The Development and Structure of the Anterior Region of the Body in the Sabellariidae, with special reference to *Phragmatopoma californica*

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Summary

Attention is drawn to the confusion which has been caused by the loose terminology of the anterior appendages in polychaetes, and more exact connotations are proposed. As the prostomium can be recognized as a comparable unit throughout the Polychaeta, a consideration of its constitution is deferred.

In the present paper the development and constitution of the anterior region of the sabellariid worms are considered. The larval development of *Phragmatopoma californica* (representing the most highly advanced genus) is described, and the structure of the adult of this species is compared with that of species belonging to other genera.

It is concluded that the opercular stalk arises mainly from the first segment; that the opercular paleae represent the notochaetae of the first two segments, and that the oral tentacles and the building organ are also developed from the first segment. The prostomium bears a single pair of tentacles.

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Introduction

The body of all polychaetes consists of a series of segments bounded by non-segmental regions; the prostomium anteriorly, the pygidium posteriorly. Each segment bears a pair of lateral lobes or parapodia from each of which extend two sheaves of chaetae. In the anterior region, this plan is usually modified, the segments often being fused one with another and to the prostomium, so that the homologies of the different parts are obscured. Much confusion has arisen regarding the terms used to denote the anterior appendages, and it is the purpose of the present studies to clarify the meaning of such terms as 'palps', 'tentacles', and 'cirri', and to investigate the fate and structure of the most anterior segments.

The following nomenclature is proposed. The *prostomium* is that region of
the body which lies anterior to the mouth and contains the brain, bears the eyes (when present), and presents no obvious signs of a segmental nature. Typically, it bears a pair of palps ventrally, and a number of antennae dorsally. The palps are innervated by nerves arising usually from the ventral or ventro-frontal region of the brain, the antennae from the dorsal or dorso-frontal region of the brain. In doubtful cases, appendages which might be referred to as either palps or antennae should be called merely ‘prostomial appendages’. Hypothetically, a segment is a unit containing the coelom arising from paired mesodermal pouches which open to the exterior by a pair of segmental organs or nephridia, provided with one or more pairs of nerves arising from a ganglion in the ventral nerve chain, blood-vessels and gonads, and which is provided with two sheaves of chaetae on each side. In all modern polychaetes this plan is greatly modified, especially in the anterior region where the presence of a segment may be indicated by the nervous system alone. It does not, of course, follow that all such nerves in the anterior region are segmental in origin. Each segment is provided with a single pair of lateral parapodia, each bearing two sheaves of chaetae; those arising dorsally being notochaetae and usually emerging from the dorsal lobe of the parapodium or notopodium; those arising ventrally termed neurochaetae usually emerge from the ventral lobe or neuropodium. Both noto- and neuropodia bear a single cirrus, that arising from the notopodium being called the notopodial or dorsal cirrus, that from the neuropodium, the neuropodial or ventral cirrus. The term ‘peristomium’ is a useful but somewhat ambiguous term, and when used should be clearly defined, since although in most instances it is synonymous with the first segment, in some polychaetes, such as nereids, what is commonly called the peristomium consists of two segments fused together. The term tentacle should be used only as a modifying word to the terms already proposed (thus: ‘antennal tentacles’; ‘tentacular cirrus’, &c.), and to filamentous structures (such as the oral tentacles of sabellariids) which cannot be homologized with any of the structures as here defined. The segment bordering, surrounding, or apparently immediately behind the mouth will be referred to here as the first segment.

Most workers seem to agree that the polychaete brain consists of three parts (Racovitza, 1896; Goodrich, 1898; Hanström, 1928; Snodgrass, 1938; Raw, 1949); but opinions differ as to whether the whole brain is presegmental or whether segmental ganglia have been added on from behind. The eversible proboscis present in many polychaetes has also been assigned a segmental origin by the Stanford school (Henry, 1947 a, b), and by Raw (1949). Nevertheless, whatever the constitution of the prostomium may be, it is quite clearly a unit comparable throughout the group; so a discussion of this subject and the origin of the proboscis may be deferred to a later paper.

