

The Post-larval Stage of *Arenicola marina*.

By

Wm. Blaxland Benham, D.Sc.Lond.,

Aldrichian Demonstrator of Anatomy in the University of Oxford.

With Plate I.

By "post-larval stage" I wish to indicate that stage in the developmental history of *Arenicola* at which the full adult number of somites has appeared, and the body is already distinguishable into (a) an anterior chætigerous region, and (b) a posterior achætous region or tail, but in which the gills are not yet completely formed or have not yet even made their appearance.

Such a stage was sent to me early in March, 1893, by Mr. Garstang, with a suggestion, which turned out to be perfectly well founded, that the worms were the young of *Arenicola*.

My hearty thanks are herewith accorded to him for his kindness in giving me the opportunity of studying them.

Two of these small worms were collected, one on February 22nd, the other on the 23rd of the same month, and he sent them to me preserved. One was stained and mounted entire, the other was cut into sections, partly longitudinal, partly transverse. An unfortunate accident to the longitudinal sections deprived me of investigating the anterior end of the worm as thoroughly as I could have wished, and though Mr. Garstang has been constantly on the look-out for more specimens, success has not crowned his efforts.

Mr. Garstang gives me the following information as to these larvæ :—“ Each was inhabiting a perfectly colourless and transparent gelatinous tube, obviously secreted by itself. The body of the *Arenicola* larva was very flexible when alive, enabling it to wriggle actively in an eel-like manner in the water—generally near the surface—when placed in a tall clear glass jar.”

“The two extremities of the body were in each of the larvæ yellow. This yellow colour was due to a number of yellow bodies or cells apparently situated in the epidermis. The blood was distinctly reddish.”

“The gelatinous tube seemed to invest the body closely, and was certainly no impediment to the animal.”

These two specimens are practically identical.

The worm is about 6·8 millimetres in length. It consists of a prostomium, without eye-spots, but with a light area or depression on each side in which is lodged the otocyst, followed by a peristomium and twenty chætigerous somites forming the anterior region, with a tail of a greater number of somites—some thirty or more—terminating in a small pygidium or anal somite.

These tail somites are difficult to enumerate, as the septa are not well developed, but each segment is surrounded by a band of gland-cells, which serve for their demarcation.

The worm is surrounded by a structureless gelatinous-looking envelope or tube (figs. 1, 4), probably secreted by these gland-cells, which are not confined to the tail, but occur in every somite; in fact, they are more abundant in the anterior somites, and here occur in two bands per somite, separated by a narrow non-glandular band (see fig. 7). This closely investing gelatinous tube seems, when taken in connection with sundry internal arrangements, such as nephridia, septa, &c., to point to an affinity with the *Chlorhæmidæ*.

As will be seen from the accompanying figures (fig. 1), the dorsal bundle contains two long capillary chætæ, of which one is longer than the other.

The peristomium is achætous; the first dorsal bundle is represented by a minute dorsal chæta (*Ch.* 2), scarcely protruding from the body, in Somite 2. At first sight the entire region between the prostomium and the first long chæta appears to be achætous, but this region is divided into two portions by a slight groove ventrally, and careful observations showed this small chæta (*Ch.* 2, fig. 1), demonstrating the composition of this region. In the adult *Arenicola* the achætous region following the prostomium has been regarded on other grounds—to wit, the existence of two septa anterior to the first bundle of chætæ—as being composed of two somites.

This small chæta, then, probably disappears in the adult, as has been shown to be the case with the anterior chætæ in some other Polychætes.

The ventral chætæ commence in Somite 3; they are much shorter than the capillary chætæ, being only about twice the length of the thickness of the body-wall. Each chæta is a sigmoid hook, with a small but distinct notch (fig. 2), the lower prong being the larger.

In the first few bundles there are only three chætæ; the number increases as we pass backwards, till in the hinder somites eight or nine chætæ constitute a bundle. Both the dorsal and ventral chætæ differ from those occurring in the adult, in which the dorsal chætæ present a series of small processes on each side (see Cunningham, Trans. Ed. Roy. Soc., xxxiii, 1888); whilst the ventral ones, as my fig. 3 shows, are without the smaller prong. Naturally the size of the chætæ differs, some idea of which difference will be conveyed by a comparison of figs. 2 and 3.

Of the thirteen pairs of gills in the adult, the present post-larval stage shows in profile only six pairs, situated on Somites 14—18. But I believe I can detect other gills on succeeding somites in the mounted specimen; however, it is difficult to be certain of the number. In the adult the first gill, which is quite small, occurs on the ninth somite (seventh chætigerous), and the last in the nineteenth chætigerous (*i. e.* the twenty-first somite). Thus the gills make their appearance from behind forwards. Each gill is at present merely a small somewhat conical papilla or eversion of the epidermis, containing a potential cavity entirely occupied by a looped blood-vessel (see fig. 5). The appearance suggests that these gills of *Arenicola* are special structures, and not, as in *Eunice* and other free-living Polychætes, modifications of the dorsal cirrus, as there is no trace of sensory hairs, which are present even in quite early stages in the development of cirri—for instance, in *Polydora*.

