

Ri 1 mit 2 + 2, Ri 2 mit 3 + 1, Ri 3 mit 2 + 1, Ri 4 mit 2 + 1, Ri 5 mit 1 + 1 Borste.

Knopfborsten sind: von L 6:1, Ri 1:2, Ri 2:1, Ri 3:1, Ri 4:1, Ri 5:1.

1. Fuß: Ri 1 mit 1, Ri 2 mit 2, Ri 3 mit 5 Borsten.

Re 1 mit 1 Si, 1 Se. Re 2 mit 1 Si, 1 Se, Re 3 mit 4 Si, 1 St, 2 Se.

2. Fuß: Ri 1 mit 1, Ri 2 mit 2, Ri 3 mit 7 Borsten.

Re 1 mit 1 Si, 1 Se. Re 2 mit 1 Si, 1 Se, Re 3 mit 5 Si, 1 St, 3 Se.

Alle 5 Se mit proximalem Dorn.

3. Fuß: Ri 1 mit 1, Ri 2 mit 2, Ri 3 mit 8 Borsten.

Re 1 mit 1 Si, 1 Se, Re 2 mit 1 Si, 1 Se, Re 3 mit 5 Si, 1 St, 3 Se.

Se von Re 1 und Re 2 mit proximalem, spitzen, von Re 3 mit stumpfem Dorn.

4. Fuß: Ri 1 mit 1, Ri 2 mit 2, Ri 3 mit 7 Borsten.

Re 1 mit 1 Si, 1 Se, Re 2 mit 1 Si, 1 Se, Re 3 mit 5 Si, 1 St, 3 Se.

Se von Re 1, Re 2 und Re 3 wie vorher.

5. Fuß: Ri 1 mit 1, Ri 2 mit 1, Ri 3 mit 6 Borsten.

Re 1 mit 1 Si, Re 2 mit 1 Si, 1 Se, Re 3 mit 3 Si, 1 St, 2 Se.

Nur proximal von Se an Re 1 und Re 2 spitze Dorne.

Furca kurz und breit mit vollzähligen Borsten.

Fundort: Station 236.

Dem *Augaptilus fungiferus* sind zunächst verwandt: *squamatus* Giesbr. und *filigerus* Claus.

#### 4. Origin and Fate of the Blood Vessels and Blood Corpuscles of the *Actinotrocha*.

By R. P. Cowles, Johns Hopkins University, Baltimore, Md.

(With 7 figs.)

eingeg. 8. April 1904.

The rudiments of the vascular system of the adult *Phoronis* make their appearance in the *Actinotrocha* some time before the metamorphosis and their development into the perfected vascular system of the adult is of considerable interest.

Although the literature furnishes us with several accounts of the anatomy and development of this system, there are points in the various descriptions which at first sight seem irreconcilable. These differences, I believe, are due to the fact that in certain *Actinotrochae* the vascular system develops more precociously than in others, for the condition that Masterman<sup>1</sup> and Roule<sup>2</sup> find in the unmetamorphosed

<sup>1</sup> Quart. Journ. Micr. Sc. Vol. 40. 1897.

<sup>2</sup> Ann. d. Sc. Naturelles Zool. 8th Series. Vol. 11—12. 1900—1901.

*Actinotrocha* corresponds, in the form I have worked on, to that of the *Actinotrocha* immediately after metamorphosis.

Some of the early investigators recognized the presence of a blood vessel along the dorsal wall of the stomach and also masses of blood corpuscles.

Metschnikoff<sup>3</sup> and E. B. Wilson<sup>4</sup> observed that the cavity containing the blood corpuscle-masses gives rise to the ring-vessel of the adult and the later papers of Caldwell and Ikeda confirm their statement.

While Masterman describes a much more complicated vascular system for the *Actinotrocha* from St. Andrews Bay than that of all the *Actinotrochae* I have examined, yet I agree with his view that the cavities of the blood vessels may be considered as vestiges of the segmentation cavity.

Fig. 1.

