itself is a later development. The anal pit therefore cannot strictly be called a portion of the blastopore, but is a growth from the ectodermic surface, it rapidly grows at the expense of the ectodermic cells which sink in as the pit forms. After this stage it is best to call it by the more suitable name of nephridial pit, as the nephridia subsequently arise in connection with it. I think the whole growth and closure of the blastopore in *Phoronis* point to this opening as being the original opening of both mouth and anus. The close relation of the anus to the terminal portion of the primitive streak points to its formerly being included within this structure as a part of the blastopore.

The formation of mesoderm in *Phoronis* is a general process in which the whole endoderm takes more or less part. In

[1] See page 505 further discussion.

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certain parts of the mesendoderm this separation is more marked than in others, especially in the regions of the endoderm lateral to the primitive streak and in that region towards what will be later the pre-oral lobe. Nevertheless the process is a general one in which there is invaginated a mesendoderm from which the mesoderm separates off over the entire surface of the endoderm.

De Selys Longchamps in his latest work (25), is also of the opinion that this process is a general one. He says "le mésoblaste de l'embryon prend son origine uniquement dans des cellules se détachant isolément de l'endoblaste . . . il y a formation, aux dépens du mésendoblaste, d'un mésenchyme primaire et persistance du blastocèle embryonnaire" (pag. 12).

It remains for me to consider several minor points in the origin of the mesoderm. Caldwell has put forward the view that the nephridial pouches give off cells which form the mesodermal lining to the posterior body cavity. In pl. 32 fig. 37 it will be seen that there are mesodermal cells already in this body cavity before the nephridial pouches are formed and while the pouches are too rudimentary to take any part in the formation of these cells. Ikeda has noticed that sometimes mesodermal cells seem as if partially detached from the ends of the pouches and about to separate off, but as I hope to show later these cells are really giving rise to the tube of the nephridial canal and take no part in the formation of mesoderm. They take on a filiform shape with numerous processes, as can be seen partially in fig. 8. But this shape is soon lost and the cells are transformed into the cuboidal cells of the nephridial canal. Contrary to Caldwell's opinion I have shown the pre-oral body cavity, if we are to consider it as such, is from the first unpaired in origin, and not paired as it would be if derived as he believed from the anterior diverticula. In returning to Caldwell's former view that the anal pit marks the old terminal position of the primitive streak, I know that this is contrary to what Ikeda has shown to be the case in *Ph. ijimai*. He has shown that in this species there is no genetic connection between the primitive streak and the anal pit, as the primitive streak has disappeared some time from the external surface of the larva before the anal pit has appeared. This is not the case, however, with the larva of *Ph. hippocrepia* and that from Faro, where the ectoblastic elements grow somewhat more slowly. The primitive streak is still marked somewhat faintly on the external surface as a slight depression of the ectoderm

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when the nephridial pit is well formed. The anus forms much later, breaking through from the posterior portion of the gut or rectum, which has formed in turn as an outgrowth of the stomach. The anus is thus a new formation, and there is no evidence to support CALDWELL's contention that this structure is also a part of the primitive streak.

ROULE (21) has attempted to divide the mesoblast of *Phoronis* into a primary mesenchyme, and a mesoderm, corresponding roughly with the larval and definite mesoderm of Annelids. Unfortunately this last structure gives rise to the "bandelettes mésodermiques" which are nothing but the diverticula of the nephridial pits which he has mistaken for mesoblast bands. The coelom he derives from the splitting of these bands, which as I hope to show is not the case, for the early coelom is at first unpaired, which would not be so if it were derived from the hollowing out of these bands. As far as I have been able to observe no distinction can be drawn between the mesoderm cells derived from the anterior and those derived from the posterior portion of the larva; they are all alike, and resemble in their irregular shape and processes the larval mesenchyme of Annelids.

3. The nephridial pit and nephridia.

In young larvae taken from the tentacles of the adult the anal or nephridial pit is well seen as a slight flattening or depression on the posterior end of the larva (pl. 31 figs. 8 and 9). From the relatively transparent condition of the ectoderm in the early stages, the development of the pit can be readily followed in surface views. It arises as a simple inpushing of the ectoderm, in the formation of which the mesoderm takes no part. In sections the pit is seen (pl. 32 figs. 30, 31, 37) to project inwards and downwards below the posterior portion of the gut or stomach. The thinnest part of the pit wall is that next the stomach, and here in places it is so thin as to seem almost as if opening into the blastocoel; careful examination, however, shows there is never an opening at this point (fig. 31). In fig. 37, which represents a coronal section through a young larva of about the age represented in fig. 8, internally the nephridial pit is seen to have divided into two lateral horns or diverticula. From these subsequently arise the nephridia. The diverticula develop as simple folds in the wall of the pit. In fig. 30 representing a sagittal section slightly lateral to the median line,

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the lumen of one of the diverticula is shown cut in the section. As the larvae grow the ends of the diverticula are drawn out into processes, and these are the rudimentary nephridia (figs. 8 and 10). By the time the rudiments of the nephridia have made their appearance, the original cavity of the pit with its median opening on the exterior has become much reduced in size. First this median opening (figs. 27, 37, 38) becomes partially obliterated, and then divides into two portions, which remain as the openings of the two nephridia. The rapid growth of the anal end of the larva separates the openings so that they come to take lateral positions, one on each side of the anal papilla (figs. 43 and 50). This obliteration of the pit is caused by the formation of the anus and rectum, which forms at this time, as an outgrowth from the stomach or gut. This forces the pit in a ventral direction, and at the same time partially closes it up.

