the last five joints being much contracted and furnished on their inferior outer margins with rows of short pectinate spines. The fifth to seventh pairs are directed backwards and increase in length posteriorly; they have strongly curved dactyla.

The uropoda are large, lamellar, and valve-like, folding over and almost completely covering the abdominal cavity; the posterior third is cut off by a transverse suture, forming a separate plate, which on its inner side bears a smaller fringed plate; these two branches thus complete the valvular flaps.

On opening out the uropods five pairs of pleopoda, each with two well-developed oblong plates all closely folded over one another, are displayed. The plates of the first two pairs are thickly fringed with fine setæ on the margins; those of the last three pairs are simply branchial.

Hab. As already noted, this species has been obtained at Stewart Island (no special locality or depth given), at Timaru in 40 fathoms, and (presumably) at or near Wanganui in the North Island.

EXPLANATION OF PLATE I.

Holognathus Stewarti, Filhol.

Fig. 1. Animal, dorsal view, nat. size.
Fig. 2. Ditto, lateral view, nat. size.
Fig. 3. Inner antenna.
Fig. 4. Outer antenna.
Fig. 5. Upper lip.
Fig. 6. Lower lip.
Fig. 7. Left mandible.
Fig. 8. Right mandible, from inside.
Fig. 9. Ditto, from outside.
Fig. 10. First maxilla.
Fig. 11. Second maxilla.
Fig. 12. Maxillipeds.
Fig. 13. Uropod.

XII.—*Origin and Fate of the Body-cavities and the Nephridia of the* Actinotrocha. By R. P. Cowles, Ph.D., Adam T. Bruce Fellow in Zoology, Johns Hopkins University, Baltimore, Md.*

Since 1846, when J. Müller discovered *Actinotrocha branchiata*, many investigators have turned their attention to the anatomy and development of *Phoronis*; but it is only within

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the last twenty-five years that a more or less careful examination of the internal anatomy of the larvæ and adults of this most interesting animal has been made.

During this time quite a number of papers have been written on the embryology of several species of *Phoronis*, and these are remarkable for the great disagreements concerning certain fundamental facts in the development. However, the conflicting nature of these descriptions, it seems to me, is probably very largely due to specific differences.

The above accounts, together with attempts to trace a relationship between *Phoronis* and the Chordates, or even the Vertebrates, through the *Actinotrocha*, have stimulated investigation, with the result that within the last two years several papers have appeared which practically agree on certain important points of special theoretical interest.

Body-cavities.—Reference to the literature published on the larval body-cavities of the *Actinotrocha* shows that our knowledge is in a very perplexing state. One investigator finds a single body-cavity, others tell us there are two, another describes three body-cavities, and one worker claims that there are five.

Roule is the only investigator who considers the *Actinotrocha* to have but one body-cavity. He denies the presence of any mesenteries in the larva of *Phoronis Sabatieri*, and says that the lining of the body-cavity has its origin from mesenchymatous cells which arise partly from the endoderm and partly from the "bandelettes mesoblastiques" (nephridial pit).

I have been able to examine the *Actinotrochæ* of *P. Sabatieri* through the kindness of M. Marc de Sélys-Longchamps, and have found that there is a mesentery present along the line of the tentacles as in other species, but that it is not very highly developed. With the material at hand I am unable to give any opinion as to the presence of a mesentery anterior to this one.

Caldwell, from a study of the development of *Phoronis Kowalevskii*, finds that the *Actinotrocha* has but two body-cavities, separated from one another by a mesentery which is inserted along the line of the bases of the tentacles. This investigator claims that the mesoderm arises partly from archenteric diverticula bilaterally placed immediately back of the blastopore, partly from the walls of the archenteron posterior to this, and partly from the posterior pits (nephridial pit), which he considers to be of endodermal origin.

Longchamps, who has recently studied the same form, denies that archenteric diverticula exist. He recognizes a transverse mesentery inserted along the line of the bases of the tentacles, a ventral mesentery in the posterior body-cavity, and an incomplete transverse mesentery separating the hood from the rest of the body. This latter, however, he believes is a secondary structure, and so considers the *Actinotrocha* to have two body-cavities—one in front of the mesentery along the line of the tentacles, and one back of this.