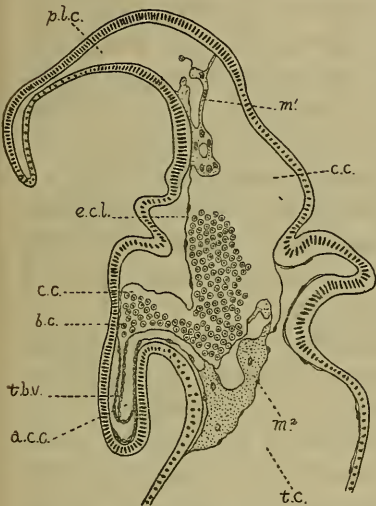


Fig. 2.

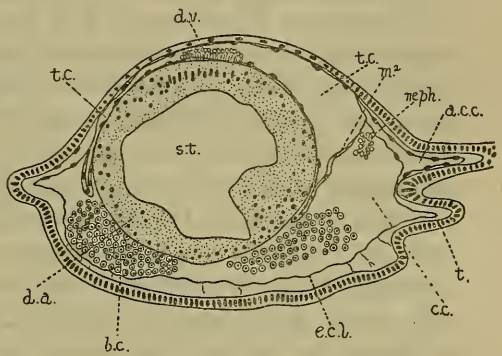


Fig. 1. Longitudinal section through an *Actinotrocha* which is almost ready to metamorphose.  $\times 225$ . *a.c.c.*, adult collar cavity; *b.c.*, blood corpuscle; *c.c.*, collar cavity; *e.c.l.*, epithelial lining of collar wall; *m<sup>1</sup>*, mesentery between collar and lobe cavities; *m<sup>2</sup>*, mesentery between trunk and collar cavities; *p.l.c.*, cavity of preoral lobe; *t.b.v.*, tentacular blood vessel of adult; *t.c.*, trunk cavity.

Fig. 2. Transverse section through the collar segment of an *Actinotrocha*.  $\times 225$ . *a.c.c.*, adult body cavity; *b.c.*, blood corpuscles; *c.c.*, collar cavity; *d.a.*, digestive area; *d.v.*, dorsal blood vessel; *e.c.l.*, epithelial lining of collar wall; *m<sup>2</sup>*, mesentery between collar and trunk cavities; *neph.*, nephridium; *t.*, tentacles; *t.c.*, trunk cavity.

The blood vessels of the adult in the *Actinotrochae* from Beaufort Harbor are represented by a dorsal blood vessel (Fig. 2 *d.v.*) running along the median line of the stomach from the dorsal insertion of the

<sup>3</sup> Zeitschr. f. wiss. Zool. Vol. 21. 1871.

<sup>4</sup> Quart. Journ. Micr. Sc. Vol. 21. 1881.

mesentery between the collar and trunk to the posterior end of the stomach, its lumen being a part of the segmentation cavity; a bunch of blood caeca formed at the posterior end of the stomach as evaginations of its splanchnic mesodermal covering; a loose sac of mesodermal tissue (at the time of metamorphosis) enclosing the larval collar-cavity and lining the somatic wall of the same and finally prolongations of the sac into the tentacles as the adult tentacular blood vessels (Fig. 1 *e.c.l.*, *t.b.v.*, Fig. 2 *e.c.l.*).

There are several important points concerning the vascular system of the *Actinotrocha* which must be taken into account in order to understand its metamorphosis into the vascular system of the young *Phoronis*. First, that the dorsal blood vessel, which is formed from the splanchnic mesodermal lining of the trunk-cavity, encloses a part of the space between the lining and the wall of the alimentary canal, i. e. the segmentation cavity; second, that this vessel ceases to exist as such posteriorly but opens into the space between the lining and the wall of the alimentary canal; third, that the wall of the stomach in the collar segment is practically free from a mesodermal lining (Fig. 2) and that the larval collar-cavity with its somatic mesodermal lining is a blood sinus; fourth, that the larval collar-cavity is a part of the segmentation cavity; and fifth, that during metamorphosis, the act of drawing the stomach and intestine into cavity of the ventral pouch causes a pressure to be exerted on the larval collar-cavity.