The Sabellariidae are one of the most specialized families of polychaetes. One of their many interesting features is the development of an operculum from the anterior segments which in the most advanced genera completely obscures the prostomium. The operculum bears two sheaves of large chaetae or paleae on each side, and though little developed in the most primitive
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genera, in the more advanced members of the family they are greatly enlarged and arranged in a radial manner on the top of the opercular stalk to form a protective crown or stopper to the tube when the worm retracts. The constitution of this operculum and the homologies of the opercular paleae have attracted the attention of previous workers (Meyer, 1887, 1888; Gravier, 1909; Johansson, 1927; Hartman, 1944), but each has arrived at somewhat different conclusions. It is interesting, therefore, to see how this region develops. All sabellariids have a long development in the plankton, their larvae often being common in many parts of the world though frequently confused with those of spionids, which they superficially resemble. Caullery (1914) was the first to distinguish the larvae of the two families, whilst Wilson (1929) made the first detailed study of the larval development (Sabellaria alveolata and S. spinulosa). Hartman (1944) gives a short account of the development of Phragmatopoma californica, and previous references to the larval stages of sabellariids will be found in this and in Wilson's paper. The development of this latter species is here described in greater detail with especial reference to the elaboration of the anterior region, and this is followed by a description and discussion of the structure of the anterior region of sabellariids in general.

Fertilizations of Phragmatopoma californica were achieved by mixing the ripe eggs and sperm, and decanting into larger vessels the young larvae that swam to the surface. Further supplies of larvae were obtained in tow-nettings taken just offshore at La Jolla, California. The structure of the adults of this and other species was studied by dissection, thick sections and histological sections. All the drawings of larvae have been made from living specimens narcotized by 7 per cent. magnesium chloride, with the aid of a camera lucida or eye-piece graticule and squared paper. The drawings of adults were made from individuals fixed in Bouin's fluid after narcotization with magnesium chloride. No noticeable contraction of the tentacles took place on fixation, and the appearance of the anterior part of the body as shown in fig. 12 is closely similar to that of the living animal. The sections were drawn with the aid of a microprojector.

The Development and Structure of the Anterior Region of Phragmatopoma californica (Fewkes)

The larval development of Phragmatopoma californica follows the same pattern as that described by Wilson for Sabellaria alveolata and S. spinulosa. Males and females occur in approximately equal numbers. The eggs when mature are purple in colour and about 75\(\mu\) across. The young troctophores begin revolving after about 12 hours and after 24 hours a recognizable prototroch has developed and the larvae can then swim off the bottom (fig. 1, A). At this time a central mass of megameres may be seen to be surrounded by a transparent layer of smaller cells containing groups of yellow pigment-granules, the number of these patches being somewhat variable. By the second
day the prototroch is better developed but is incomplete mid-dorsally and remains so throughout life. The gut which has by now appeared soon acquires a stomodeal opening, and a number of chaetae are erupted from the postero-

Fig. 1. Larval development of *Phragmatopoma californica*. A, trophophore, showing central mass of megameres and patches of pigment granules amongst the peripheral micromeres. B, C, young chaetigerous larvae, showing elaboration of the gut, chaetal sacs, and prototroch. B in dorsal view, C in optical section.

lateral region of the larva (fig. 1, B and C). The patches of yellow-brown pigment increase in number and are irregularly scattered throughout the ectodermal layer. At this stage a weak telotroch may also be seen and the bright red pigment of the eye-cups has appeared. The chaetae, which are from the first of the barbed type characteristic of all sabellariid larvae, rapidly
increase in number and when the larva is 36 hours old the single pair of chaetal
sacs from which they arise may be clearly seen (fig. 1, c). Five or six chaetae
are borne on each side in larvae two days old (fig. 2) but there may be as many
as 30–40 long barbed chaetae on each side by the time the larva is ready to
metamorphose. When three or four days old
the larva has become clearly lop-sided, the
head overhanging the mouth (figs. 2, 3), and
this appearance is later accentuated by the
development of the oral lappets (figs. 4, 5).
By this time the telotroch is better developed
and the ‘grasping cilia’ may also be seen.
These are apparently formed by three or four
adjacent cilia clinging together, and retain the
barbed chaetae against the side of the body
when swimming. These grasping cilia can re-
lease the barbed chaetae which are thrust out-
wards and forwards in response to abnoxious
stimuli, or when braking (fig. 3). The telo-
troch becomes stronger as the larva develops
and is often quite prominent in old planktonic
larvae. The prototroch becomes strongly
developed and the mouth, stomodaeum, and
the regions of the oral lappets also become
strongly ciliated. A pair of red eye-spots is
usually recognizable by the time the larva is
four days old, but in many larvae only one is
formed at first, and this is always on the left
(as in fig. 3). The yellow-brown pigment-
patches become grouped along the prototroch
and telotroch and are scattered over the head
and pygidium, but are never present on the
segmental region of the body. Dark stellate
chromatophores, on the other hand, appear
in the trunk region. At first three rows may
be recognized and these demarcate the three
segments usually known as the parathoracic segments of the adult (figs. 4,
5, 6). These three parathoracic segments are the first to be clearly delimited,
the abdominal segments gradually becoming recognizable behind this region
with increasing age (figs. 7, 8, 9). The segments anterior to this parathoracic
region, with which we are chiefly concerned here, are peculiar in that they
are not distinguishable until later in development.

