

# Giant Pelagic Larvae of Phyllodocidae (Polychaeta, Annelida)

ALEXANDER B. TZETLIN\*

*Department of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow, Russia*

**ABSTRACT** The microscopic anatomy of giant pelagic larvae of Phyllodocidae was studied using routine histological, SEM, and TEM techniques. The larvae consist of two distinct regions: a large spherical trochophore measuring up to 2 mm in diameter and a posterior, long (up to 10 mm length), narrow rudiment of the adult body with up to 120 segments. The larvae have an unusual mixture of larval and adult features, including a very complex, well-developed brain and ganglia in the ventral nerve cord, and only a single pair of protonephridia located in the hyposphere of the trochophore. A muscular pharynx is not developed. The intestinal wall, especially in the trochophore region, consists of endodermal cells containing considerable nutritive material in the form of yolk-like globular inclusions. The digestive tract of all larvae was empty. The position of the frontal sensory organ and the prototroch, the structure of the parapodia and setae, and the three pairs of tentacular cirri dictate inclusion of the larvae in the family Phyllodocidae. The relatively enormous size and unusual pattern of development of the adult body may be adaptations for a long pelagic life and rapid settlement of the species, which inhabits slopes of islands and underwater mounts located far apart. *J. Morphol.* 238:93–107, 1998. © 1998 Wiley-Liss, Inc.

**KEY WORDS:** pelagic larvae; Phyllodocidae; Polychaeta, Annelida

The Phyllodocidae is a large family of polychaetes including both benthic and pelagic forms, traditionally considered as a group that has retained some archaic characters (Ushakov, '72; Pleijel, '91; Eibye-Jacobsen, '93). Since Kleinenberg (1886) first described metamorphosis of the phyllodocid *Lopadorhynchus*, the development and metamorphosis of Phyllodocidae have been under intensive investigation, and these data have been discussed in the scope of evolutionary morphology of invertebrates: the origin of adult nervous system in Trochozoa (see Meyer, 1898; Beklemishev, '64; Åkesson, '67), larval and postlarval metamorphism (see Ivanov, '28; Sveshnikov, '78), evolutionary relationships of the pericalimma (endolarva) larva and true trochophore (see Minichev and Starobogatov, '72; Salvini-Plawen, '80, '88), and the origin of larval and adult nephridia in annelids (Bartolomaeus, '94). A number of detailed studies in morphology, development, and ultrastructure of phyllodocid larvae have been published (e.g., Åkesson, '67; Lebsky, '70, '74; Blake, '75; Cazaux, '75, '85; Ospovat, '78; Lacalli, '81, '86, '88; Ushakova and Evdonin, '85; Zavarzina and Tzet-

lin, '86; Bartolomaeus, '87, '89, '94; Smith and Ruppert, '88; Smith, '92), but only a few species have been investigated: *Phyllodoce mucosa*, *P. maculata*, *P. fragilis*, *Eulalia viridis*, *Eteone longa*, and finally *Lopadorhynchus* spp. There are no or only poor, fragmentary data on the larval morphology and development of most of the 20 or so genera and more than 200 species of the family.

Here, we describe some aberrant giant larvae from the plankton samples of the Soviet expedition vessels *Academic Petrowsky*, *Professor Vodyanitsky* and *Odyssey*, collected during 1983–1985. All of the larvae were found in the northwestern part of the Indian Ocean from the Seychelles to the Gulf of Aden. The material had been

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\*Correspondence to: Alexander B. Tzetlin, Dept. of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow 119899, Russia.

E-mail: sasha@atzetlin.home.bio.msu.ru (home)  
Tzetlin@l.inv.bio.msu.ru (office)

kept in a 4% formaldehyde solution since its collection more than 10 years ago. Preservation of the tissues is thus not perfect but sufficient to provide data on larval structures.

The numerous studies of phyllodocid morphology (cited above) make it possible to supplement our results with up-to-date information on this subject.

#### MATERIALS AND METHODS

About 20 specimens of unidentified aberrant larvae were found in the samples collected by Dgedy net and pleuston trawl during the 1983–1984 voyages of the Russian research vessels *Academic Petrovsky*, *Professor Vodyanitsky*, and *Odyssey*. All larvae were collected in the northeast Indian Ocean from the Seychelles to the Gulf of Aden (Table 1). The material was fixed in total together with the whole planctonic sample in a solution of 4% formaldehyde in sea water. It remained in the solution for 10 years. Larval specimens selected for histological and TEM studies were postfixed in 1% osmium tetroxide, dehydrated in a series of alcohol and acetone dilutions, and embedded in Epon. Semithin sections (two sagittal and two transversal series) were made from larvae N 1–4, (from Seychelles, 04°31'18 S, 55°13'5 E, depth 0–10 m, 19 Dec., 1983, R/V *Academic Petrovsky*, voyage N 14), with glass knives on a Dupont Ultracut microtome and stained in 1% toluidine blue. Ultrathin sections for TEM observations were cut on an LKB-3 Ultracut microtome with diamond knives, stained in lead citrate and uranyl acetate, and then examined with a JEM-100b microscope.

#### RESULTS

Although the material was collected at different times and localities, all of the larvae were similar, allowing a general description of their morphology.

##### *External morphology*

In overall appearance the larvae consisted of a large trochophore body bearing a rudiment of adult trunk on its vegetative pole. The trunk rudiment comprised 100 or more setigerous segments and a pygidium (Fig. 1; see also Fig. 4A).

*Trochophore region.* The trochophore region is spherical, ranging in diameter from 1.0–1.5 mm. Its episphere bears a ciliated sensory organ consisting of a transverse strip of cilia on the frontal surface. Two ocelli flank it. The highly developed prototroch consists of densely spaced cilia up to 66  $\mu$ m in length. The mouth lies just posterior to the prototroch and is surrounded with a ciliary field (Fig. 1). No neurotroch is seen. The lower hyposphere forms a collar that covers the first segments of the rudimentary adult trunk.

*Rudiment of adult trunk.* The length of the rudiment is correlated with the number of setigerous segments present and, in different specimens, segments ranged from 33–120. The maximum length observed in our specimens was 12 mm. Setigerous segments each bear uniramous parapodia, each equipped with an aciculum and six compound heterogomph setae, as well as dorsal leaf-shaped and ventral parapodial cirri (Fig. 2A,D). The setal shaft exhibits numerous long acuminate teeth (see Fig. 5B).