The lining of the former he finds has its origin from mesoderm-cells arising in a diffuse manner from the walls of the archenteron; the lining of the latter, he seems to think, may arise from cells of the nephridial pits.

Menon's paper deals only with the full-grown *Actinotrocha*, and his study leads him to believe that this creature has three body-cavities, separated from one another by two complete transverse mesenteries corresponding to the incomplete mesentery and the mesentery along the line of the tentacles of which Longchamps speaks. He also recognizes the existence of a ventral mesentery and indications of a dorsal mesentery in the posterior body-cavity.

Masterman, from a study of the early stages in the development of *P. Buskii*, considers that five body-cavities are represented in the *Actinotrocha*—one median anterior and two pairs of body-cavities back of this one. According to his account of the anatomy of the *Actinotrocha*, however, there are but three body-cavities, which he calls the preoral, collar-, and trunk-cavities. He describes the same mesenteries that Menon speaks of, and beside these a dorsal mesentery in the collar-cavity.

Ikeda's description of the body-cavities of the Japanese *Actinotrochæ* is of special interest because he is the first to describe a mesodermal sac arising immediately in front of the mesentery along the line of the tentacles. This sac makes its appearance rather late in the life of the larva and, after metamorphosis, gives rise to the lining of the supraseptal cavity of the adult. Ikeda finds the same mesenteries in the *Actinotrocha* that Longchamps does, and also describes the mesentery back of the preoral lobe as incomplete. He has scarcely anything to say concerning the origin of the mesenteries, but he finds that the mesoderm arises, in part at least, from two bilaterally placed archenteric diverticula.

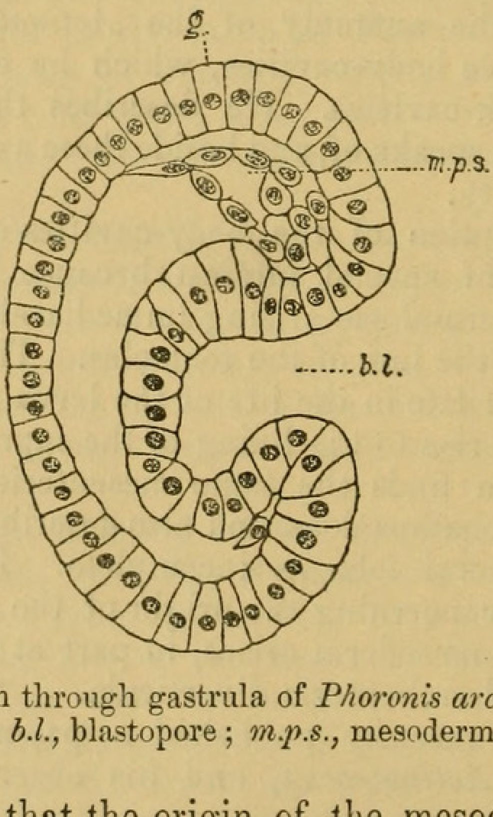
Goodrich has recently published a paper on the body-cavities of the *Actinotrocha*, and his observations confirm those of Ikeda.

From the above review of the recent literature on the body-cavities and mesenteries of the *Actinotrocha* it is seen that all but Roule, and possibly Caldwell, recognize the presence of a mesentery between the cavity of the preoral lobe and that of the collar. Longchamps, Ikeda, and Goodrich agree that this structure is incomplete, and the former considers it to be a secondary structure. Menon, and probably Masterman, on the other hand, consider it to be a complete mesentery.

I have studied the two *Actinotrochæ* found in the harbour of Beaufort, North Carolina, and I am inclined to think that one of these is the *Actinotrocha* of *Phoronis architecta.* In both species there is an incomplete mesentery between the preoral lobe and the collar-cavities and a complete one between the collar- and trunk-cavities. The trunk-cavity contains a ventral mesentery, and in one species indications of a dorsal mesentery, but there is no sign of a dorsal mesentery such as Masterman describes for the collar-cavity.