When the critical stage in the metamorphosis is being passed through, the blood corpuscle-masses break up and are driven by the pressure on the collar-cavity to the points of least resistance. As a rule, some of the blood corpuscles are squeezed up into the dorsal region of the collar-cavity where the dorsal blood vessel ends and invariably some of the blood corpuscles pass from the larval collar-cavity into the cavity between the wall of the alimentary canal and its mesodermal covering. In fact, as soon as the critical stage occurs, the splanchnic mesodermal lining in the trunk-segment becomes separated from the wall of the alimentary canal and thus allows the blood corpuscles to move about between these two layers throughout its extent.

The dorsal blood vessel (»Mediangefäß« [Cori<sup>5</sup>], »afferent vessel«, [Benham<sup>6</sup>]) and the ring-vessel with its tentacular vessel are completely formed structures at this stage. The dorsal vessel is still freely open posteriorly into the space or sinus between the stomach wall and

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<sup>5</sup> Zeitschr. f. wiss. Zool. Vol. 51. 1891.

<sup>6</sup> Quart. Journ. Micr. Sc. Vol. 30. 1889.

its mesodermal covering and blood corpuscles are carried back and forth from it to the sinus by the contraction and expansion of the former. Anteriorly the dorsal vessel can plainly be seen opening into the ring-vessel (larval collar-cavity).

The origin of the connection between the dorsal vessel and the ring-vessel and the manner in which the blood corpuscles find their way into the former are questions which have not been very satisfactorily elucidated. To my mind, the *Actinotrochae* from Beaufort Harbor present no great difficulties in the way of understanding how these processes take place. The dorsal blood vessel opens posteriorly into the sac-like sinus around the loop of the alimentary canal and it seems probable from an examination of sections of the critical stage that it is also open anteriorly. Assuming that such is the condition, it will open into the space between the mesodermal lining and the wall of the gut. This space, however, is in free communication with the larval collar-cavity (adult ring-vessel) which contains the blood corpuscles. Under these conditions the blood corpuscles can pass into the dorsal blood vessel from either end.

Shortly after the critical point in the metamorphosis, the mesodermal lining on the left side of the oral limb of the "U" shaped alimentary canal begins to show indications of becoming a blood vessel and when the metamorphosis is completed, a definite vessel (Fig. 3 *e, f*) is seen which opens posteriorly into the spacious blood sinus around the loop of the alimentary canal. Anteriorly before reaching the transverse septum, it divides into two branches which run obliquely upward along the sides of the alimentary canal almost encircling the same; these finally open into the ring-vessel of the suprasedal cavity. The vessel described becomes the efferent vessel of the adult and its branches become part of the recipient vessel (Fig. 3).

Above it is stated that I believe the stage in the development of the blood vessels which Masterman and Roule describe for the *Actinotrocha* corresponds to the stage which is found in the metamorphosed *Actinotrocha* from Beaufort Harbor. These two observers recognize a ventral blood vessel along the stomach but such a structure is not present in the Beaufort *Actinotrocha*. It, however, makes its appearance just after metamorphosis and is undoubtedly the same as the efferent vessel of the adult which has just been described.

Masterman also speaks of a "ring-sinus" connecting the dorsal vessel with the ventral vessel at the posterior end of the stomach and a "postoral ring-sinus" which does the same at the anterior end of the stomach. The former is undoubtedly identical with the spacious blood sinus, which has been described above, as surrounding the loop of the

alimentary canal. The latter makes its appearance after the metamorphosis in the *Actinotrocha* from Beaufort Harbor, and I am quite sure it represents the branches of the efferent vessel which pass up around the oesophagus and become continuous with the recipient vessel of the adult (Fig. 3 *ef.b*). It must be mentioned, however, that Masterman says these branches open into the dorsal blood vessel (afferent vessel of adult) which is not the case in the form on which I have worked.