TABLE 1. Material examined

R/V, voyage	Date	Latitude	Longitude	Type of net	Depth (meter)	Number of spec.	Comments
<i>Academic Petrovsky</i> , vo. N 14	04.11.1983	12°05,5'N	45°40'E	Pleuston trawl	0	4	Gulf of Aden
<i>Academic Petrovsky</i> , vo. N 14	23, 11, 1983	11°44,5'N	45°10,5'E	Djedi net	10–0	1	Gulf of Aden
<i>Academic Petrovsky</i> , vo. N 14	23, 11, 1983	11°44,5'N	45°10,5'E	Djedi net	500–100	4	Gulf of Aden
<i>Academic Petrovsky</i> , vo. N 14	24, 11, 1983	11°45,7'N	45°55'E	Pleuston trawl	0	4	Gulf of Aden
<i>Academic Petrovsky</i> , vo. N 14	19, 12, 1983	04°31'18 S	55°13'5 E	Djedi net.	10–0	5	Seychelles (Silhouette)
<i>Academic Petrovsky</i> , vo. N 14	19, 12, 1983	04°31'18 S	55°13'5 E	Djedi net.	50–25	1	Seychelles (Silhouette)
<i>Prof. Vodyanitsky</i> , vo. N 16	1.05, 1984	0°26,3'N	56°00'E	Djedi net.	50	1	Underwater mountain "Equator"
<i>Odyssey</i> , vo. N 33	30, 5, 1984	10°12,00'N	56°04'E	Djedi net.	100–0	1	Underwater mountain "Error"

GIANT LARVAE OF PHYLLODOCIDAE

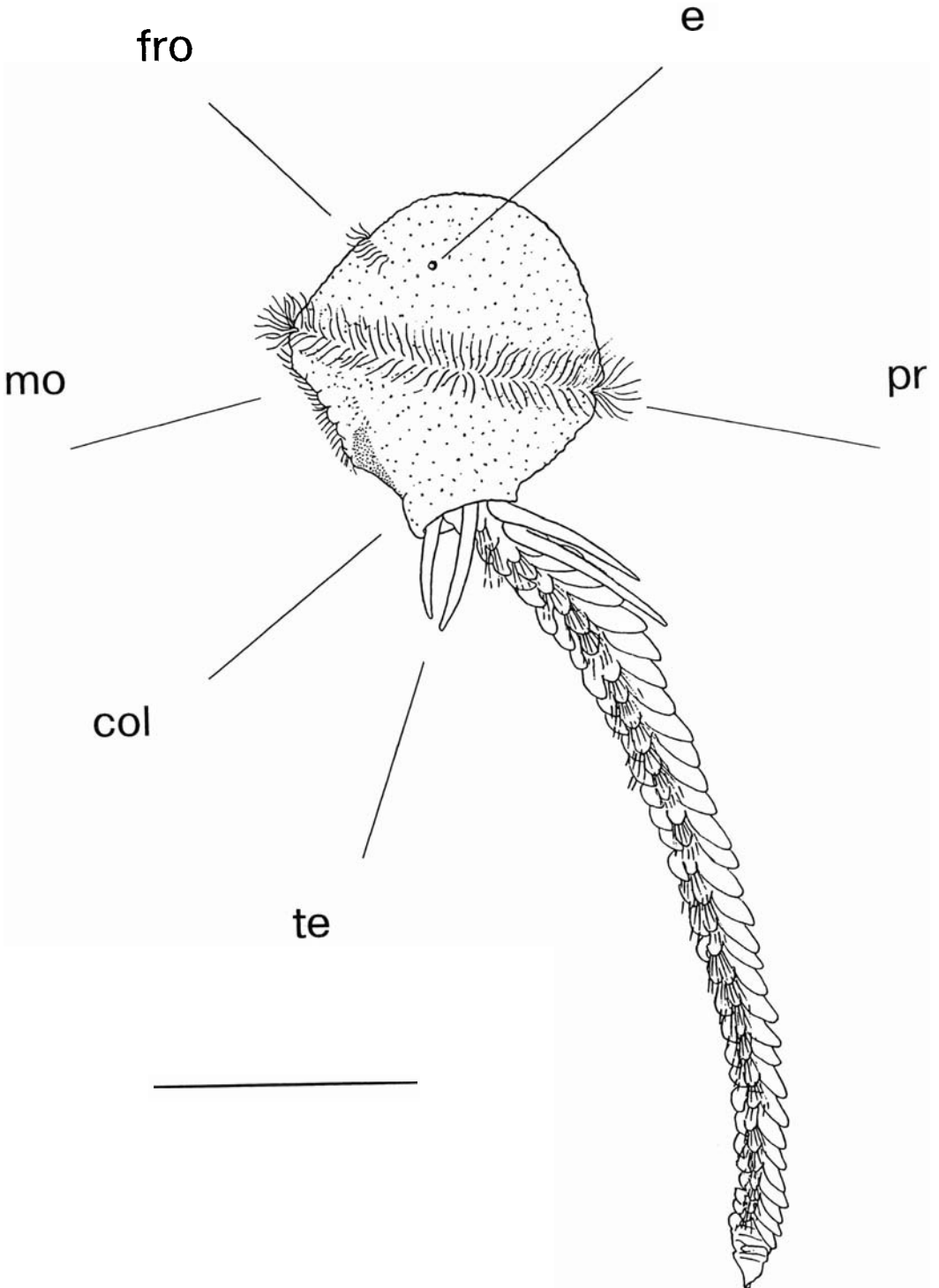


Fig. 1. Giant larva of Phyllocodidae g. sp. with 36 setigerous segments. Lateral view. Col, collar; te, tentacular cirri; e, eye; fro, frontal organ, mo, mouth. Scale=500  $\mu$ m.