Thus the part of the head overhanging the mouth or ‘oral hood’ consists of
two tiers: (1) the prototrochal band, (2) the oral lappets on each side of the
mouth. The mouth is bounded posteriorly by a U-shaped area which in later
larvae may be recognized by its glandular nature to be the tube-building
FIG. 3. Ventral view of a young larva with chaetae extended. Note the greater development of the prototroch, the telotroch with 'grasping cilia', and the oral lappets developing under the chaetal lobes.

FIG. 4. Ventral view of a larva showing the development of the oral lappets. Note also the greater development of the telotroch, the distribution of pigment patches along the prototroch and non-segmental regions of the body, and the three lines of stellate chromatophores demarcating the future parathoracic segments.
organ of the adult (figs. 7, 10). The long barbed chaetae arise, as already noted, from a single pair of chaetal sacs, and these together with the building organ belong to the first segment. The lateral lips probably also belong to this segment, but it is not impossible that they represent true palps.

Before the building organ becomes clearly recognizable a pair of appendages may be seen growing out from the head in the dorso-lateral region just behind or at the end of the prototroch (figs. 6, 7, 8). It is difficult to homologize these appendages in the larva, but since in the adult they are innervated from the brain-mass they are presumably prostomial in origin, but in the
present state of our knowledge it is impossible to say whether they should be regarded as palps or antennae. When well developed they may be seen to have a ciliated groove communicating with the mouth. The groove passes over the parapodial lobes bearing the barbed chaetae, and under the prototrochal band, conveying the phytoplankton on which the larva feeds into the mouth (figs. 7, 8). The yellow pigment-patches which have been noted to be characteristic of the asegmental regions of the body, appear on the distal half of each tentacle along the dorsal side, and this may be regarded as additional evidence that these appendages are in fact prostomial in origin (fig. 8).
As growth proceeds, the three parathoracic segments acquire sheaves of long spear-shaped chaetae characteristic of the adult, and large mobile feet bearing uncini grow out from the abdominal segments (figs. 8, 9). The complementary bundles of chaetae are not recognizable until later. In many larvae a single barbed chaeta may also be seen arising from the last parathoracic seg-

![Diagram of a larva in ventro-lateral view.](image)

**Fig. 7.** A larva in ventro-lateral view, showing the further development of the prostomial tentacles and oral region. Notice the mid-ventral groove of the tentacle leading under the hood to the mouth, the U-shaped building organ (here buckled into a W owing to the flexure of the trunk), and the parathoracic chaetae.

ment (fig. 8). About the same time ventral cirri may be seen growing out from the first parapodial lobes, and soon afterwards the barbed chaetae begin to break off and fall out, gradually being replaced by flattened chaetae or paleae, simpler in structure than those of the adult. A segment between the first segment and the first parathoracic segment at last becomes apparent, a single sheaf of chaetae being protruded on each side about the time of settling (fig. 10).

Under natural conditions the larva probably settles out of the plankton as much as 2 months or even longer after the initiation of development. The barbed chaetae have by then been completely replaced by flattened paleae, and the prototroch and telotroch are lost. The caudal tail grows out and is
provided with a pair of dark patches of pigment probably acting as eye-spots, the young worm being able to walk backwards with the aid of the mobile legs.