Once the rectum is formed, the nephridial pit rapidly disappears, and nothing remains but these diverticula having separate openings, one on either side of the anus. A depression, however, for some time marks the former position of the pit, on the external surface, below the anal papilla. The rudiments of the nephridia rapidly lengthen out into bulbshaped tubes (pl. 31 figs. 10 and 15). The nuclei in the walls of these tubes are large and readily distinguishable, and largest at the growing end of the bulb. As the tubes lengthen, they lose their bulb-like character, and assume the typical appearance of the nephridia, as in fig. 12. Figs. 11, 16, 25 and 29 represent various stages in this change. The solenocytes develop as direct outgrowths of the tube wall, and are at first large and irregular. They soon aggregate at the distal end of the tube, where they take on the appearance they present in the fully formed nephridium. Fig. 28 represents the fully developed larval condition. The solenocytes are therefore especially developed cells of the nephridial wall, and so with the nephridium are of ectodermic origin. In the early stages of their development they often appear to throw out irregular protoplasmic processes as in fig. 11. These processes have, no doubt, given rise to their being mistaken for mesodermic cells of the blastocoel in which the nephridia lie free at this time. In the later stages, as in figs. 12 and 28, the solenocytes are more regular in form, and in the living condition look not unlike a small cluster of grapes at the end of the long nephridial tube (fig. 55).

The lumen of the nephridium forms early, and is seen almost from the first as a clear space in the centre of the mass of

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cells composing the rudiment of the nephridium. The exact steps by which the organ composed of a few cells is transformed into the many celled one of the fully grown larva are somewhat difficult to follow, but it is doubtless from the rapid division of these cells composing the nephridial rudiment, since their nuclei rapidly decrease in size as the nephridia develop.

The solenocyte tubes form late, and apparently very shortly before the nephridium becomes functional. The external openings of the nephridia on the ectodermal surface are remarkably small. I have never been able to observe them, either in sections or in whole preparations, although the spot where this opening is situated is readily distinguishable on the surface of the larva from a collection of pigment about it.

In the larva of *Ph. hippocrepia* the nephridial pit is much deeper and better marked than in the Sicilian larva (fig. 46 and compare figs. 38 and 37). In *Ph. Sabatieri*, ROULE has denied strongly the existence of this structure, but DE SELYS LONGCHAMPS (25) has since found it well marked in this species. He has also found evidences of the pit in the small and peculiar larva of *Ph. Mülleri*, where it develops in a manner similar to the way its develops in other larvae. MASTERMAN has also found it in the larva in which he formerly denied its existence. There is no doubt therefore that in all Phoronid larvae it is present in the early stages. The merit of its rediscovery since the time of CALDWELL is due to IKEDA, who was also the first to show that the nephridia arose in connection with it.

The exact morphological significance of the nephridial pit is not obvious, as there is no similar structure in any of the animals to which *Phoronis* may be related, to be compared with it.

SCHULTZ (23) regarded it as the rudiment of the ventral pouch or metasome, which of course appears much later, as IKEDA has pointed out. It has several times been mistaken for the formation of a proctodaeum, and this mistake is the more readily made from its close relation to the rectum or gut. It is worthy of note that in the Trochophore larva the gut opens on the exterior at the ventral end of the larva in a large and conspicuous proctodaeum of ectodermal origin, into this proctodaeum open on either side the head-kidneys some distance from its external orifice[1]. Now the relationship of

[1] E. B. WILSON was the first to call attention to this condition in the Trochophore of *Hydroides*. I have confirmed this on good number of species, as *Pomatoceros*, *Eupomatus*, and it is probably the case in all typical Trochophores.

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the developing nephridia of *Phoronis* to the anal or nephridial pit is similar to the relationship existing between the head-kidneys and the proctodaeum in the Trochophore. As there are many resemblances between the Actinotrocha larva and the Trochophore it is not impossible that the anal pit in the young Actinotrocha represents the proctodaeum of the Trochophore. There is certainly no proctodaeum in the Actinotrocha, as the anus is a new formation appearing rather late at a period when the larva has developed at least two pairs of tentacles. This tends to support this view.

From the foregoing account of the origin and development of the nephridial pit it will be seen that it has nothing to do with the formation of mesoderm in the posterior part of the larva. It is solely an ectodermal structure which gives rise to the nephridial tubes, these in turn giving rise to the solenocytes. The distal ends of the nephridia hang free in the blastocoelic space in which they develop, lying entirely outside the coelom, which at this stage is quite small, the solenocytes having already formed on the ends of the comparatively long nephridial canals, while the coelom is still represented by a very small space on the dorsal side of the gut. At no stage during their development do the nephridia open into the blastocoelic space in which they lie.