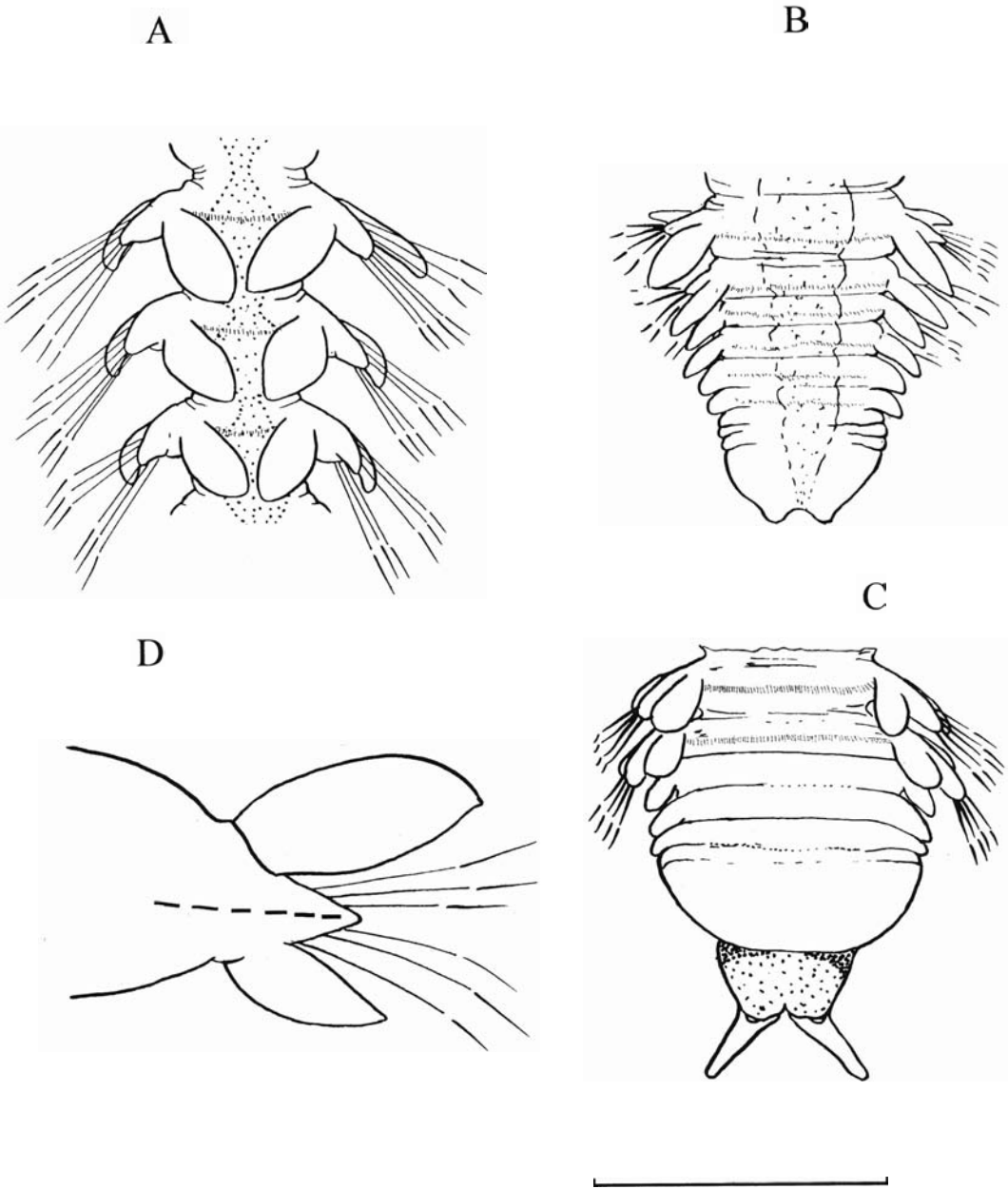


Fig. 2. Giant larva of Phyllodocidae g. sp. Fragments. **A:** Middle region of the trunk rudiment, dorsal view. **B:** Posterior region of the trunk rudiment, 35 setigerous segments. **C:** Posterior region of the trunk

rudiment with rudiments of anal cirri, 90 setigerous segments. **D:** Parapodium of the trunk rudiment. Scales: A=350  $\mu$ m, B=160  $\mu$ m, C=400  $\mu$ m.

Aciculae approach 132  $\mu$ m in length and 3.5  $\mu$ m in thickness. The proximal setal region up to articulation is about 130  $\mu$ m long. The first three segments, partially covered

by the throchophoral collar, bear four pairs of tentacular cirri in a pattern of 1-2-1. Pygidial structure varies with the number of setigerous segments. Specimens with 70-

100 segments bear two small pygidial cirri, whereas those with 35–55 segments have only two small papillae at the pygidial end (Fig. 2B,C).

### *Internal morphology*

**Epithelium and cuticle.** A simple tall epithelium delimiting the trochophore region is overlain by a larval cuticle in which diffuse collagen fibers make up an amorphous matrix penetrated with numerous epithelial microvilli. Cuticle thickness in the trochophore region is ~200 nm. The epithelium varies in height from 37  $\mu\text{m}$  on the frontal side to 43  $\mu\text{m}$  on the side of trochophore, opposite the mouth. The epithelium of the episphere and posterior hyposphere is rich in glandular cells that contain large oblong cisternae filled with secretory product. (Figs. 3,6A, B, D).

The adult trunk rudiment is covered by a thin epithelium ~3  $\mu\text{m}$  in height. The overlying cuticle, 0.4  $\mu\text{m}$  thick, is of the "adult" type, exhibiting several mutually orthogonal layers of collagen fibers (Fig. 7).

**Digestive tract.** A mouth surrounded by a ciliated field opens into the larval intestine. The intestine exhibits a wall consisting of tall, ciliated cells, apparently lacking microvilli, and containing yolk-like reserve vacuoles averaging 22  $\mu\text{m}$  in diameter. The intestinal lumen consists of a narrow space between these cells. A mass of endoderm almost completely occupies the internal cavity of the trochophore region ( Figs. 3, 8).

A rudiment of muscular axial proboscis lies in the episphere, forming a compact structure dorsal to the endodermal mass (Figs. 3, 6C). Its lumen is covered with the "larval type" cuticle. A poorly developed basal membrane surrounds the rudiment and is partly covered by cytoplasmic extensions of mesodermal cells.

In the hyposphere, the lower part the spherical mass of trochophoral endodermal cells becomes the intestine of the rudimentary adult trunk. The intestinal lumen is quite narrow here (Figs. 3, 5B). At the termination of the pygidium the ectodermal anus establishes a complete intestinal tube (Figs. 2, 3, 5D, E).

Intestinal cells of the rudimentary adult trunk are also filled with vacuoles containing yolk-like reserve materials, but here, the

vacuoles are only half the diameter (100  $\mu\text{m}$  on average) of those present in trochophore-region intestinal cells. The vacuoles gradually decrease in number and size from trochophore to pygidium.

The intestinal lumen passing through the midpart of the segments narrows to a diameter of 6.6  $\mu\text{m}$ . The rudiment intestinal epithelium generally exhibits a few short surface microvilli, although intestinal cells in posterior segments to the pygidium and the meristematic zone lack microvilli. Moreover, epithelial cells in this distal region of the intestine project freely into the lumen and do not contact each other. No specimens examined contained food remains in their intestinal lumen.

**Nervous system.** The nervous system consists of a well-developed brain, circumesophageal connectives, and a ventral nerve cord. The brain, subepithelial in the larval episphere, consists of massive frontal lobes that contain neuropil, distinctly divided into frontal and posterior areas (Figs. 3, 6B). Optic lobes (optic ganglion), which are posterior to the frontal lobes, contact the eyes directly. Circumesophageal connectives originate in the brain, extend two roots around the endodermal mass, and join in the ventral part of the trunk rudiment, in the region covered by the collar. Posteriorly the circumesophageal connectives exhibit two pairs of segmental trunk ganglia. A third pair, located ventrally on the third setigerous segment, comprises the first ganglionic pair of the well-developed, extensively ganglionated ventral nerve cord (Fig. 5C). Each ganglion of the ventral nerve cord contains ~180–200 neurons, whereas interganglionic regions of the cord lack neuron cell bodies (Figs. 3, 5C, D).

**Trunk rudiment.** The body wall of the trunk rudiment is composed of epidermis and a longitudinal muscle layer consisting of four bands, ventral and dorso-lateral pairs (Figs.4, 7). Longitudinal myocytes are arranged into a monolayer with their narrow surfaces resting on the basal lamina and their nuclei located in noncontractile extensions (Fig. 7).

Additionally, parapodial muscle complexes and bundles of oblique muscle are present in each segment of the trunk rudiment.