The *Actinotrocha* which has just completed its metamorphosis has only one ring-vessel (larval collar-cavity) but the young *Phoronis* when it is twelve hours old possesses both the recipient and distributing vessels; these vessels, I believe, arise by the fusion of the walls of

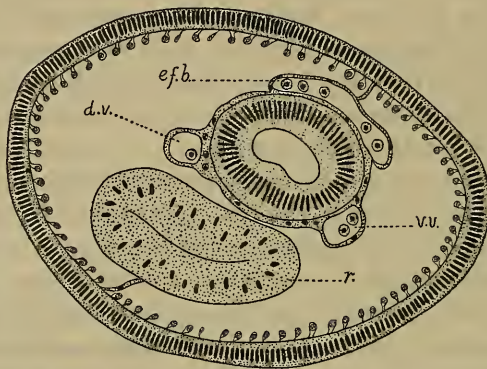


Fig. 3. Transverse section through the anterior region of an *Actinotrocha* which has just completed its metamorphosis.  $\times 360$ . *d.v.*, dorsal blood vessel (afferent blood vessel); *v.v.*, ventral blood vessel (efferent blood vessel); *r.*, rectum; *ef.b.*, branches of efferent vessel which are continued into the recipient vessel of the adult.

the single ring-vessel in the metamorphosing *Actinotrocha* and by the subsequent separation of the two parts along the line of fusion.

**Blood Corpuscles:** The red blood corpuscles of the adult *Phoronis* make their appearance in the young *Actinotrocha* and when the latter becomes fully developed, they are usually present as one or two pairs (according to the species) of conspicuous red masses in the larval collar-cavity (Fig. 2 *b.c*).

All the earlier observers describe these masses of blood corpuscles but E. B. Wilson is the first to discuss their origin. According to his view, they develop in solid masses, adhering to the stomach wall near the base of the tentacles.

Caldwell<sup>7</sup> tells us in a general way that the blood corpuscles

<sup>7</sup> Proc. of the Roy. Soc. Vol. 34. 1882, 1883.

"arise from the mesoblast cells in front of the septum" while Menon thinks that they have their origin from the splanchnopleure, covering the stomach and its diverticulum. Ikeda describes a totally different origin for these masses and says that they arise from "gigantic mesoblast cells in the body cavity of the larvae with one or two pairs of tentacles". Since the publication of his paper, however, Ikeda<sup>8</sup> has rejected this view but he has not as yet published anything on the subject.

There are two different *Actinotrochae* found in the waters of Beaufort Harbor which I shall designate as Species, *A.* (probably that of *Phoronis architecta*) and Species, *B.* Species, *A.*, which is the smaller of the two, is the more favorable for the study of the origin of the blood corpuscles and in this form, the latter make their appearance

Fig. 4.

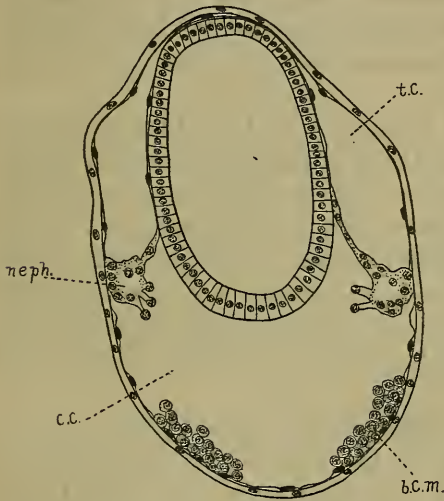


Fig. 5.



Fig. 6.

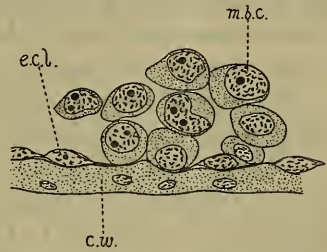


Fig. 4. Transverse section through a young *Actinotrocha* with 12 tentacles.  $\times 440$ . *c.c.*, collar cavity; *b.c.m.*, mesodermal blood corpuscle masses; *neph.*, nephridium; *t.c.*, trunk cavity.

Fig. 5. Section through mesodermal blood corpuscle masses.  $\times 1250$ . *c.w.*, collar wall; *e.c.l.*, epithelial lining of collar wall; *m.b.c.*, mother cell of blood corpuscles.

Fig. 6. Same as Fig. 5.

during the 14 tentacle stage. (The fully developed *Actinotrocha* of this species has 18 tentacles.)

*Actinotrocha*, Species, *A.* with 16 tentacles invariably has blood corpuscles and they are present in the so-called collar-cavity as two masses more or less closely applied to the ventro-lateral wall of the

<sup>8</sup> Journ. of the Col. of Sc. Imp. Univ. Japan. Vol. 13. Pt. 4. 1901.

stomach. In some cases, however, they are separated from the wall by a considerable space.