4. The development of the body cavity.

The body cavity of the trunk region makes its appearance in larvae of about the age represented in fig. 8 (*tr.c*). It appears first as a small collection of cells on the dorsal side of the rectum, or gut, close under the ectoderm. At the time when they are first distinguishable, they consist of a small mass of cells, some ten to fifteen in number, closely applied to the wall of the gut. Whether they are derived from this structure, or are only a local accumulation of the scattered cells of the blastocoel at this point, I have been unable to determine. Although I have repeatedly looked for them in larvae of this age, I have never observed the actual steps in their origin. From their close connection with the wall of the gut at the time of their appearance, I believe they are really derived from this structure. They are at first closely packed together, but a small space soon makes its appearance in their midst, and this is the beginning of the trunk coelom. In pl. 32 fig. 36 this is well seen as a small space surrounded by cells on the dorsal surface

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of the rectum (*tr.c*). This is from the first unpaired, and as it rapidly grows it surrounds the rectum on either side, so that in advanced stages these lateral portions meet on the median ventral line, forming the ventral mesentery. Thus the trunk coelom soon comes to consist of a large unpaired dorsal portion, and two lateral parts surrounding the gut (figs. 33, 39, 41).

In a series of coronal sections, represented in pl. 31 figs. 19 to 24, taken through a young *A. branchiata*, the shape of this cavity can be clearly followed.

The first section passes through a ventral plane, so that the ventral wall of the gut just appears cut in the section. The ventro-lateral portions of the coelom (*tr.c.v*) appear as two narrow slit like sacs one on either side of the gut. As the sections gradually proceed dorsalwards these lateral portions get larger till they finally join in the dorsal cavity (*tr.c.d*). While the coelom is surrounding the gut it is at the same time extending on to the dorsal portion of the stomach, so that it soon comes to fill up all the remaining space in the posterior end of the larva. There is never any trace of a dorsal mesentery in the dorsal portion of the coelom (figs. 14, 35, 40, 42, 45). Cowles (6) in a late stage of *A. architecta*, has figured (fig. 5) what may be a dorsal mesentery in this cavity, but it is of a very doubtful nature, and has, I think, no bearing on the double origin of the cavity.

In larvae of the same age and size, the shape of the coelom varies very much. In some it is well developed, while in others of the same relative size it is still small. In some it is even imperfect. In these last it is the dorsal wall that seems to be wanting, so that in these larvae the coelom seems to consist of two lateral portions surrounding the gut in communication with a dorsal cavity which is in free connection with the original blastocoelic space. I believe that this condition is quite abnormal if it really exists during life. It is certain that in the majority of larvae it is possible to see both in sections, and still more readily in suitably cleared whole preparations, that the dorsal wall of the coelom is quite intact throughout. If this condition does exist during life, and De Selys Longchamps claims it does, I think no importance is to be attached to it. De Selys Longchamps has never been able to find this cavity perfect in the early stages, and in the dorsal region and also in an anterior direction, it is always up to a later date in free communication with the blastocoel. Certainly, in most of the larvae

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I have examined this is not the case, as I have already stated, for in transparent larvae such as those represented in figures 17, 18 and 49, the dorsal wall of the coelom can be seen quite plainly in the living state. In the development of *Asterina gibbosa* Mac Bride (16 pag. 368) has drawn attention to the number of abnormal ways in which the coelomic sacs frequently arise in this Echinoderm. One abnormality frequently found, consists in the coelomic epithelium of the gut breaking up into a mass of cells having the appearance of mesenchyme, which choke up the lumen of the coelom. This abnormality may take place at any stage in the differentiation of the coelom. I think this observation is of great interest when taken in connection with the frequency with which the epithelium of the coelom in *Phoronis* lying against the gut is found wanting (fig. 34). Mac Bride has also noted the irregular manner in which the various portions of the coelom often arise in different parts of one and the same larva, and we might justly expect some similar variation in *Phoronis* which possesses so remarkable a life-history. The embryology of animals that pass through a more or less protracted larval development has repeatedly shown us that everything in early development is sacrificed to the immediate needs of the larva. For instance in *Unio* the organisation of the Glochidium is distinctly foreshadowed in the segmentation long before the actual appearance of the Glochidium stage. So in *Phoronis* the development of the coelom may be somewhat modified.

As already stated the nephridia are well developed while the coelom is yet small. They are from the first outside this structure, and ventral and lateral to it. As the coelom grows its lateral portions soon force the nephridia against the inner wall of the ectoderm, and away from the gut. In section (pl. 32 fig. 47) a few cells of the nephridial canal of one side are shown close to this lateral portion of the coelom.