Larval mesenchyme consists of cells whose meandering extensions turn around the in-

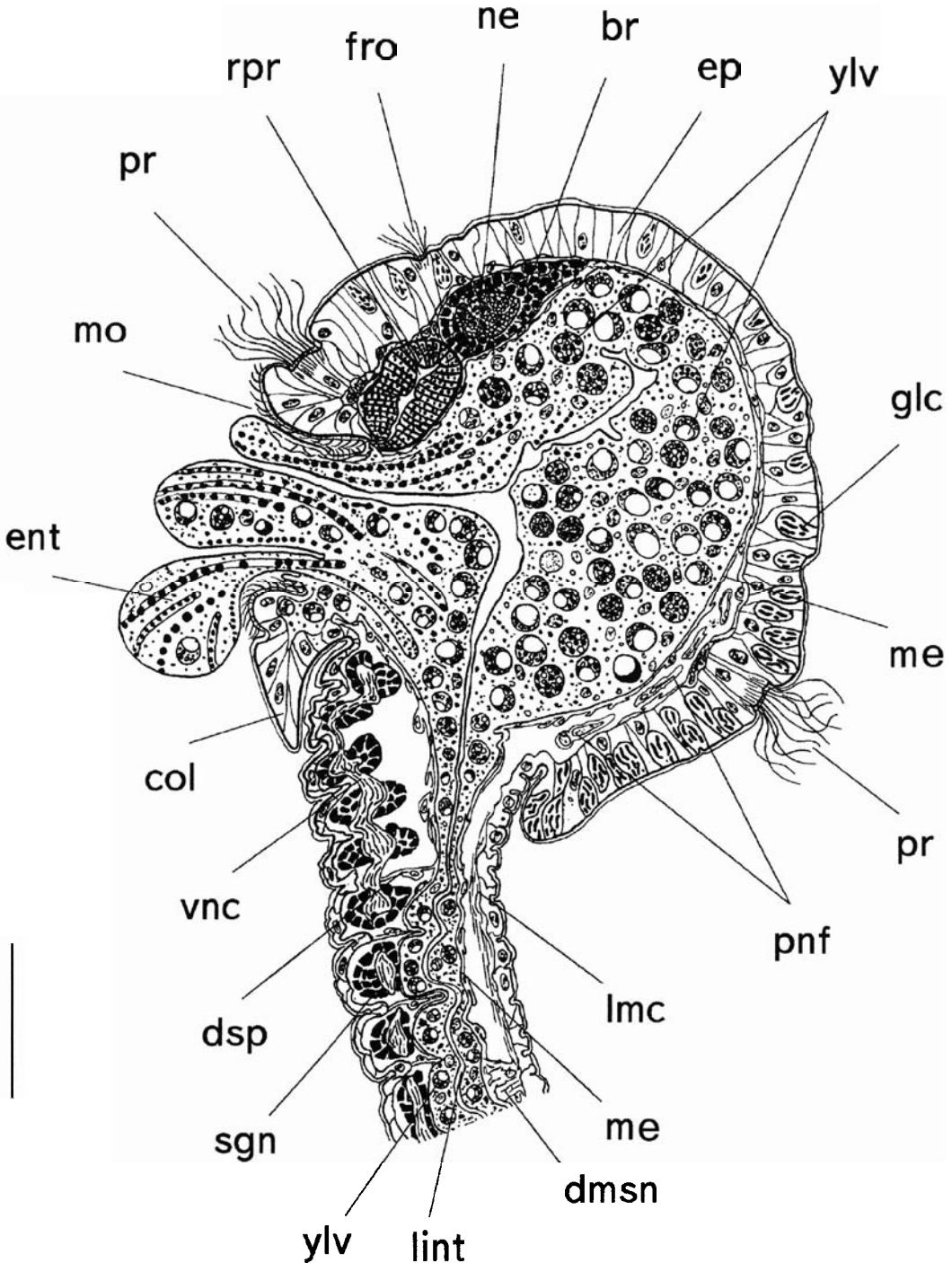


Fig. 3. Giant larva of Phyllodocidae g. sp. Sagittal section. Part of the trochophore endodermis is everted from the mouth. Br, brain; col, collar; dmsn, dorsal mesenterium; dsp, septum; ep, epidermal epithelium; fro, frontal organ; glc, gland cell; lint, intestinal lumen;

lmc, longitudinal muscle cell; me, mesoderm; mo, mouth; ne, neuropil; pnf, protonephridium; pr, prototroch; rpr, proboscis rudiment; sgn, segmental ganglia; vnc, ventral nerve cord; ylv, yolk-like vacuole. Scale=700  $\mu$ m.

GIANT LARVAE OF PHYLLODOCIDAE

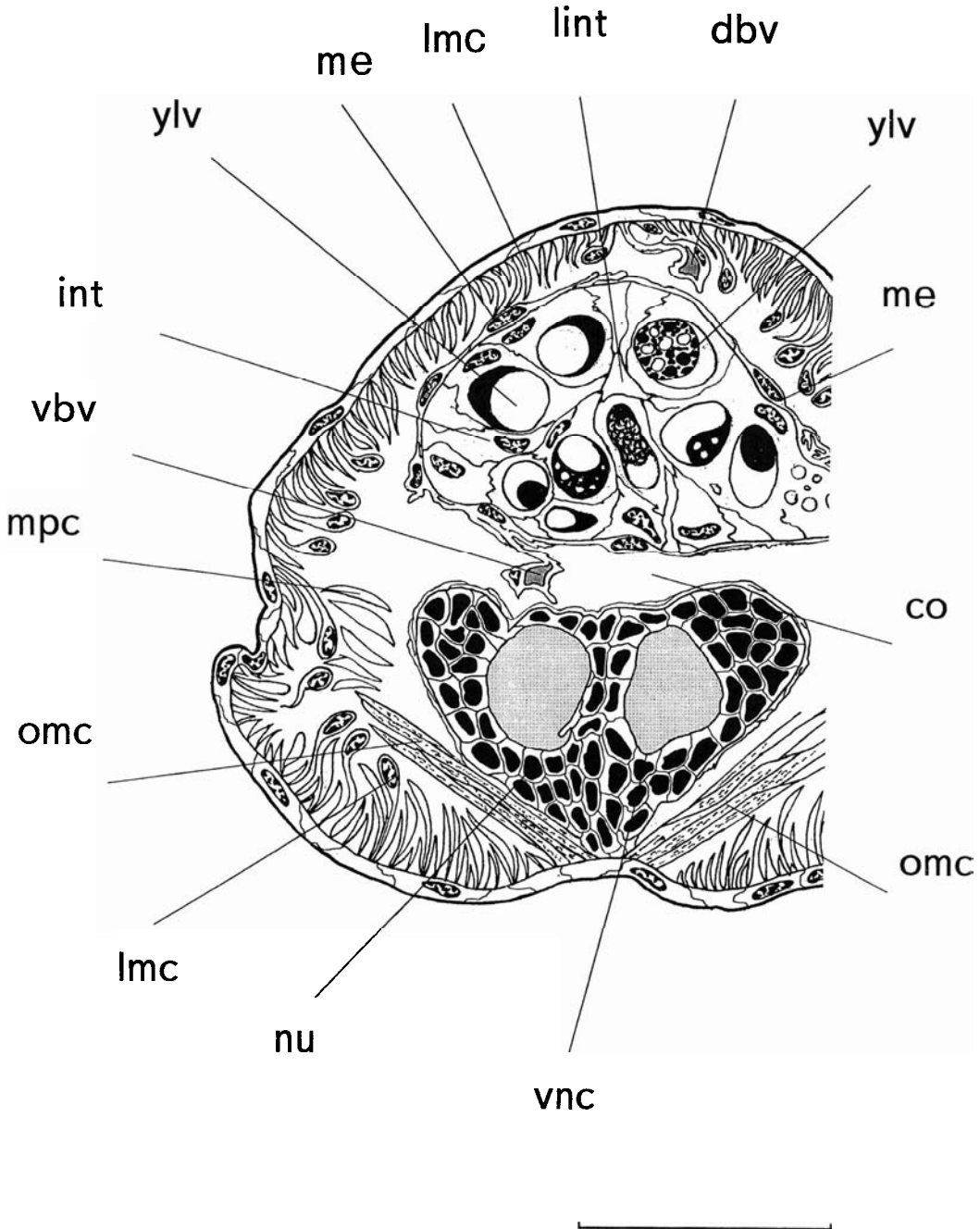


Fig. 4. Larva of Phyllococidae g. sp. Transverse section through middle region of the trunk rudiment. Slightly schematic, after TEM reconstruction. Co, body cavity; dbv, dorsal blood vessel; int, intestine; intes-

tinal lumen; lmc, longitudinal muscle cell; mpc, muscle of parapodial complex; me, mesoderm; nu, nucleus; omc, oblique muscle; vbv, ventral blood vessel; vnc, ventral nerve cord; ylv, yolk-like vacuole. Scale = 50  $\mu$ m.