The transverse section of a larva with 12 tentacles in a plane just posterior to the base of the tentacles but anterior to the mesentery always shows two masses of cells bilaterally placed and closely applied to the mesoderm lining the ventro-lateral somatic wall (Fig. 4 *b.c.m.*). Occasionally I have found cells in these masses situated very close to the mesodermal lining, which were decidedly spindle-shaped in form and whose nuclei resembled those of the cells of the mesodermal lining, both in shape, size and internal structure (Fig. 5 *e.c.l.*, Fig. 6). These cells are not very rich in cytoplasm. Most of the cells, however, are almost three times the size of the cells lining the somatic wall, the cytoplasmic part of the cell having increased in size to a greater extent than the nucleus. Most of the nuclei have large deeply staining nucleoli (Fig. 5 and 6 *m.b.c.*). In some specimens, parts of these masses of cells are apparently in the act of wandering across the body cavity to the position the blood corpuscle-masses occupy in the fully formed *Actinotrocha*.

I have sectioned some 15 or 20 larvae with 12 or 14 tentacles and with one exception, I have found that when the mesodermal masses are present on the ventral body wall, there are no blood corpuscle-masses present in the larva and that when the blood corpuscle-masses are present, there are no mesodermal masses. In the exception which I have mentioned small blood corpuscle-masses were found applied to the stomach wall and masses of cells bilaterally placed were found on the ventral somatic wall but these cells had already taken on the character of blood corpuscles.

Ikeda has described a "mesoblastic cell mass" which he evidently considers as giving rise to the adult body cavity and its position is very similar to that of the mesoblastic masses that I have described above. They are both products of the mesodermal lining of the ventral somatic wall and are situated between the plane of the bases of the tentacles and the plane of the somatic insertion of the mesentery between the collar and trunk. Although Ikeda does not touch upon the very early origin of the adult body cavity yet it seems probable that he considers it as arising from a single mass of cells. The mesodermal masses that I have described above are paired and bilaterally placed and they are present only in the young larva of 12 or 14 tentacles (Fig. 4). Furthermore, in the larva with 12 or 14 tentacles there is no sign of the beginning of the adult body cavity. Although these mesodermal masses, which give rise to the blood corpuscles, according to my observations, have a similar position to the

rudiment of the young adult body cavity yet I am convinced that they do not give rise to it.

In Species, *A.*, there is no intimate relation between the masses of blood corpuscles and the nephridia such as has been described by Masterman for the species from St. Andrews Bay and by Longchamps<sup>9</sup> for *Actinotrocha branchiata*. In the larva of 16 tentacles the blood corpuscles, however, are closely applied to the stomach wall in the region of the digestive area. There is no mesodermal epithelium covering that part the surface of the stomach which lies within the collar-cavity, and the blood corpuscles seem to be so intimately related to the digestive areas that I am inclined to believe that they receive nourishment from them (Fig. 2).

While the blood corpuscles vary in size and undoubtedly multiply by karyokinetic division yet I have never found the "large and somewhat coarsely granular" and the "smaller finely granular" corpuscles that Ikeda speaks of nor in this species have I found any "gigantic mesoderm cells" in the region of the blood corpuscle-masses. Very large cells in close relation to the blood corpuscle-masses are

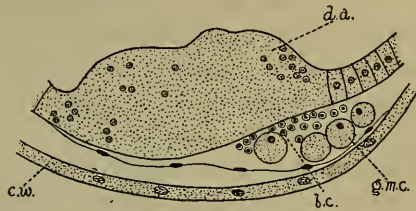


Fig. 7. Transverse section through the digestive area of an *Actinotrocha*.  $\times 450$ . *b.c.*, blood corpuscle; *c.w.*, collar wall; *d.a.*, digestive area; *g.m.c.*, gigantic mesoderm cell.

found in some specimens of *Actinotrocha*, Species, *B.* (Fig. 7 *g.m.c.*). These cells resemble those which are present in the old gastrula of Species, *A.* and which arise from the wall of the archenteron, but they are not as coarsely granular as the latter. Although in *Actinotrocha*, Species, *B.*, the cells are found, in most cases, closely associated with the blood corpuscles, I have never seen them in process of division and I do not believe that they give rise to blood corpuscles. Their occurrence is quite variable but so far as I have observed, they are not present in the *Actinotrochae* which are ready to metamorphose. They are not phagocytes nor are they pigment cells and the only name which I feel justified in giving them is large free mesoderm cells. Frequently they are also found in the posterior end of the trunk-cavity.