There seems to be more or less inclination on the part of those who have investigated the *Actinotrocha* since the appearance of Masterman's paper to doubt the correctness of the latter's observation as to the five-fold origin of the body-cavities from the enteron.

Fig. 1.



Sagittal section through gastrula of *Phoronis architecta,* × 704. *g.*, ganglion; *b.l.*, blastopore; *m.p.s.*, mesodermal preoral sac.

I do not find that the origin of the mesoderm in *Phoronis architecta* agrees with Masterman's account for *Phoronis Buskii,* nor do I find that the mesoderm arises from archenteric diverticula. My observations agree more closely with those of Longchamps, but we differ concerning the origin of the lining of the preoral lobe and the lobe-collar mesentery.

As in the form studied by Longchamps, the anterior and lateral borders of the blastopore are most active in giving rise to mesoderm-cells, and in the gastrula-stage, where the blastopore-lips have closed up somewhat, the mesoderm-cells which have arisen from the anterior border of the blastopore become arranged into a definite sac (fig. 1). Later this sac bends around the anterior end of the archenteron, so as to become horseshoe-shaped, and its anterior wall becomes the lining of the preoral lobe, while its posterior wall becomes the lobe-collar mesentery. At this stage the latter is complete, and it remains so until the preoral lobe begins to take on the shape of the hood. The larva of *Phoronis architecta* is an exceptionally favourable one for studying the origin of this mesentery, because of the spacious blastocœl, and there is not the least doubt but that it is a definite structure and that it has not a secondary origin.

In the larva of *Phoronis architecta* the lining of the collar-segment does not arise as it does in the preoral lobe. It has its origin largely, or possibly entirely, from isolated mesoderm-cells, which come from the lateral lips of the blastopore. These cells, however, do not form a complete lining to the collar-cavity, but arrange themselves on the somatic wall, leaving at least the lateral and ventral walls of the stomach free from any lining. This condition continues throughout the life of the *Actinotrocha* (fig. 2). The early stages that we have been considering show no sign of the mesentery which is found between the collar- and trunk-cavities of the fully-formed *Actinotrocha*. In fact, the trunk-segment does not exist at this time.

I am still in doubt as to the origin of the lining of the trunk-cavity and also as to the manner in which the mesentery arises between the latter and the collar-cavity. In larvæ with two pairs of tentacles the trunk-cavity is not present, but in larvæ with the beginnings of four pairs of tentacles it makes its appearance. This stage in the development of the *Actinotrocha* of *Phoronis architecta* is very difficult to obtain, however, and I have never taken but one specimen (fig. 3).

Longchamps has called attention to a figure of a young *Actinotrocha* in Hatschek's 'Lehrbuch' which shows the lining of the trunk-segment arising from two cœlomic sacs. Hatschek does not describe the origin of these sacs, but Longchamps asks whether or not the lining of the trunk-cavity may not arise from part of the "diverticule ectoblastique" (nephridial pit).

I believe that the cavity of the trunk is formed in the following manner:—As the tentacles grow out and increase in number the posterior region of the larva about the rectum increases greatly in length. In doing the latter the mesodermal lining of the collar is drawn away from the somatic

Fig. 2.

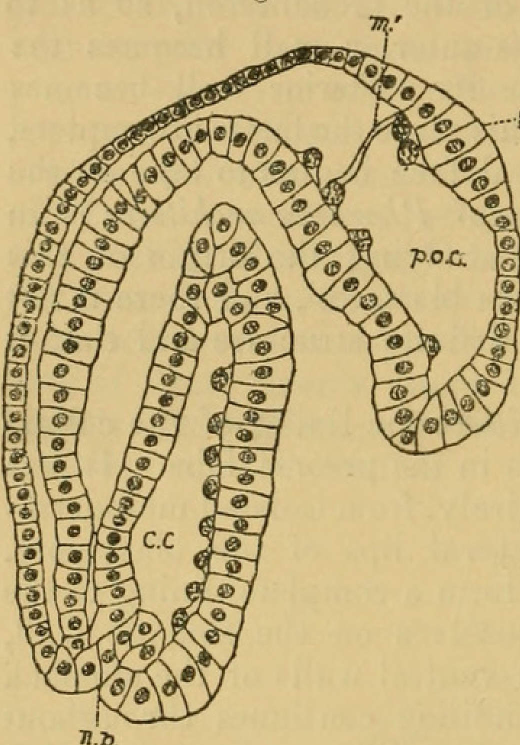


Fig. 3.