**Fig. 8.** A slightly later larva seen from the right side, showing the ciliated groove of the prostomial tentacle passing to the mouth. The first parapodial lobes of the abdominal region bearing uncini, and the single barbed parathoracic chaeta may also be seen.

**Fig. 9.** A late planktonic larva in dorsal view, showing the replacement of the barbed chaetae by simple paleae, and the development of the three pairs of mobile parapodial lobes in the abdominal region.

representing the parapodia of the first three abdominal segments, moving about quite actively for a short time after settling. After a brief phase of such activity, tube building commences and the caudal tail becomes normally
reflexed. The three stages in the life-history are shown diagrammatically in fig. 11. The dorsal region of the first segment has by then begun to grow very rapidly so that the prostomium and the prostomial tentacles are pushed into a ventral position. This dorsal extension carries the paleae upwards and they eventually become arranged in an opercular crown on top of a thick stalk or peduncle. At the same time the ventral face of this stalk becomes elaborated to form a system of feeding tentacles leading to the mouth.

Adult structure

In the adult the paleae become arranged to form an almost complete crown on top of the stalk, forming a very effective stopper to the tube when the animal retracts. On the ventral side a large number of tentacles are arranged in rows, and each with a ciliated groove conveys particles through collecting channels to the mouth (fig. 12). A sheaf of simple chaetae emerge in the ventral region on each side of the building organ, and a pair of small protrusions representing the notopodial cirri of the same segment may be seen in the corresponding dorsal region. A second pair of sheaves also emerging from the ventral region may be seen a little farther back, and a pair of rather better developed notopodial cirri may be seen in the corresponding dorsal region.

The opercular chaetae or paleae are arranged in three series of concentric and almost complete rings. They arise from two pairs of paleal sacs, the outer and middle rows from one, the inner row from the other. The paleal sacs are embedded in the dorsal muscle of the most anterior segments and plunge right back into the second segment or the first parathoracic segment, one pair passing back slightly farther than the other. The paleae are produced continuously, the paleae from each sac fanning out into one portion of a hollow cone bisected by a plane through its axis, the paleae arranged in ascending age, the youngest towards the dorsal side. The apposition of the two pairs of paleal sheaves, one pair of which is concentric to the other, produces the virtually complete crown of the operculum, the paleae from above appearing to be arranged in concentric split-rings, the main break occurring where the new paleae are moving up
from beneath. The arrangement of the paleae and the structure of the anterior region is shown in figs. 12, 13, 14.

Thus in the adult *Phragmatopoma californica* there are two pairs of chaetal

![Fig. 11. Three phases in the career of an advanced sabellariid: A, planktonic stage; B, settling stage; C, adult stage. Prostomial tissue stippled.](image1)

![Fig. 12. Structure of the anterior region of *Phragmatopoma californica*. A, ventro-lateral view, showing relation of the oral tentacle system on the ventral side of the opercular stalk to the mouth and prostomial tentacles (inset illustrates pattern of ciliary currents whereby food particles are conveyed to the mouth). B, dorso-lateral view showing the arrangement of the opercular paleae and the reduced dorsal cirri of the first two segments.](image2)

sheaves forming the opercular paleae, a small sheaf of simple chaetae emerging ventrally on each side near the building organ, and another similar pair emerging ventrally in the next segment. The following segment, which is the first parathoracic segment, possesses the usual arrangement of sheaves of chaetae.
Details of the nervous system will not be described here, since the detailed studies of Collis (1952) on Sabellaria alveolata, which agree with those of Johansson on the same species and with observations made by the present writer, will be appearing elsewhere in the press.