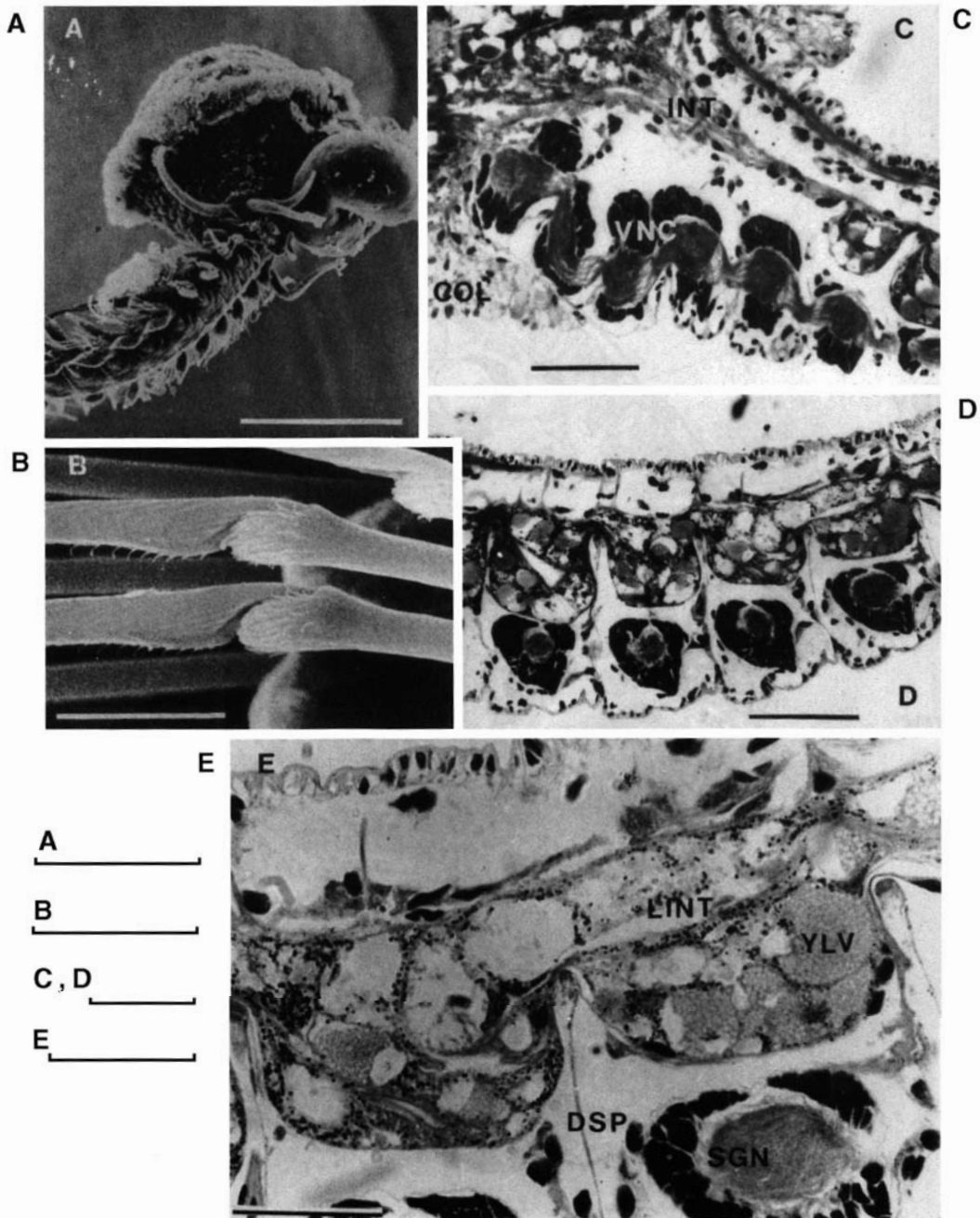


Fig. 5. Larva of *Phyllococidae* g. sp. **A**: General view. Trochophore entodermal intestine is partially everted from the mouth. SEM. **B**: Compound setae (parapodia) of the midregion of the trunk rudiment). SEM. **C**: Detail of parasagittal section, hyposphere and anterior region of the trunk rudiment, semithin section. **D**: Detail of para-

sagittal section, midregion of the trunk rudiment, semithin section. **E**: Detail of the same section, intestine and septa. Col, collar; dsp, septum; int, intestine; lint, intestinal lumen; sgn, segmental ganglion; ylv, yolk-like vacuole. Scales: A = 400 μm, B = 8 μm, C, D = 94 μm, E = 24 μm.