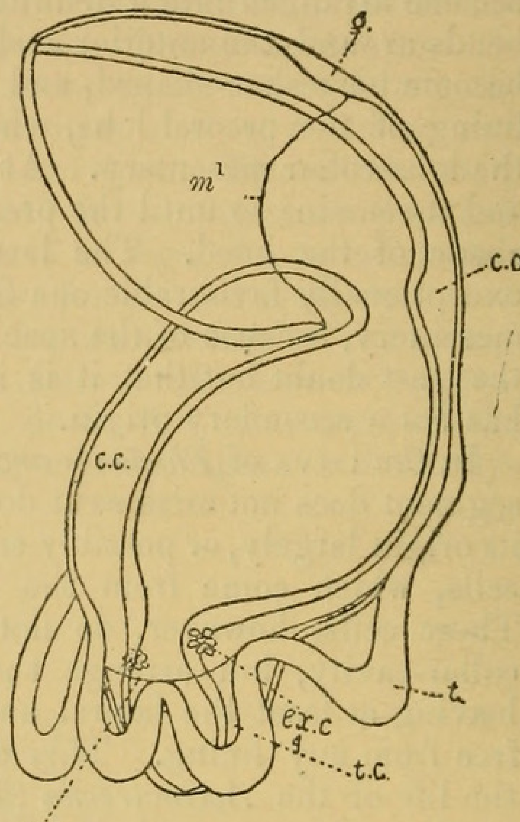


Fig. 2.—Longitudinal section through young larva, not quite sagittal, × 704. *c.c.*, collar-cavity; *g.*, ganglion; *m.*[1], mesentery between lobe- and collar-cavities; *n.p.*, nephridial pit; *p.o.c.*, cavity of preoral lobe.

Fig. 3.—Young larva of *Phoronis architecta*; three pairs of tentacles and beginnings of the fourth pair, × 225. *c.c.*, collar-cavity; *ex.c.*, excretory cells; *g.*, ganglion; *m.*[1], mesentery between lobe- and collar-cavities; *m.*[2], mesentery between collar- and trunk-cavities; *t.*, tentacle; *t.c.*, cavity of trunk.

wall in the region back of the tentacular band, and a cavity is left containing the rectum, part of the stomach, and the proximal part of the nephridial diverticula. At the same time this is taking place certain cells, which may have their origin from the base of the nephridial diverticula, give rise to the lining of the cavity of the trunk. As to the manner of the origin of these cells, I am still in doubt. I have not been able to find two cœlomic sacs which Hatschek has figured, and I have hunted for them in larvæ where the diverticula are just beginning to form and also in larvæ with two, four, and six tentacles. In one specimen with two tentacles, however, 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 (fig. 4).

One thing is certain—the fully developed trunk-cavity of the *Actinotrocha* has a distinct mesodermal lining, consisting of a somatic and a splanchnic layer (fig. 5). As far as I know, all *Actinotrochæ* have a ventral mesentery; this tends to support the view that the lining of the cavity of the trunk has its origin in a sac which grows around the rectum and posterior part of the stomach. Whether or not the fact that there is an indication of a dorsal mesentery in the posterior region of some of the fully developed *Actinotrochæ* (fig. 5) has any bearing on the double origin of the cavity of the trunk I cannot say, for I have never seen the very young larvæ of these forms.

Besides the larval body-cavities there is a mesodermal sac discovered by Ikeda, which arises between the mesodermal lining of the collar-cavity and the ventral ectoderm at a rather late stage in the development of the *Actinotrocha* (fig. 5). I have nothing to add to Ikeda's description of this structure, the cavity of which becomes the supraseptal cavity of the adult.