**DISCUSSION**

Many diverse views have been expressed regarding the origin and homologies of the opercular paleae. Most workers seem to agree that they are derived from the first segment, but differ in opinion as to which the first segment really is. Some believe that although the paleae may be referred to a single segment, the opercular stalk may actually be formed from more than one segment. Quatrefages (1848), Grube (1877), Meyer (1887, 1888), Gravier (1909), McIntosh (1922), Fauvel (1927), Johansson (1927), and Hartman (1944), all agree that the opercular paleae belong mainly to one segment. Johansson, however, believes that there may be several segments anterior to this 'paleal segment' which have fused to the prostomium, and that they also may have contributed to the opercular stalk and to the series of paleae. Meyer and Gravier conclude that the operculum represents the notopodia of the first segment. Hartman concludes that the paleae represent both the notopodia and the neuropodia of a single segment, and that the heavy crotchets

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**Fig. 13.** Stereo-section of the anterior of Phragmatopoma californica to show the relationships of the operculum and opercular stalk, the oral tentacle system, and the prostomial tentacles. The letters refer to the approximate position of the sections shown in fig. 14.
which are present in the operculum of some genera (*Lygdamis* and *Idanthyrsus*) represent the notopodia of another segment, the first small chaetal sheaf emerging on each side of the building organ being the neurochaetae of this latter segment. The extra bundle of chaetae which she claims to be embedded in the opercular stalk of *Sabellaria* does not exist.

![Fig. 14. Sections through the anterior region of an adult *Phragmatopoma californica*.](image)

**A.** through the 1st parathoracic segment, showing the spear-shaped chaetae emerging from the notopodium and arising near the ventral nerve cord, and the ventral chaetae arising dorsally. The chaetal sacs of the opercular paleae in this and following sections may be seen in the dorsal longitudinal muscle-blocks. **B.** through the 2nd thoracic segment, showing the base of ventral chaetae and the tissue of the building organ. **C.** 1st thoracic segment, through the building organ. **D.** through the mouth and cerebral ganglia. **E.** through the base of the opercular stalk. **F.** through the distal end of the opercular stalk, showing arrangement of paleae.

In both *Sabellaria* and *Phragmatopoma* the opercular paleae arise from two pairs of sacs, and although in *Sabellaria* the paleae are arranged in three rows, the middle and inner rows arise from a single sac (Watson, 1910 *a, b*; Hartman, 1944; Ebling, 1945). As the notochaetae and the neurochaetae of each segment arise each from a single sac it is reasonable to infer that the paleae represent either the neurochaetae and the notochaetae of a single segment, or the components of two segments. It has been seen that one paleal sac projects back very slightly more than the other in both *Sabellaria* and *Phragmatopoma*, and
also that the first two visible segments have one pair of sheaves only. The simplest possible explanation of the origin of the paleae is to refer them to the missing sheaves of these two segments. The question then arises whether these represent notochaetae or neurochaetae, but in the present state of our knowledge it is quite impossible to say to which they should be ascribed. It may be argued that they are clearly notochaetae because of their dorsal position, but on the other hand they show obvious resemblances to the parathoracic spear-shaped chaetae, which, although emerging in a dorso-lateral position, arise near the ventral nerve cord. The shorter chaetae which emerge in the ventro-lateral position in each of the first five segments arise in a more dorsal position, and this is clearly shown in fig. 14, A. This suggests that the notochaetae and neurochaetae are actually reversed, not only in the abdominal region, as Hartman has suggested, but throughout the segmental region of the body. On this hypothesis the opercular paleae and the spear-shaped parathoracic chaetae are thus all neurochaetae, and in support of this suggestion it may be pointed out that in less advanced families, large specialized chaetae tend to be characteristic of the neuropodium rather than the notopodium, and it is only in the most advanced families such as the Sabellidae and Serpulidae that uncinis occur in the dorsal lobe in the anterior part of the body. Although sections of sabellarioids do suggest that the neuro- and notochaetae have in fact become transposed, there is as yet no real evidence that such transposition has occurred either in this family or in the anterior region of sabellids and serpulids, and it is probably safer in these instances to call the chaetae which emerge from the notopodium, notochaetae, and from the neuropodium, neurochaetae, although further research may show that reversal has in fact taken place.

However, it seems quite clear that the paleae are derived from two segments, since if they represented the components of a single segment the existence of a further segment must be invoked, and there is no anatomical or developmental evidence for this assumption. Mention must also be made of a number of nerves running forwards from the circum-oesophageal commissures described in *Sabellaria alveolata* by Johansson and more recently by Collis, and it is the presence of these nerves which prompted Johansson to postulate the existence of as many as five segments in the operculum. Apart from these nerves, which may not necessarily be segmental in origin, the existence of further segments is not indicated by any other structure either in the larva or the adult as already noted.