In *Actinotrocha*, Species, *B.*, the blood corpuscle-masses are four in number; one pair in the same region as those of Species, *A.*, and the other, in the anterior dorso-lateral part of the collar-cavity. All that I am able to say concerning the origin of the blood corpuscles in this

<sup>9</sup> Arch. de Biol. Vol. 18. 1902.



species is that the anterior pair of masses develop later in the life of the *Actinotrocha* than the posterior pair.

Roule tells us that the nephridia end internally at the level of the oesophagus in the *Actinotrocha* of *Phoronis Sabatieri* and he shows this in a figure. I have made cross sections through this region and have found masses of cells in much the same place as Roule has shown. These cells seem to me to be blood corpuscles but I must say that I have had opportunity to examine very few specimens of *Phoronis Sabatieri* and only one showed these masses of cells.

## 5. Das Cerebralganglion und die Leibeshöhle der Gordiiden.

Von Dr. Max Rauther, Assistent am zoologischen Institut in Jena.

(Mit 4 Figuren.)

eingeg. 11. April 1904.

Die systematische Stellung der Gattung *Gordius* ist bis auf den heutigen Tag unaufgeklärt. Von den meisten älteren Forschern<sup>1</sup> wurde sie der Klasse der Nematoden zugerechnet. Daß diese Vereinigung unnatürlich sei, haben sämtliche neueren anatomischen Untersuchungen dargetan; aber auch zu andern Vermaliengruppen schienen deutliche Beziehungen völlig zu fehlen. Schon Cuvier<sup>2</sup> hatte allerdings dem Wurm seinen Platz provisorisch am Ende der Annelidenklasse angewiesen. Seitdem wurde die Annelidenverwandtschaft oft wieder angedeutet (Dufour<sup>3</sup>, Camerano<sup>4</sup>, u. a.). Auch Vejdovský<sup>5</sup> bezeichnet in seiner ersten *Gordius*-Arbeit (1886) diesen Wurm als einen degenerierten Anneliden; in seiner letzten (1894) schiebt er die Entscheidung über die Verwandtschaftsbeziehungen jedoch der Embryologie zu. Keinem dieser Forscher ist es gelungen, die Homologie der Organisation beider Wurmtypen, weder im allgemeinen, noch im einzelnen, durchzuführen. Der Mangel des Cerebralganglions und der Schlundkommissur, einer sicher gekennzeichneten sekundären Leibeshöhle und der »Segmentalorgane«, der scheinbar ganz abweichende Bau des Genitalapparates, ließen derartige Bemühungen eitel erscheinen. Zu diesem Schlusse gelangen auch die Autoren<sup>6</sup> der neuesten anatomischen und embryologischen Untersuchungen.

<sup>1</sup> Vgl. u. a. Schneider, A., Monographie der Nematoden. 1866.

<sup>2</sup> Règne animal, 1. édit. T. II. 1817.

<sup>3</sup> Ann. des Sc. nat. Sér. II. T. VII. 1831.

<sup>4</sup> 1888, Ricerche intorno alla anatomia ed istologia dei Gordii, Torino; später (1897, Monografia dei Gordii, Mem. Accad. Sc. Torino V. 47) zieht C. vor, *Gordius* mit Nectonema an die Basis der Nemathelminthen zu stellen.

<sup>5</sup> Zeitschr. f. wiss. Zool. Bd. 43 (1886), 46 (1888) und 57 (1894).

<sup>6</sup> Montgomery, H., The Adult Organisation of *Paragordius varius*. Zool. Jahrb. Anat. XVIII. 1903, p. 464: »In view of these facts the *Gordiacea* cannot be

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