At this time the relative proportions of the nephridia and the coelom are well shown in pl. 31 figs. 13, 18, pl. 32 figs. 44, 49, 53 and 54. Finally in pl. 33 figs. 56 and 58 these relationships are again shown in a diagrammatic figure. From the inspection of these figures it will be seen that the nephridia with their solenocytes project some distance into the blastocoelic space in front of the coelom, and that it is only by the growth of this structure in the fully formed Actinotrocha that the anterior wall of the coelom comes close up to the heads of these organs. By the time this stage is reached a con-

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siderable readjustment of the relationships of the various organs in the larva has taken place. This is brought about principally by the outgrowth of the anal region, and the formation of the tentacles. These last arise in pairs, towards the dorsal surface, the most dorsal pair always being the youngest. This is also the case, as CALDWELL pointed out, with the tentacles of the adult, but the adult tentacles at the same time grow laterally, new pairs arising both ventrally and dorsally to the first pair, so that the most ventral of the adult tentacles are not necessarily the oldest. Increase in size seems to correspond with the number of tentacles and their size, as MASTERMAN has shown. About this time the cuticle of the young larvae becomes very opaque and granular, and this added to the greater rapidity of movement acquired by the larva when it has attained two pairs of tentacles make it very difficult satisfactorily to follow the internal changes taking place in living material. The larvae roll themselves up in a ball on the slightest irritation. The rapid outgrowth of the tentacles also adds to the difficulty as they render it impossible to obtain satisfactory side views of the animal.

By referring to pl. 31 fig. 18, it will be seen that the body of the larva can be roughly divided into a pre-oral lobe, and a main trunk region. The pre-oral portion consists of a flexible hood which is often carried folded down over the mouth, on the trunk region. Into the hood, the blastocoelic cavity of the trunk extends, being crossed in all directions by the processes of the mesenchymatous cells which are quite numerous in this portion of the cavity.

The trunk region is composed of the main portion containing the stomach, and a posterior anal papilla, containing the gut or rectum, the nephridia, and the true coelom; and is separated from the stomach portion but faintly, by the line of outgrowth of the tentacles. Thus the body cavity of the pre-oral hood and the trunk, exclusive of the space of the true coelom partially surrounding the gut, is blastocoelic in character. With the growth of the larva the true coelom, which is at first a small sac on the dorsal side of the gut, increases at the expense of this blastocoelic cavity, until in advanced stages the only remaining part of it is the collar space, and the cavity of the hood. The collar cavity[1] which has given rise to so much discussion, is certainly not coelomic, as

[1] The collar cavity of MASTERMAN, not the true coelomic cavity of this region, the preseptal cavity.

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Ikeda has shown that it is transformed later into the ring vessel of the adult. De Selys Longchamps has moreover made it clear, that this cavity is distinctly blastocoelic. It has therefore nothing to do with the true coelom, but is probably formed from the remnants of the blastocoelic space in the trunk region not taken up by the true coelom, which is the space surrounding the line of insertion of the tentacles, into which it extends a short distance. Its formation takes place I think in the following manner. As the coelomic sac forms and grows round the gut, and at the same time spreads on to the posterior portion of the stomach, it will be seen from the inspection of pl. 31 fig. 18, that the original blastocoelic space of the larva is confined to the tentacles, and the part of the trunk region about the stomach. Now shortly after this, the anal region starts to grow much more rapidly than the rest, so that the anal papilla containing the gut and coelom is drawn out, so that this part of the larva comes in time to be the largest. The part of the blastocoel surrounding the base of the tentacles thus comes to occupy an anterior instead of a posterior position in the larval trunk. When the fully formed Actinotrocha stage is reached, this space is seen surrounding the larva like a collar at the base of the tentacles, where it retains its position until transformed into the adult ring vessel during metamorphosis. It is plain this cavity is not truly coelomic, the epithelial lining on the stomach is always imperfect, and numerous wandering cells found throughout it denote its haemocoelic nature. The septum between this cavity and the trunk region is formed by the anterior wall of the true coelom of the trunk region which has moved forward.

Contrary to the opinion of De Selys Longchamps I have tried to show that the trunk coelom and the cavity of the collar are never in communication, as the true coelom of the trunk is a closed sac from the first. Late in development only does the true coelom of the collar region form, which Masterman never observed, and this during metamorphosis is transformed into the adult supraseptal cavity. The origin of this cavity is very difficult to observe, in all the material I have been able to collect it is unformed and only in the late stages of the Actinotrocha is it well established. As far as my observations go they would seem to strengthen the statement of Schultz (21) that this cavity is derived by segmentation from the ventral anterior prolongations of the trunk cavity into the collar region. It is hard to see why it should

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should not possess a ventral mesentery like the trunk cavity. I think De Selys Longchamps fails to recognise the true morphological import of this space, as it is only in a very wide sense that it can be called a schizocoele. Schultz claims that in the Actinotrocha regenerating after injury it always arises as two anterior diverticula of the trunk coelom, and in some of my sections the trunk coelom projects forward in this region in a manner that is somewhat suggestive of this, for at this period the cavity has not appeared, while in stages a little later the preseptal cavity has made its appearance and rapidly increases in relative size during further development. But the whole subject needs reconsideration and further investigation. Ikeda first described this cavity and Goodrich (**11**) has given a very excellent and detailed description of it, but neither of these authors made any observations on its development. Ikeda mentions it as "already formed in the fully developed larva of every type as a space running along the inner side of the tentacular circle above the septum", and sending a prolongation into each of the tentacles. Goodrich has shown that the cavity terminates dorsally in two horns, which run forward in advanced larvae some distance on either side of the median line towards the ganglion of the preoral lobe. In any case, whatever may be the origin of this cavity, it is at least as much a coelomic cavity as that of the trunk region, for the primitive origin of the coelom in *Phoronis* as a pouch or pair of pouches from the archenteron has long been lost if ever possessed by this animal. Two coelomic cavities at least can be made out in the larva of *Phoronis* not counting the haemocoelic cavity of the preoral lobe and the collar.