The precocity of development of the first segment as compared with the delayed appearance of the following segment in the larvae of *Phragmatopoma californica* has already been emphasized, and the stalk of the operculum (as distinct from the opercular paleae) in the adult seems to be mainly contributed by the first segment. An evolutionary series in the elaboration of the operculum may be traced from *Cryptopomatus* through *Lygdamis* and *Sabellaria* to *Phragmatopoma* (fig. 15). In *Cryptopomatus* the operculum and the paleae are hardly developed. In *Phalacrostromma, Cryptopomatus, Lygdamis, and*
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*Idanthyrsus* heavy hooked chaetae (crotchets or nuchal hooks) are also present in the opercular crown, but these seem to belong to the outer row of paleae of *Sabellaria* and *Phragmatopoma* and do not indicate the presence of another segment in the operculum. The prostomium which is hardly recognizable in the adult *Phragmatopoma* is more prominent in the more primitive genera. It is relatively large in *Cryptopomatus*, and in *Lygdamis* is produced into a process projecting forwards between the opercular lobes. In the higher genera the prostomium is inseparably fused with the opercular stalk, and it is difficult to define its limits. However, the rows of eye-spots which run forwards in the mid-ventral line from the bases of the prostomial tentacles in *Sabellaria*, probably arise from prostomial tissue. The oral tentacles which are developed from the ventral side of the opercular stalk from the first segment are absent in *Phalacrostemma* and arranged in a relatively simple manner in such genera as *Lygdamis*, but are much more elaborate in *Sabellaria* and *Phragmatopoma*. For the synonomy of these genera the reader is referred to the work of Johansson (1927).

The single pair of prostomial tentacles have a feeding function in the larvae, and also in the adults of the most primitive genera such as *Phalacrostemma*, but are reduced in importance with the elaboration of the oral tentacle-system in the more advanced genera. The prostomial tentacles appear to be directly comparable to similar structures in the spionids and other related families, but it is proposed to discuss these relationships in another paper.

**Conclusion**

The constitution of the anterior region of the sabellariid worms may thus be interpreted as follows.

**Prostomium.** Usually reduced in the adult and partly or wholly concealed by the development of the operculum. In the larva, well developed and provided with one or two pairs of red eye-spots and a strongly developed prototroch. One pair of long tentacles with a ventral ciliated gutter communicating with the mouth and used for feeding arises from the end or just

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**Fig. 15.** Evolution of the opercular crown in Sabellariidae. A, *Lygdamis*; B, *Sabellaria*; C, *Phragmatopoma*. The arrow indicates the generation of the paleae, the youngest at the base of the stalk or dorsal. Inner row of paleae, black; middle row, stippled; outer row, unshaded.
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posterior to the prototroch. In the adult these tentacles are important for feeding only in *Phalacrotestema*, but in most genera are probably mainly sensory.

**Segment 1.** Hypertrophied and constituting the main part of the opercular stalk. In the larva it is prominent and bears a pair of chaetal sacs from which long barbed chaetae protrude. These sacs correspond to one of the pairs of chaetal sacs which in the adult bear the opercular paleae—probably those giving rise to the inner and middle rows. All the opercular paleae correspond with the chaetae emerging from the notopodium of succeeding segments, and in the absence of further evidence may be referred to as notochaetae. The complementary sheaves are not recognizable in the larva; in the adult they protrude ventrally on each side of the building organ, which belongs mainly to this segment, although glandular tissue extends back into the second segment. The segment contains a normal arrangement of vascular and nephridial systems.

**Segment 2.** In the larva this segment is late in appearing, but in the adult it contains the normal complement of organ systems. One of the pairs of chaetal sheaves is represented by the outer whorl of opercular paleae, corresponding with the chaetae which emerge from the notopodium of succeeding segments, and may be regarded as notochaetae. The complementary sheaves are simple and emerge in a ventro-lateral position.

The following segment is the first parathoracic segment (in Hartman’s terminology, and equivalent to Johansson’s ‘first paleal-bearing thoracic segment’); it bears a normal complement of organ systems, spear-shaped chaetae corresponding to the opercular paleae emerging dorsally, and simple chaetae emerging ventrally.

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