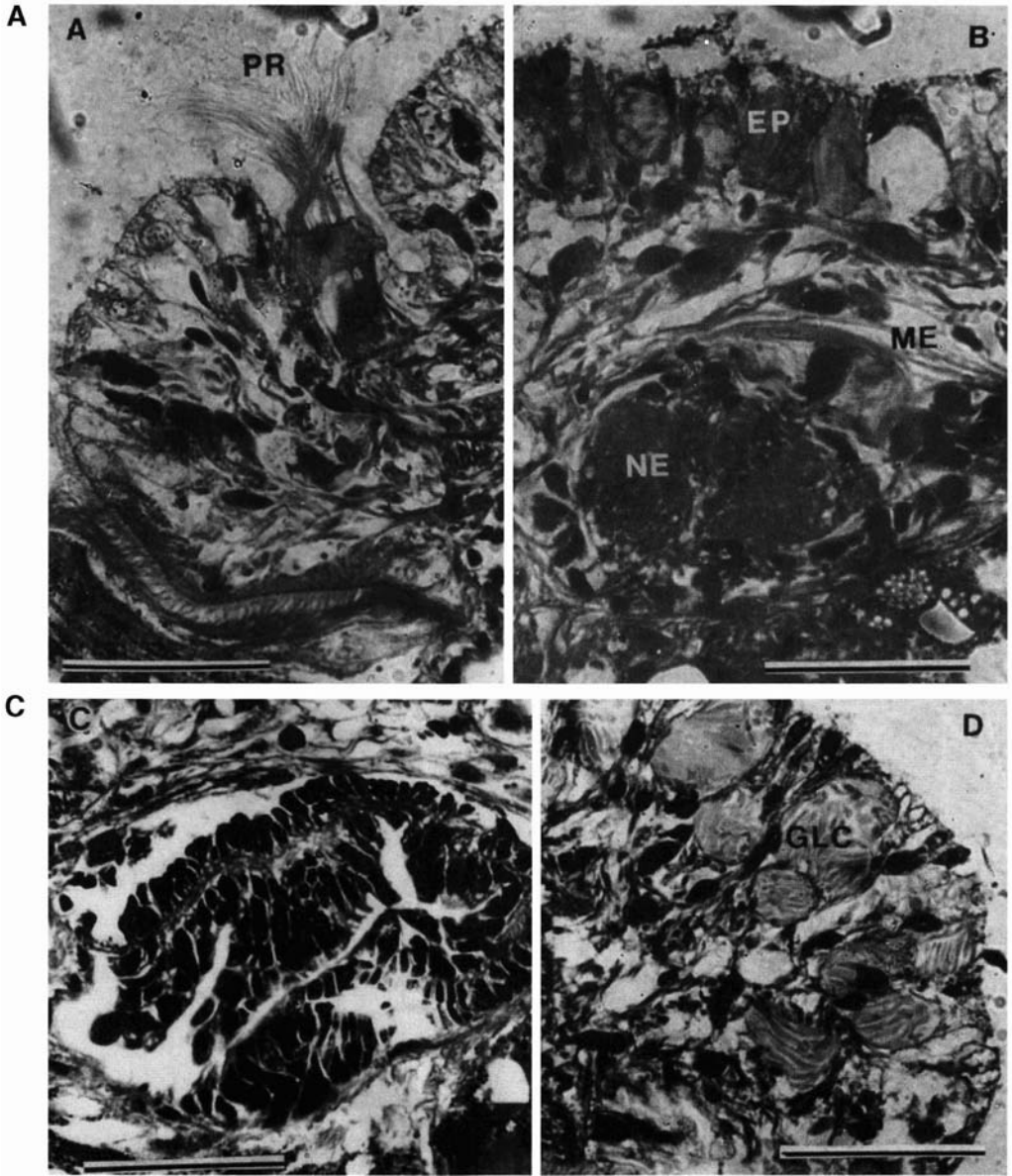


Fig. 6. Larva of Phyllodocidae g. sp. Details of the sagittal section through trochophore region. **A:** Protroch and mouth with entodermal intestine partially everted from the mouth. **B:** Brain. **C:** Proboscis rudiment.

**D:** Gland cells in the epidermis of the trochophore, semithin section. Ep, epidermal epithelium; glc, gland cell; me, mesoderm; ne, neuropil; pr, protroch. Scale = 50  $\mu$ m.

testine, muscular proboscis rudiment, and the brain, passing through the intercellular spaces of the larval body (Figs. 8, 9). Intersegmental septa of the trunk rudiment,

formed by myocytes are only developed ventrally and the coelomic space above the intestine remains open over the length of the entire body.

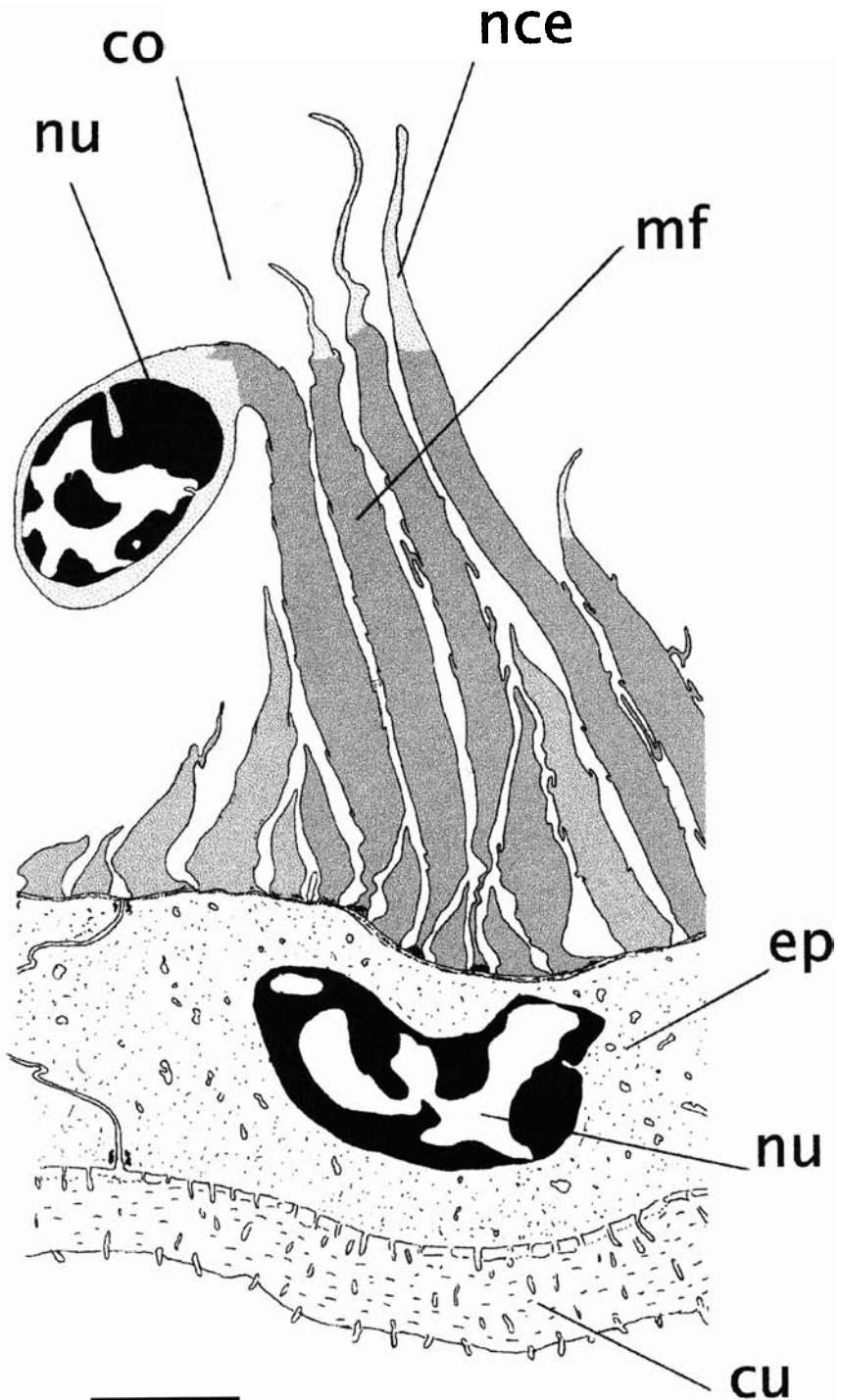


Fig. 7. Larva of Phyllodocidae *g. sp.* Fragment of the body wall of the trunk rudiment, transverse section. Ventro-lateral muscle band (after TEM). Co, body cavity; cu, cuticle; ep, epidermal epithelium; lmc, longitudi-

nal muscle cell; nu, nucleus; mf, contractile part of the muscle cell, nce, noncontractile part of the longitudinal muscle cell. Scale = 1  $\mu$ m.