Harmer (**13**) has recently advanced reasons for considering the preoral cavity also a modified coelomic space, he suggests that this cavity never acquires full development, from the fact that this portion of the larva is not represented in the adult, being thrown off during metamorphosis. In very young larvae especially those of Sicilian species, pl. 31 figs. 26 and 27, I have already pointed out how well marked this cavity is, and in the American species *A. architecta*, Cowles (**6**) has found it even more pronounced. As development proceeds the sac-like nature of the cavity becomes less and less distinct. And this would lend support to this suggestion of Harmer's that it was originally coelomic. It is however at no stage so well marked and distinct as the coelom sac of the trunk region. Frequently in the early stages as I have remarked (p. 495)

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it is very irregularly formed, and in the later stages it is always in free communication with the haemocoelic space of the collar region, and for these reasons I am inclined to consider it with Selys Longchamps as a true haemocoel. It certainly on the other hand bears a striking resemblance to the preoral cavity of the Enteropneusta and *Cephalodiscus* in its general configuration, and in the manner in which the muscle cells develop in relation with it.

For the same reason it may be argued that the preseptal coelom makes its appearance late in development, because it represents the small preseptal coelom of the adult, including the lophophore and the tentacles, which are only required late in development. In this connection Ikeda has observed that the part of the larval tentacle thrown off during metamorphosis is that in which the preseptal coelom is wanting.

Caldwell was of opinion (3) that the trunk body-cavity took its origin in the masses of cells derived from the nephridial diverticula — "in a paired mass of cells which grows out from the first formed sacs (posterior diverticula) and remains separated from the latter by a septum" (pag. 376). This view is now impossible for reasons which I have already mentioned. For it will be seen that at the time the body-cavity arises the nephridial diverticula are some distance from this structure in a ventral direction. I have never observed anything in sections that would tend to support this view.

Hatschek in his Text book of Zoology gives a diagrammatic figure of a young Actinotrocha larva, in which the trunk cavity is represented as consisting in a pair of coelomic sacs one on either side of the gut. This figure has given rise to considerable comment in the recent literature of *Phoronis*; unfortunately it was published without any description. In certain views of the larva, especially ventral views, the two lateral portions of the coelom certainly give a very misleading impression that the coelom is paired as shown in this figure. For instance, fig. 58 which is taken from a reconstruction model of *A. branchiata*. Here the two lateral portions of the coelom which are about to meet on the ventral line certainly look like separate sacs (fig. 57). I believe Hatschek was misled in considering the coelom paired from the examination of the larva from the ventral surface. Masterman (18) shows the trunk coelom arising from two lateral masses of cells on the dorsal side of the archenteron. These masses are at first solid and form part of the

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gut wall. I have shown that in the larvae I have studied the first rudiments of the coelom occur much later, and are as far as I can determine unpaired; this by no means precludes the possibility of their paired nature at an earlier date though I have never observed any indications of this.

Ikeda (**14**) whose careful work has done so much towards elucidating difficult points in the development of *Phoronis* unfortunately passes over the origin and early history of this cavity, and only treats of it when it is already well formed, passing from a stage in which there is no septum in the trunk region to one in which this septum is well advanced. Cowles (**6**) states that in larvae of *Ph. architecta*, he has noticed an arrangement of mesodermal cells on the dorsal side of the gut which may be the beginning of the trunk coelom. He says in larvae "with two tentacles I have found an arrangement of mesodermal cells on the dorsal side of the intestine which seems to be the beginning of a sac; this however is not paired. Whether or not this sac and its cavity give rise to the lining and cavity of the trunk, I cannot say for I have found but a single specimen in which this condition exists".

The views of De Selys Longchamps on the nature of the trunk cavity I have already discussed. I should however like to point out again, that if the body cavity of the trunk is in free communication with that of the collar region (the haemocoel) how is it that only the posterior cavity develops into a real coelom, and the other forms haemocoel? Both these cavities are according to his account formed from the original space of the blastocoel, yet why if they are all one, do the mesodermal cells of one form a coelomic lining, and the same cells in the other form blood vessels? I have tried to show that this is a mistake, that these two cavities are essentially different; from the first the trunk coelom in normal larvae is completely closed. By the growth of this closed sac in a forward direction the septum of the trunk-collar region is formed.

5. The development of the nephridia in late stages.

I have little to add to the account given by Goodrich (**11**) of the structure of the nephridia in the Actinotrocha larva; this account has been confirmed in all its essential details by De Selys Longchamps (**25**) and Cowles (**6**). The shortening of the nephridial canals in the larva, once it has begun to assume the form of the Actinotrocha, is very rapid, and is caused by the

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compression of the collar space and the great outgrowth and development of the anal region. The nephridial canals are short and thick (pl. 32 fig. 51) as compared with their condition in earlier stages. The heads of the nephridia project inwards and forwards into the collar haemocoel between the preseptal coelom and the stomach wall, here they end in short y-shaped branches not unlike the nephridia of some Polychaets. To these branched ends the solenocytes are attached, their tubes opening into the lumen of the nephridial canals.