The epidermis is at this stage a single layer of cells, and varies, as it does in the adult, in different parts of the somite. In the non-glandular band (figs. 4 and 7) the cells whose outlines are not recognisable are flattened, and the nuclei are oval with their long axes parallel with the surface of the body. In the glandular band, however, the epidermis is thicker (fig. 5), and consists of narrow, deeply staining cells, compressed between large gland-cells. The nuclei of the former are small and circular, and of the latter compressed against the side of the cell. Viewed from above, the epidermis presents the appearance of fig. 7.

Wirèn (Kongl. Svensk. Vet. Akad. Handlingar, 22, pl. i, figs. 1—23) has described a similar difference in the epidermis cells between the ridges and those constituting the ridges in the adult. Probably these glandular bands of the post-larval stage become broken up into the polygonal areas or ridges of the adult.

I would here call attention to the strongly marked grooves, each followed by a distinct ridge, in the anterior somites; in this ridge the chætæ are inserted. This is true of both the post-larval stage and of the adult, and one would at first sight regard these grooves as intersegmental grooves, so that the chætæ appear to have the rather

abnormal position of the anterior margin of the somite. But such is not in reality the case; dissections of the adult, as well as observation of the nephridia of this present stage, indicate that the chætæ, and thus the ridge and groove, are in the middle of the somite, for in the anterior regions of the adult are certain complete septa, the last of which is placed midway between the third and fourth bundles of chætæ, the next anterior midway between the second and third bundles. The anterior end of the nephridium in the somites containing these organs lies about midway between consecutive bundles of chætæ—where, in fact, the septum would occur. I am unable to distinguish the septa in the present mounted specimen.

Of internal structures I will draw attention more particularly to the vascular system. Wirèn (loc. cit., p. 38, et seq.) has shown that in the adult *Arenicola* the dorsal and ventral blood-vessels are merely local enlargements of a continuous perienteric sinus, from which the axial portions are slightly nipped off. *Now at this post-larval stage I find no sinus.* Both the dorsal and the ventral vessels are quite distinct from the wall of the gut, as the camera drawing (fig. 4) shows. From these axial vessels branches pass right and left to the wall of the gut (diagrammatically shown in fig. 8), where they subdivide to a slight extent, and give rise to a but feebly developed plexus below the cœlomic epithelium.

I have already, in discussing the perienteric blood-sinus of certain earthworms,* referred to the improbability of its being a primitive feature, as is sometimes held. Here in *Arenicola*, at any rate, we have a network preceding ontogenetically the sinus of the adult.

Other vessels pass to the gill as shown; the dorso-branchial vessel passes straight to the gill, curves round at the apex of the latter, and after two or three twists passes to the ventral vessel. Another vessel passes to the nephridium, but I have not traced its origin. The blood-vessels are covered by cœlomic epithelium, which, in the case of the ventral trunk and the ventro-branchial vessel, consists of rounded cells with brownish granular contents and a round nucleus; they are, in fact, chloragogenic cells: elsewhere the cœlomic epithelium is flat.

In the body-wall the circular muscles are already present, and the epidermis rests directly upon them—the subepidermic tissue described by Wirèn has not yet made its appearance.

The longitudinal muscles are interrupted at three points, ventrally at the nerve-cord and dorso-laterally at the level of the dorsal chætæ. The oblique muscles so characteristic of Polychætæ are attached at these same points (see fig. 4).

* Quart. Journ. Mic. Sci., xxxiv, *A New English Genus of Aquatic Oligochætæ* (Sparganophilus).

As to the separate existence of a somatic cœlomic epithelium I feel some doubt; apparently the inner ends of the cells giving rise to the longitudinal muscles are themselves the lining of the cœlom, so that these cells are *myocœlomic*.

The *nephridia* are confined to Somites 6—10, though there may be traces of them in other somites. I believe I can distinguish a small one, for instance, in Somite 5. They have thus the same position as in the adult, where they occur in the fourth to eighth chætigerous somites, *i. e.* Somites 6—10.