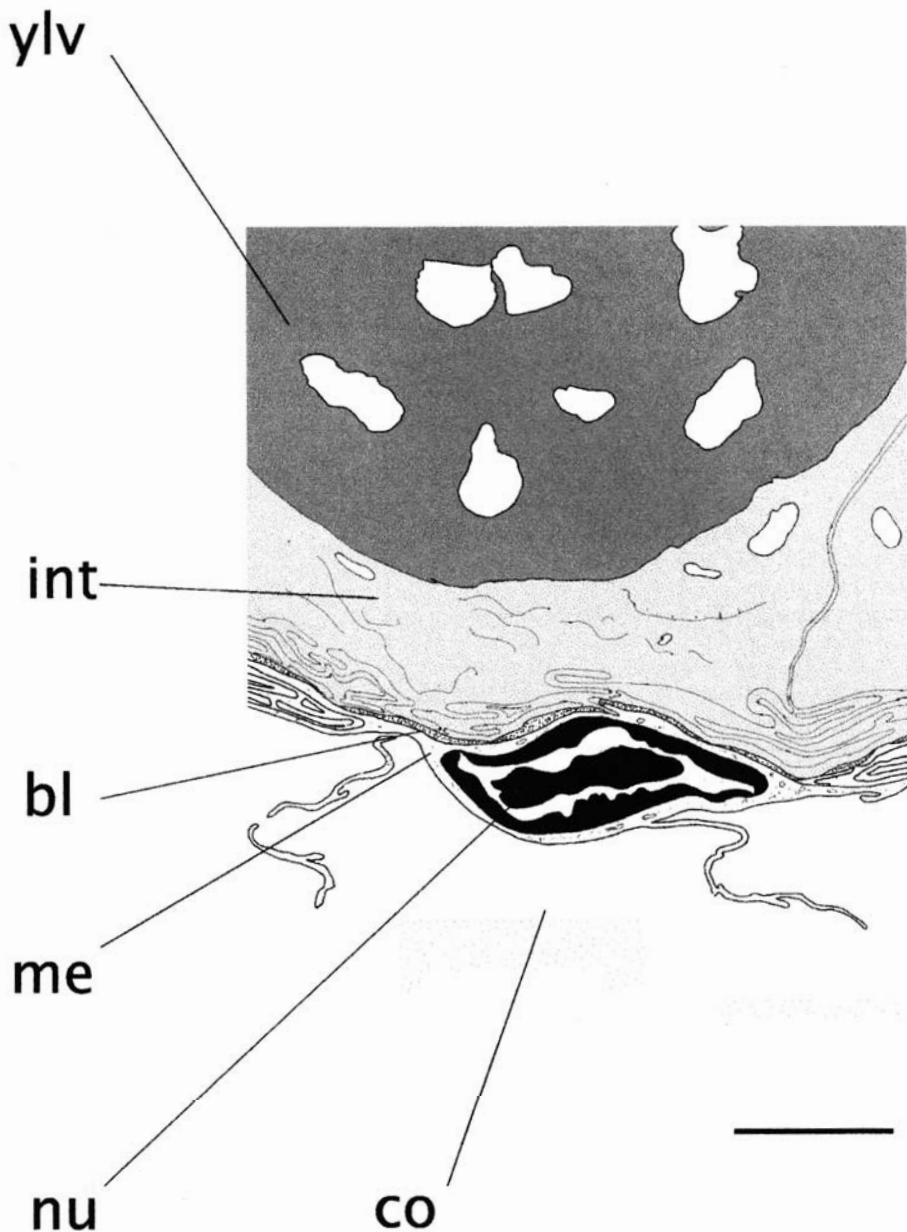


Fig. 8. Larva of Phyllococidae g. sp. Detail of entodermal intestine epithelium with yolk-like vacuoles and mesoderm in the hyposphere of trochophore region. Sag-

ittal section. After TEM. Bl, basal lamina; co, body cavity; int, intestinal cell; me, mesoderm; nu, nucleus; ylv, yolk-like vacuole. Scale = 1  $\mu$ m.

**Excretory system.** A pair of protonephridia is present in the trochophore region of the larva. Each of the 10–15 terminal cells has a cilium surrounded by a filtration weir of 15 microvilli (microvillar rod). Distally, the microvillar rod is surrounded by a proto-

plasmic cap, formed by a nephridial duct wall cell (Fig. 9). Duct cells are ciliated but only extend a few scattered microvilli into the relatively large duct lumen ( $\sim 4 \mu$ m in transection). It was not possible to determine the number of cells forming the chan-