In *A. branchiata* the heads of the nephridia are divided into three such branches (pl. 32 fig. 52), terminating in bell-like funnels which are apparently closed. Into these bell-like funnels the tubes of the solenocytes project, as well as being attached to their lips and sometimes the outside portions of the funnel. It is difficult in some sections to make out if these funnels are really closed, and these structures undoubtedly have given rise to the statements about the nephridia opening into the blastocoel. In fig. 52, which is an accurate drawing of a section, they will be seen to be closed, and I have never been able to find that they are ever open into the blastocoel.

It is well known that in the adult *Phoronis* there are two organs that function as nephridia, which open into the oral and the anal chamber of the trunk coelom respectively by means of large ciliated funnels. Caldwell (3), Ikeda (14), Goodrich (11) and De Selys Longchamps (25) agree that the canals of the adult nephridia are derived during metamorphosis from those of the larval organs, which subsequently acquire openings into the coelom, in the adult functioning both as nephridia and as genital ducts.

Of equal importance with the early growth of the nephridia and the origin of the solenocytes is their final fate. The adult organs acquire openings into the coelom comparatively late in development in some manner unknow at present. If the openings of these organs should be formed from growths of the coelomic epithelium, then these adult nephridia of *Phoronis* would resemble the compound nephridia of some Polychaets described by Meyer (19).

It was my intention on commencing this work to follow in detail if possible the growth of these coelomic funnels, but lack of material has rendered this impossible although I made it a special point to obtain material that might show the growth of these funnels. Their formation must evidently take place rapidly, the critical stage

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being passed through in a very short time. The material I have obtained always shows these structures already formed or probably soon to appear. The critical stage takes place some time after metamorphosis when the young worm has almost assumed the adult form. The nephridial canals are found just after metamorphosis, as Ikeda (**14**) and Goodrich (**11**) have observed, one on either side of the anus somewhat reduced in size, in the position they hold in the adult worm. The solenocytes have disappeared, there is no doubt that they drop off into the collar haemocoel before the nephridia lose connection with this space.

In *A. branchiata* after metamorphosis the larval funnel-like ends of the nephridia are seen unchanged, although the solenocytes have disappeared. It is possible the coelomic funnels may be formed by the further growth of these structures, it is certain at this time no trace of the funnels can be seen as separate growths of the coelomic wall. I hope however to return to this point in a future paper.

6. Summary and conclusion.

It has been shown that in the young larva of *Phoronis* the nephridia develop as outgrowths of the diverticula into which the nephridial or anal pit divides, that the solenocytes form as direct outgrowths of certain cells of the sides and ends of the nephridial canals. As the nephridial pit is entirely an ectodermal structure, the nephridia and solenocytes, as outgrowths of it, are also of ectodermal origin. In the early stages the nephridial canals are long and slender openings at the posterior end of the larva on either side of the anus. During development there is a considerable shortening and thickening of these canals, and their external openings move forward until in the Actinotrocha larva they open behind the ring of tentacles on the anterior end of the trunk, where they project inwards and forwards between the preseptal coelom and the gut wall, into the haemocoelic space of the collar region. They are closed, never communicating with the blastocoelic space in which they lie. During metamorphosis the canals of the larval organs persist as the canals of the adult nephridia, which acquire openings into the coelom by means of ciliated funnels of unknown origin. The main coelomic cavity of the larva, the body cavity of the adult, appears a little after the nephridia as a small space on the dorsal side of the rectum and is from the first unpaired. Only after metamorphosis do the nephridia come into relation with it.

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Material and Methods.

The material used in the present work was obtained partly at Plymouth, England, and partly from the small Pantano near Faro, Messina. The Faro larvae probably belong to the species *Ph. psammophila*, but their identity is not certain. Two distinct Actinotrocha larvae are found at Faro at different seasons of the year, so that in the Pantano there are at least two species of the adult worm. I have been able to find only one of these, which seems to resemble *Ph. psammophila* very closely. The other may be *Ph. kowalevskii* the young stages of which are at present unknown.

It is note-worthy that while in the Plymouth species, *Ph. hippocrepia*. all stages up to the free-swimming stage are frequently found in the tentacles of a single adult, in the Sicilian species on the other hand all the larvae found in the tentacles of one worm are all at the same stage of development. The Faro larvae are also more difficult to raise, and I could never succeed in getting them past the one tentacle stage when raised from the egg; the Plymouth larvae are readily reared to a later stage. The Faro larvae soon cease to grow although at this time a large Actinotrocha is very abundant in the Plankton of the Pantano, and has been described by Goodrich (**11**) as possessing 14 tentacles.

I am greatly indebted to Mr. Marc de Selys Longchamps for various stages of *A. branchiata*, which have been of great service to me. For fixing I have found strong Flemming's and Hermann's fluid answer best. Sublimate gives poor results, at least for the segmentation stages, causing the cells to assume a rounded and unnatural shape quite unlike their appearance when fixed with Flemming's solution. With Sublimate-Acetic acid I have obtained preparations that resemble the drawings given by Ikeda (**14**) of the segmentation stages of *Ph. ijimai*. For sections I have used both the ordinary Paraffin method and the modified Paraffin-celloidin method. For the study of whole mounts I have found fresh material cleared with acetic acid and glycerine, and stained with methyl green very satisfactory for temporary use.