My observations on the fate of the body-cavities and mesenteries of the *Actinotrocha* agree with those of Ikeda. The preoral lobe and the lobe-collar mesentery are lost during metamorphosis, the collar-cavity and its lining become the ring-vessel of the adult, the cavity of the mesodermal sac between the mesodermal lining of the collar-cavity and the ventral ectoderm becomes the supraseptal cavity of the adult, the trunk-cavity, including the cavity of the ventral pouch, is transformed into the infraseptal body-cavity, and the mesentery between the collar- and trunk-cavities becomes the transverse septum of the adult.

Nephridia.—Caldwell was the first to describe the nephridia of the *Actinotrocha*, although earlier investigators saw the bunches of excretory cells at the ends of the nephridial canals. The account which Caldwell gives us is very brief, but he makes the observation that the nephridial canals end blindly within the collar-cavity.

Longchamps's view agrees with that of Caldwell, while Masterman and Menon find that the nephridial canals of the *Actinotrocha* open into the collar-cavity through one or more

Fig. 4.

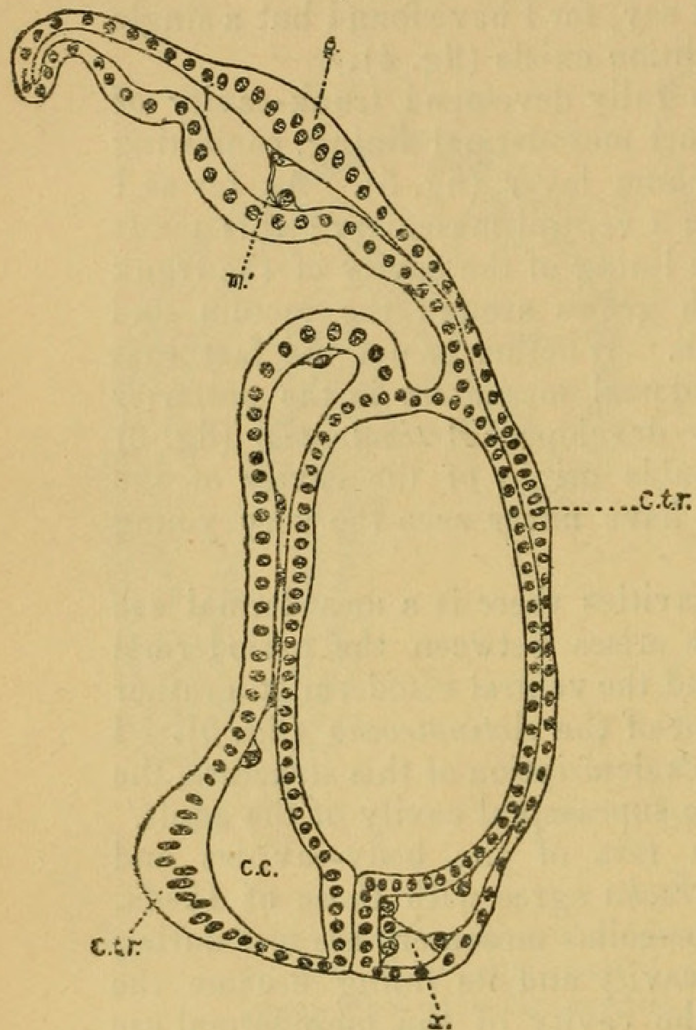


Fig. 5.