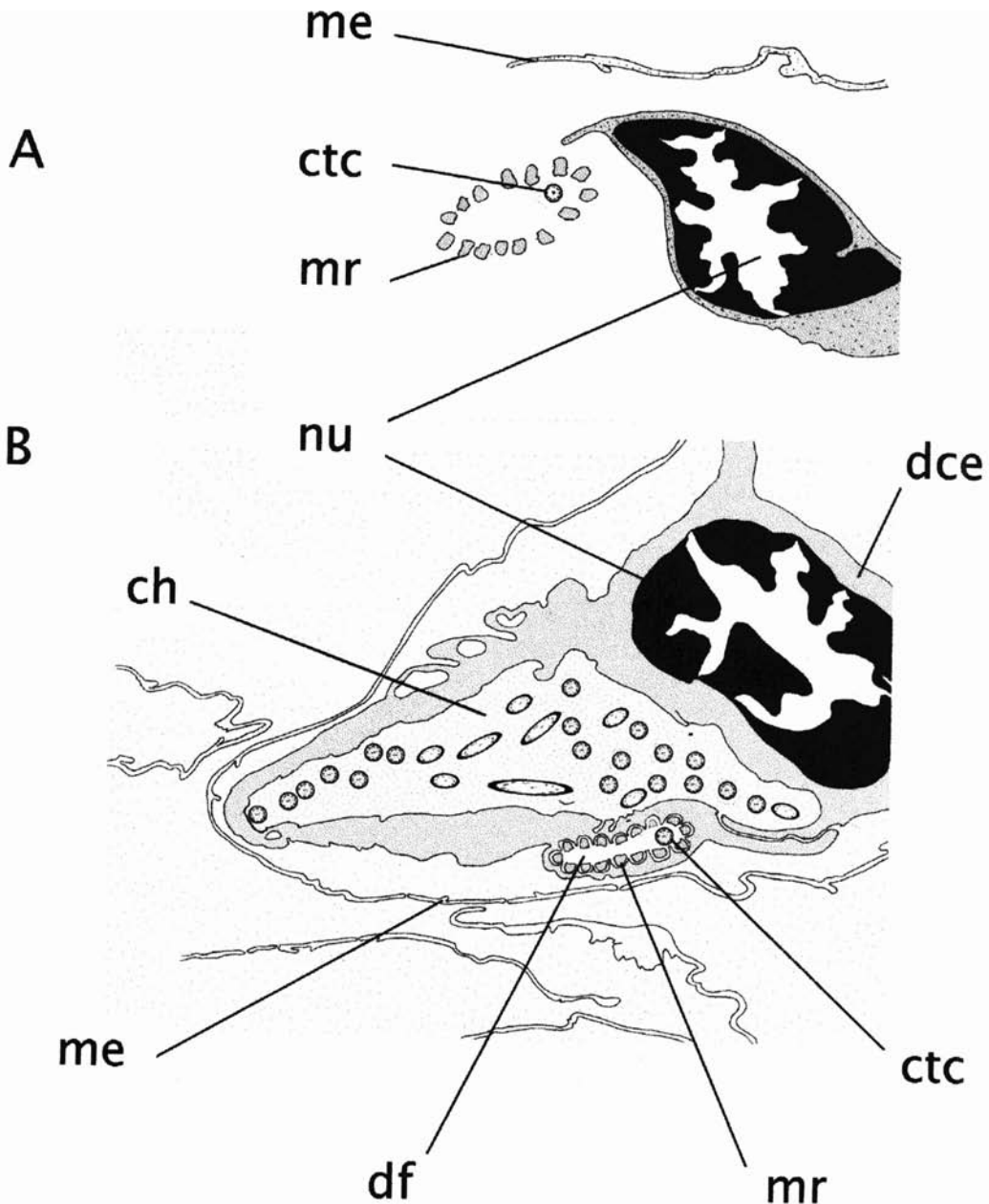


Fig. 9. Larvae of Phyllodocidae g.sp. Details of protonephridium. **A:** Filtration weir and nucleus of terminal cell. **B:** Nephridial duct, transversal section with distal part of the filtration weir surrounded by protoplasmic

cap of the channel cell. After TEM. Ctc, cilia of the terminal cell; ch, channel of the protonephridium; dce, distal duct cell; df, distal part of the filtration weir; me, mesodermal cell; mr, microvillar rod; nu, nucleus. Scale = 1.2  $\mu$ m.

nel. An ECM was not observed associated with the microvillar weir, but this may be artifact. No excretory organs were found in trunk segments.

#### DISCUSSION

Several characters dictate the inclusion of this distinctive pelagic larva in the family Phyllodocidae. These are the position and

structure of the frontal sensory organ; absence of an apical tuft of cilia; a collar, formed by the hyosphere, covering the first setigerous segments of the trunk rudiment (Cazaux, '75, '85; Sveshnikov, '78; Lacalli, '81; Zavarzina and Tzetlin, '86); shape and localization of tentacular cirri on the first three segments (tentacular formula 1-2-1); uniramous parapodia with foliose prominent dorsal cirri and compound heterogomph setae with setal shaft exhibiting numerous long acuminate teeth (Pleijel, '93); and displacement of the first two pairs of segmental ganglia of the ventral nerve cord onto circumesophageal connectives (Lebsky, '70; Ospovat, '78; Eibye-Jacobsen, '93).

Furthermore, the distinctive body cavity, lacking a peritoneum, covered by somatic longitudinal muscles, and exhibiting incomplete septa formed by myocytes, is typical for phyllodocids as is the monolayer of longitudinal myocytes that form the body wall (Zavarzina and Tzetlin, '89; Bartholomaeus, '94; Ivanov and Tzetlin, in prep.). Protonephridia also resemble those reported from phyllodocids: the 14-15 regularly spaced microvillar rods forming the terminal cell weir are identical to protonephridia from the phyllodocids *Eulalia viridis*, and *Phyllodoce (Anaitides) mucosa* and *P. fragilis* examined by Lebsky ('74), Smith and Ruppert ('88), and Bartholomaeus ('89). However, these larvae from the Indian Ocean show an unusual combination of larval and adult features. Normally, nectochaetae of phyllodocids have no more than 10 segments (Sveshnikov, '78; Cazaux, '85) with rudiments of prostomial appendages usually appearing on segments 10-12 (Ospovat, '78), but two cases of polysegmented phyllodocid nectochaetae have been reported, namely, the larvae of *Lopadorhynchus* (see Åkesson, '67) and pelagic larvae of *Phyllodoce sp.* described by Blake ('75). However, the *Lopadorhynchus* larvae have no more than 15 segments and adults have maximally 35. Larvae with 13 segments have the full number of episphaerial antennae and a well-developed muscular axial proboscis. The pelagic phyllodocid nectochaetae found off the Northern California coast by Blake ('75) had up to 22 segments. The larvae with 12-22 segments already had four antennae of the adult type on the episphere and a well-developed muscular axial proboscis.

In contrast, the pelagic larvae described in this study had over 100 segments. They also exhibited several well-developed organs

that correspond to those of adult bottom-dwelling phyllodocids. For example, the brain is subdivided into anterior and posterior regions. The posterior division is connected with eyes and the well-developed neuropil runs to the circumesophageal connectives. All these characters are comparable to those seen in adult *Eulalia viridis* (Lebsky, '70) and rather more complicated than the central nervous system usually present in trochophore and metatrochophore larvae (Åkesson, '67; Ospovat, '78; Lacalli, '88). Furthermore, the paired segmental ganglia are also similar to those of adult *Eulalia viridis* (Lebsky, '70; Ushakova and Evdonin, '84). Tentacular cirri, parapodia, muscle cells of the parapodial complex, and serially arranged muscular elements correspond to those of phyllodocid adults (Pleijel, '93) while prostomial appendages are still absent.

One pair of protonephridia, located in the hyosphere, is typical for phyllodocid trochophores. Normally, these protonephridia disappear in the two-segment-stage metatrochophore, along with the appearance of serial segmental nephridia (Bartholomaeus, '89). Conversely, larvae examined in this study have protonephridia in the hypochere at least until the development of 100 or more segments, which still do not exhibit their own serial nephridia. The protonephridia in the hyosphere more closely resemble adult segmental nephridia of *Phyllodoce mucosa* than they do larval protonephridia (Bartholomaeus, '89) in terms of the number of terminal cells and the diameter and construction of the channel.

Despite well-developed myocytes forming the body wall and incomplete septa, mesodermal cells that surround the intestine both in the trochophore and in the trunk rudiment are nonspecialized cells bearing numerous lamina-like flattened cytoplasmic extensions, typical for larval mesoderm of polychaetes. Basal laminae are weakly developed.

I believe that the planktotrophic larvae undergo two stages of development before settlement occurs: (1) growth of an actively feeding, exceptionally large trochophore and (2) development of the trunk rudiment. If these larvae were lecithotrophic, we would expect the adults to produce large oocytes. However, neither oocytes nor mature eggs with a diameter >1.0 mm have been described from phyllodocids or from polychaetes in general.

In lecithotrophic larvae, yolk material is usually located not only in endoderm but also in tissues of mesodermal origin (Zavarzina and Tzetlin, '91; Tzetlin, in prep.). Yolk-like material was observed in the intestines of actively feeding pelagic trochophores of *Lopadorhynchus* (Akeson, '67). In these larvae, we have only found yolk material in the intestine, not in any other tissues.

The presence of larvae in the coastal area of the Seychelles Islands and the Gulf of Aden and as well as in the area of undersea mounts (Error, Equator) leads me to the suggestion that the unknown benthic adult stage of these phyllodocids inhabits the floor of the shelf and slope zone of the Indian Ocean.

The very large size and unusual pattern of development of the adult body may be an adaptation for an extended pelagic life and a rapid settlement of a species that inhabits the slopes of islands and undersea mountains located far from each other. It is also likely that the delayed appearance of prostomial appendages and the muscular axial proboscis, both structures needed for benthic life or at least for macrophagy, reflect the extensive period of active filter feeding by the pelagic stage. The very few findings of the larvae do not give real matter for comparison with geographical distribution of other midoceanic invertebrate larvae (Scheltema and Rice, '90; Scheltema, '92).

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