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Explanation of Plates 31—33.

Lettering.

an anus.
bl blastopore.
col.c collar cavity.
corp.m blood corpuscle mass.
ect ectoderm.
Int intestine.
m mouth.
mes mesoderm.
m.f mesenchymatous fibres.
nep.c canal of nephridia.
nep.p nephridial or anal pit.
oes oesophagus.
per peritoneal lining of trunk cavity.
pl.c plastic corpuscles.
pre.c preoral cavity.
pre.l preoral lobe.
rec rectum.
seg.c segmentation cavity.
sol solenocytes or excretory cells of the nephridia.
stm stomach.
t'.t''.t''' first, second and third larval tentacles.
tr trunk.
tr.c trunk or main body cavity.
tr.c.d dorsal portion of the trunk coelom.
tr.c.v ventral or lateral portions of the trunk coelom.
v.gr ventral groove or primitive streak.
v.mes ventral mesentery.

All the figures have been drawn under an oil immersion, giving an approximate magnification of 700 ×. They are roughly proportional to one another.

Plate 31.

Fig. 1—4. *Phoronis hippocrepia*, Sections of blastulae.
Fig. 5—7. *Phoronis hippocrepia*, Sections of gastrulae. In fig. 5, the section is taken through a region slightly posterior to the point where the blastopore lips are meeting.
Fig. 8—10. *Ph. psammophila*. Young larva collected in the Tow Faro Messina.
Fig. 11 and 12. *Ph. psammophila*, Nephridium early stage. The solenocytes are seen arising from the sides and ends of the nephridial canal.
Fig. 13. *Ph. psammophila*, Dorsal view showing the trunk cavity and the nephridia. The connection of the two lateral portions of the trunk coelom dorsal to the rectum is shown.
Fig. 14. *Ph. branchiata*, Median section showing the ventral portions of the trunk coelom.
Fig. 15 and 16. *Ph. hippocrepia*, Nephridium early stage.

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Fig. 17. *Ph. hippocrepia*, Lateral view of a young larva showing the trunk coelom and nephridia.
Fig. 18. *Ph. hippocrepia*, Same view of a larva slightly older then the last.
Fig. 19—24. *Ph. branchiata*, A series of consecutive sections through a young larva with two pairs of tentacles.
Fig. 25. *Ph. psammophila*, Nephridium early stage.
Fig. 26. *Ph. psammophila*, Lateral view of a whole preparation.
Fig. 27. *Ph. psammophila*, Dorsal view of the previous.
Fig. 28. *Ph. hippocrepia*, Nephridia 48 hours after the larvae have left the tentacles of the adult.
Fig. 29. *Ph. psammophila*, Nephridium early stage.

Plate 32.

Fig. 30. *Ph. hippocrepia*, Sagittal section of a young larva from the tentacles of the adult.
Fig. 31. *Ph. hippocrepia*, Sagittal section slightly later stage.
Fig. 32. *Ph. hippocrepia*, Coronal section slightly oblique.
Fig. 33. *Ph. hippocrepia*, Median section of a larva with two pairs of tentacles.
Fig. 34. *Ph. hippocrepia*, Median section.
Fig. 35. *Ph. branchiata*, Transverse section showing tentacles and body cavity.
Fig. 36. *Ph. hippocrepia*, Median section of the same larva as that shown in Fig. 34, this section being more median.
Fig. 37. *Ph. psammophila*, Coronal section showing anal pit.
Fig. 38. *Ph. hippocrepia*, Similar section to that of Fig. 37.
Fig. 39. *Ph. hippocrepia*, Section through the same larva as that shown in Fig. 33, this section being taken through a plane more median to that of the former.
Fig. 40. *Ph. branchiata*, Transverse section through the collar region.
Fig. 41. *Ph. hippocrepia*, Section showing the lateral portion of the coelom.
Fig. 42. *Ph. branchiata*, Transverse section.
Fig. 43. *Ph. hippocrepia*, Transverse section through the posterior region of young larva, showing the nephridial canals, tentacles and the preoral lobe folded back on the trunk.
Fig. 44. *Ph. hippocrepia*, Section slightly lateral to the median line.
Fig. 45. *Ph. hippocrepia*, Section showing the nephridial pit, part of the trunk coelom, and one of the nephridial canals.
Fig. 46 and 47. *Ph. hippocrepia*, Two consecutive sections through a larva just free from the tentacles of the adult.
Fig. 48. *Ph. branchiata*, Transverse section.
Fig. 49. *Ph. hippocrepia*, Dorsal view.
Fig. 50. *Ph. hippocrepia*, Oblique section through a young larva of about the same age as that represented in Fig. 49.
Fig. 51 and 52. *Ph. branchiata*, Section through one of the nephridial canals, and the blood-corpuscle mass of the fully formed Actinotrocha. Fig. 51 shows the solenocytes and the branched funnel ends of one of the nephridia.
Fig. 53. *Ph. hippocrepia*. Whole preparation seen from the dorsal surface. A younger stage than that shown in Fig. 49.
Fig. 54. *Ph. hippocrepia*. Dorsal view of a whole preparation.