But though they have the same position, they are very different in shape. I have previously figured this organ in the adult (Quart. Journ. Mic. Sci., xxxii, pl. xxv, *The Nephridium of Lumbricus, &c.*), and the present fig. 6 may be compared therewith. In place of the great wide sac there is in the post-larval stage quite a simple narrow tube, running nearly in a straight line from the nephridial pore, situated behind the ventral bundle of chætæ, forwards to the nephrostome, about midway between that bundle and the preceding one. The tube is, however, divisible into two regions, according to the presence or absence of concretions. The former (fig. 6, *a*) forms rather more than half the whole length of the tube. The organ is ciliated throughout.

The nephrostome is perfectly simple, so far as I can judge; is without lips, so that we cannot speak of a "funnel" in the usual sense of the word.

With regard to the alimentary tract, it presents exactly the same regions as in the adult. The narrow œsophagus passes back from the pharynx (? if this is eversible) into a wide "stomach," occupying Somite 7 and part of 8. Into the hinder part of this a pair of cone-like diverticula open, each diverticulum being longitudinally ridged internally. Immediately after the stomach the gut presents a series of pouches on each side, as in the adult. This sacculated region extends through four or five somites, and is succeeded by the narrow intestine, which suddenly dilates in the "tail," and here occupies nearly the whole cavity of the body.

DESCRIPTION OF PLATE I,

Illustrating Mr. Benham's paper on "The Post-larval Stage of *Arenicola marina*."

FIG. 1.—View of the larva mounted whole (from a camera drawing, under Zeiss *aa*, occ. 2). $\times 38$. The animal is lying on its right side anteriorly, but is twisted in Somite 13, so that it presents its dorsal surface upwards. The dorsal chætæ of the right side are seen as far forwards as Somite 8. The ventral chætæ are seen anteriorly, but have not been represented after Somite 13. The rudimentary gills are seen in Somites 14 to 21. The somites in the "tail" are indistinct except towards the anus. The dark shading round the animal represents the structureless envelope secreted by it. *Ch. 2*. Rudimentary dorsal chætæ of Somite 2. *div*. The diverticulum of stomach of the left side. *d. ch. l.* The dorsal chætæ of the left side. *d. ch. r.* The dorsal chætæ of the right side. *int'*. Narrow intestine. *int*². Wide intestine. *m.* Mouth. *æs.* Œsophagus. *oto.* Area deprived of pigment, below which is situated the otocyst. *Pros.* Prostomium. *sac.* Sacculated region of intestine. *stom.* Stomach.

FIG. 2.—One of the ventral chætæ from a transverse section. (Camera, Zeiss D. 4.) $\times 500$.

FIG. 3.—One of the ventral chætæ of an adult *Arenicola*. (Camera, Zeiss B. 4.) $\times 150$.

FIG. 4.—Transverse section through middle region of the body, about Somite 16. (Camera, Zeiss D. 2.) $\times 200$. [The intestine has probably shifted a little from its natural position. The oblique muscles are not cut through in the section drawn, but I have added them from neighbouring sections.] *Bl. ves.* Blood-vessels passing to and from the gill (which is not represented in the section). *chlor.* Chloragogen cells around the ventral blood-trunk. *circ. musc.* Circular muscle of the body-wall. *dors. v.* Dorsal blood-trunk. *epid.* Epidermis. *int.* Intestine. *long. mus.* Longitudinal muscles of the body-wall. *n. cells.* Nerve-cells. *n. fi.* Nerve-fibres. *nu. circ.* Nuclei of circular muscles. *nu. long.* Nuclei of longitudinal muscles. *obl. mus.* The oblique (or transverse) muscle. *splanch.* Nuclei of visceral cœlomic epithelium. *vent. ves.* Ventral blood-trunk.

FIG. 5.—A section through a gill. *ep.* Epidermis, in which is a number of gland-cells (*gl. c.*). *circ. mus.* Circular muscles of the body-wall. *Bl. ves.* Branchial vessels.

FIG. 6.—A portion of Fig. 1 more highly magnified. It represents one of the somites containing a nephridium. (Camera, Zeiss D. 2.) $\times 200$. The body-wall and the intestine are represented by the shading. The chætæ of two neighbouring somites are included in order to show the relative position of the nephridial pore and funnel. *a.* The excretory region. *b.* The "duct."

FIG. 7.—A portion of the body-wall viewed from the surface; it shows one of the glandular bands (*b*) bounded by the narrow non-glandular rings (*a, a*) which occur in each somite. *gl.* Gland-cells.

FIG. 8.—Diagrammatic transverse sections of the body to show vascular system in the branchial region on the right side, and the intestinal vessels on the left side. *Br. ves.* Branchial vessel. *Dor. ves.* The dorsal trunk. *Vent. ves.* Ventral trunk. Both are quite separate from the wall of the intestine (see Fig. 4). *d. int. ves., v. int. ves.* Vessels passing from these trunks to and from the plexus in the wall of the intestine (*int. cap.*).