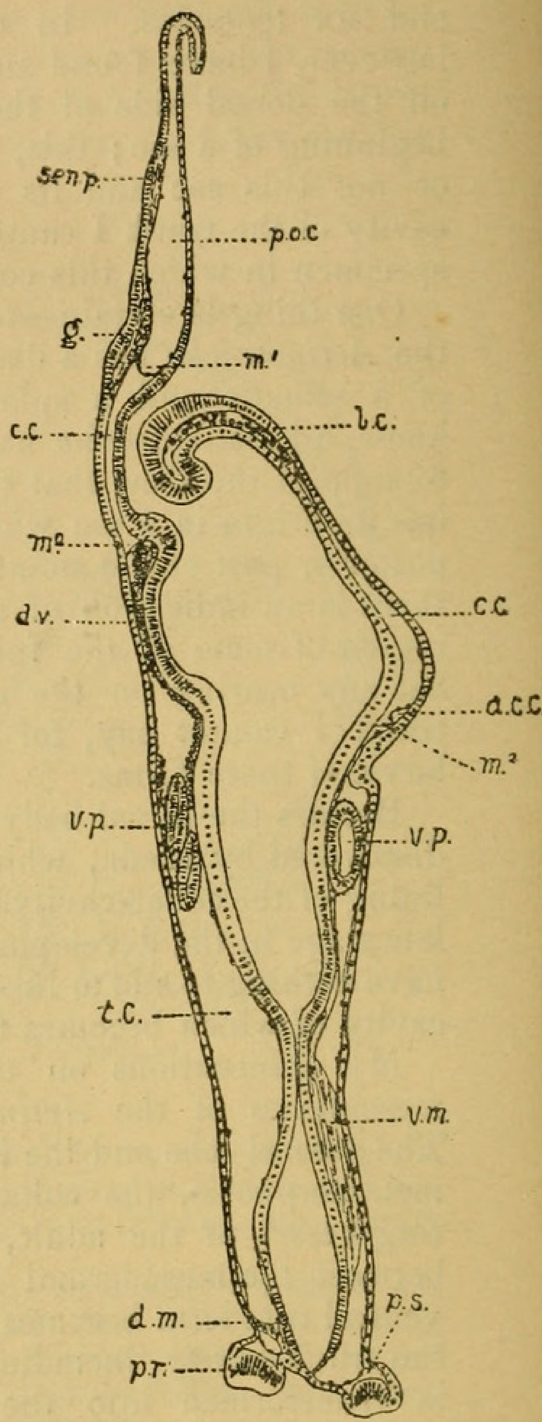


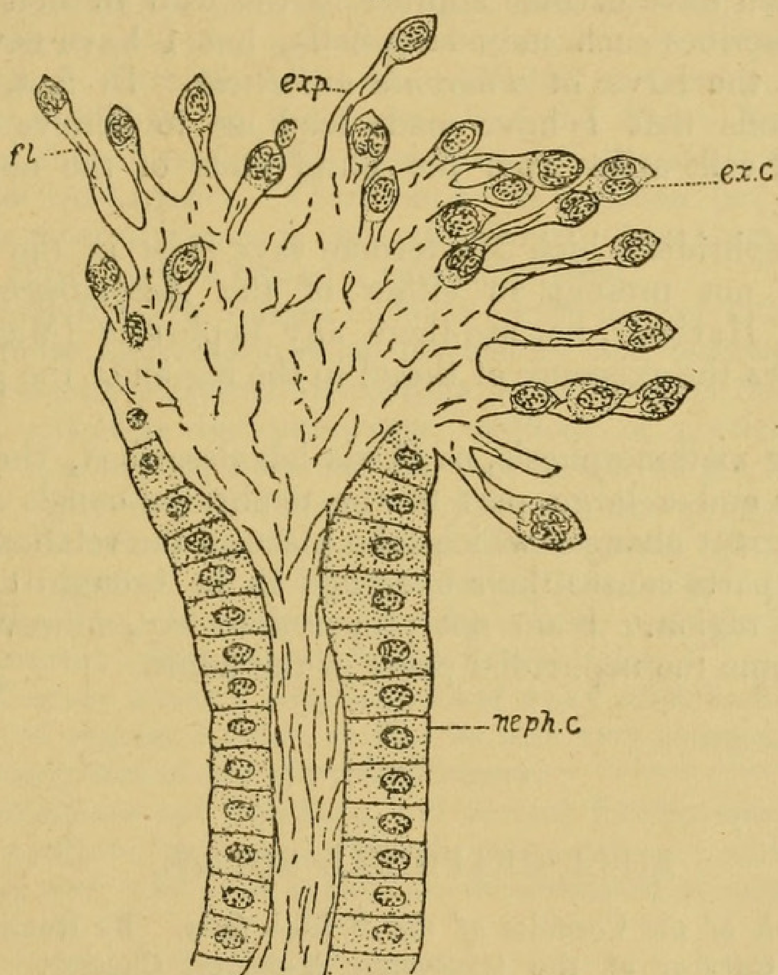
Fig. 4.—Longitudinal section through larva with two tentacles, × 704. *c.c.*, collar-cavity; *c.t.r.*, ciliated tentacular ring; *g.*, ganglion; *m.*[1], mesentery between lobe- and collar-cavities: *x.*, indication of a mesodermal sac.