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Plate 33.

Fig. 55. *Ph. branchiata*. Actinotrocha larva showing the nephridia and solenocytes and the lateral portions of the trunk coelom.

Fig. 56. *Ph. hippocrepia*, Diagrammatic reconstruction of a young larva.

Fig. 57. *Ph. branchiata*, Actinotrocha larva. Ventral view of the same larva as that shown in Fig. 55.

Fig. 58. Model of a young larva of *Actinotrocha branchiata*, reconstructed from the series of sections part of which are shown figs. 19—24 pl. 31. It is represented as partially cut open and seen from the ventral surface. *oes* oesophagus, *m.f* muscle fibres running from the ectoderm to the oesophagus, *nephr.* nephridia with solenocytes, *t* first pair of tentacles, *pre.l* preoral lobe, *rec* rectum, *tr.c.v* ventral portions of the trunk coelom which are about to meet on the ventral median line.

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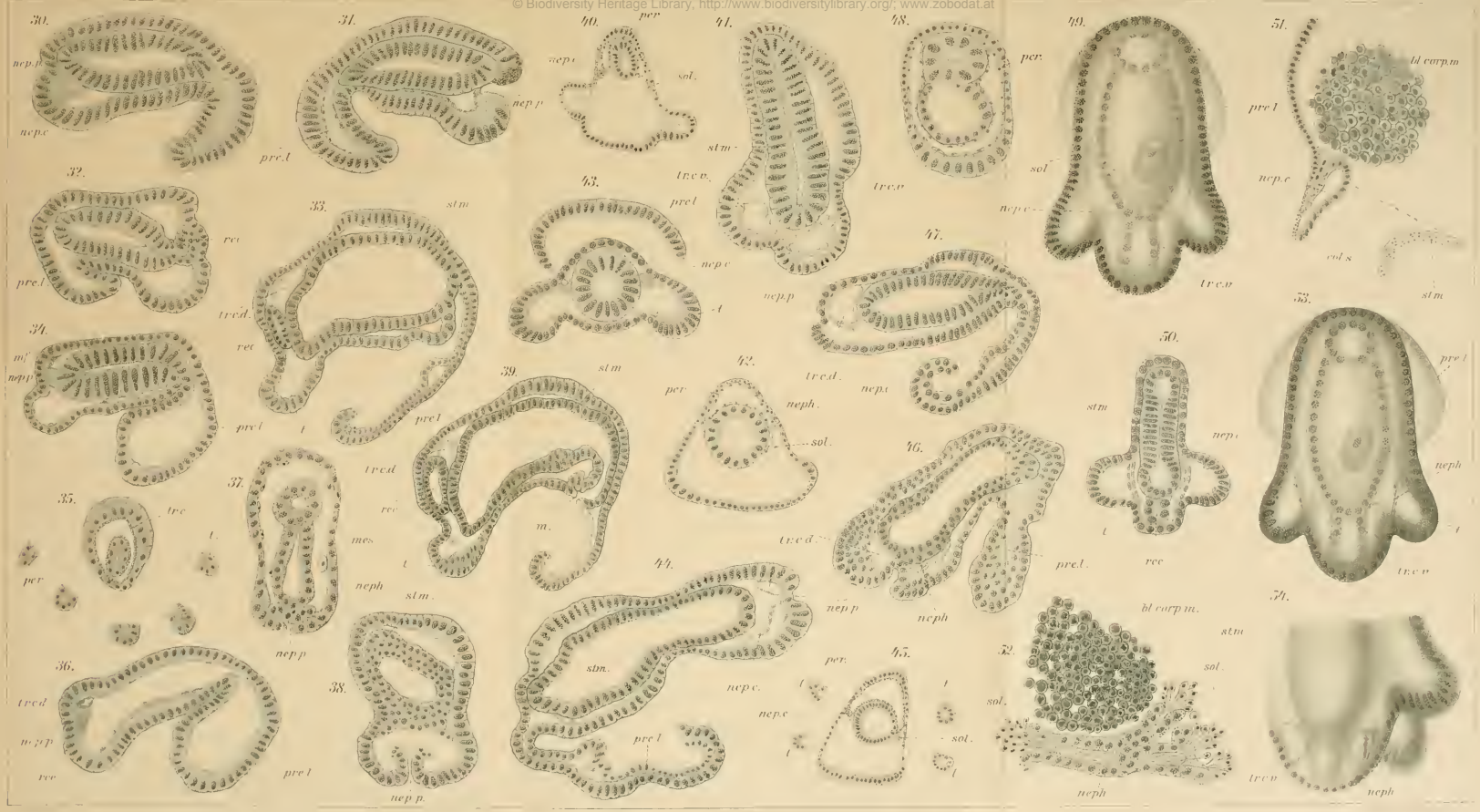

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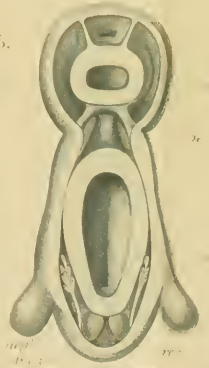

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