Fig. 5.—Longitudinal section through an *Actinotrocha* from Beaufort Harbour, × 112. *a.c.c.*, adult collar-cavity; *b.c.*, blood-corpuscles; *c.c.*, larval collar-cavity; *d.m.*, indication of dorsal mesentery; *d.v.*, dorsal blood-vessel; *g.*, ganglion; *m.*[1], mesentery between lobe- and collar-cavities; *m.*[2], mesentery between collar- and trunk-cavities; *p.o.c.*, preoral body-cavity; *p.r.* perianal ring; *p.s.*, perianal sinus; *sen.p.*, sensory papilla; *t.c.*, trunk-cavity; *v.m.*, ventral mesentery; *v.p.*, ventral pouch.

funnels. Ikeda and Roule, on the other hand, tell us that they end blindly.

Goodrich has recently published a paper on the nephridia of the *Actinotrocha,* and has given a very complete and accurate description of their anatomy. My observations on these organs for two different species of *Actinotrochæ* confirm his work in nearly every detail. I find that the nephridial canal does not open by funnels into the collar-cavity, but that it ends in a thin-walled bulb, from the surface of which many thin-walled tubular processes or excretory cells radiate (fig. 6).

Fig. 6.



Longitudinal section through nephridium of an *Actinotrocha* from Beaufort Harbour, × 1200. *ex.c.*, excretory canal; *ex.p.*, excretory process; *fl.*, flagellum; *neph.c.*, nephridial canal.

These are really continuations of the blind end of the nephridial canal, and the lumen of each process is continuous proximally with that of the latter, but distally it is closed by a cell-like structure possessing one or more nuclei (fig. 6, *ex.c.*). Each tubular process contains a flagellum which arises from the cell at the tip of the former. Goodrich claims that there is but one nucleus at the end of each process, but I find in the *Actinotrocha* of *Phoronis architecta* that there may be two. (This conclusion is not drawn from bent nuclei, although I admit that such exist.)

It is, I think, a fairly well-established fact that the posterior pit (fig. 2, *n.p.*) and its wall become transformed into the nephridial canals of the *Actinotrocha*, and if we assume that the pit is of ectodermal origin, which seems to be the case in *Phoronis architecta,* we may say that the canals are of ectodermal origin. There is still some doubt as to whether the tubular processes or excretory cells arise from the blind ends of the nephridial canals, or whether they represent mesoderm-cells which have become applied to the wall in that region. Ikeda describes such mesoderm-cells, but I have never seen them in the larvæ of *Phoronis architecta.* In fact, all the observations that I have made lead me to believe that the excretory cells arise from the blind ends of the nephridial canals.

The nephridia which Masterman says exist in the preoral lobe are not present in either of the *Actinotrochæ* from Beaufort Harbour, nor are there any nephridia (Masterman now denies the existence of these) in the region of the perianal ring.

During metamorphosis, as Ikeda has described, the excretory cells and a large part of the nephridial canals are lost, and the great changes which take place in the relation of the different parts causes their openings to be brought closer to the anal region. I am not prepared to say, however, that they become the nephridial pores of the adult.

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Since the first publications of the Ray Society appeared in 1844, the Society has published a long series of valuable monographs, chiefly, but not exclusively, dealing with the Fauna of the British Islands; and the concluding volume of Mr. Newstead's great work on the Coccidæ has just appeared, under the management of Mr. John Hopkinson, F.L.S., who succeeded to the post of Secretary on the death of Rev. Prof. Wiltshire last year.

The Coccidæ, or Scale-Insects, are extremely destructive in gardens,