



Morphological variation of axial non-muscular proboscis types in the Polychaeta

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Abstract

The fine structure of mouth parts was studied in 19 species from 13 genera belonging to the three families that are known to have a soft non-muscular axial proboscis: Orbiniidae, Opheliidae, and Scalibregmatidae. Four types of mouth structures divergent from the simple non-muscular axial proboscis were found. (1) A bubble-like symmetrical ciliated proboscis was found in both *Ophelia* and *Euzonus*, genera in the subfamily Opheliinae. A similar mouth structure is known for Paraonidae, Capitellidae, and some Maldanidae. (2) A folded symmetrical axial proboscis with well-developed ciliated lobes that form a complicated structure with intricate patterns; the mouth opening is terminal, and the whole structure is symmetrical. Orbiniidae, Scalibregmatidae, and *Travisia* (Opheliidae) have this type. (3) An asymmetrical dorsal lobed proboscis. The plane of asymmetry is dorsoventral. It is a tongue-like lobed or flattened eversible structure. The mouth opening is situated below and behind it. When inverted into the pharyngeal cavity, the entire structure is rooted dorsally. It is found in all studied species of *Ophelina* and *Polyophthalmus* and in *Armandia brevis*. (4) Oral tentacles (about 12 ciliated tentacles). When retracted, the oral tentacles are situated dorsally in the pharyngeal cavity, similar to the folds of an asymmetrical lobed proboscis (type 3). Contractor muscles and vascular vessels are found inside the cavity of the tentacles. This type is found in *Armandia maculata* and *A. leptocirrus*. A tentative scheme of transformation of the soft axial proboscis is presented. Three main trends of proboscis transformation in the Scolecida are discussed: (1) enlargement of the ciliated surface of the proboscis by the development of numerous folds and intricate patterns, (2) appearance of an asymmetrical proboscis, and (3) transformation of the asymmetrical dorsal lobed proboscis into oral tentacles.

Key words: Opheliidae, Scalibregmatidae, Orbiniidae, Polychaeta, axial non-muscular proboscis

Introduction

An axial non-muscular proboscis is present in many of the sand- or mud-swallowing species of Arenicolidae, Maldanidae, Capitellidae, Opheliidae, Orbiniidae, and Paraonidae (Tzetlin & Purschke 2005). These proboscides are composed of epithelial, glandular, and sensory cells but the musculature is weakly developed (Purschke 1988; Saulnier-Michel 1992). Arenicolidae, Maldanidae, and Capitellidae have unciliated epithelia, whereas Paraonidae, Orbiniidae, Scalibregmatidae, and Opheliidae bear cilia on the surface of the proboscis. Eversion of the proboscis is achieved by changes in hydrostatic pressure in the anteriormost compartments of the body cavity. The pressure increase is effected by contractions of the musculature of the body wall and is limited to the anterior part of the body cavity by a strong muscular septum (diaphragm or gular membrane). This structure is found in Capitellidae, Arenicolidae, Opheliidae, and Scalibregmatidae

(Ashworth 1902; Tampi 1958; Purschke & Tzetlin 1996). The proboscis is withdrawn by the activity of retractor muscles.

In this paper we differentiate between the terms “mouth opening” and the opening of the soft axial proboscis (“proboscis opening”). When the proboscis is retracted, the mouth opening is a hollow surrounded by lips that lead to the digestive tract. When the proboscis is everted from the mouth opening, the hollow that leads to the posteriormost parts of the digestive tract (proboscis opening) is located on the top of the axial proboscis.

During ontogeny, individuals of *Arenicola marina* (Linnaeus, 1758) (Arenicolidae) and *Scoloplos armiger* (Müller, 1776) (as well as other Orbiniidae) pass through a juvenile stage possessing dorsolateral ciliary folds and a ventral pharyngeal organ (Eisig 1914; Anderson 1959; Purschke & Tzetlin 1996). Later in development these structures are replaced by axial non-muscular proboscides. Interestingly, in some species of Maldanidae the adults have a foregut with a typically developed ventral proboscis and dorsolateral folds (e.g., *Nicomache minor* Arwidsson, 1906), whereas other species exhibit various stages of development of axial proboscis-like structures in addition to more-or-less reduced ventral pharynges (e.g., *Nicomache lumbricalis* (Fabricius, 1790), *Praxillela praetermissa* (Malmgren, 1865) or even possess only a non-muscular axial proboscis (*Axiothella rubrocincta* (Verrill, 1900) (Tzetlin 1991). A similar situation was observed in the Orbiniidae by Eisig (1914).

Detailed morphological studies are rare and ultrastructural investigations have been made in only one species, *Notomastus latericeus* M. Sars, 1850 (Capitellidae) (Michel 1972; Saulnier-Michel 1992). Anatomical diversity of axial non-muscular proboscides in different families of polychaetes is still poorly known, and perhaps underestimated as a taxonomical character. At least three modifications of the non-muscular axial proboscis are known: (1) an axial bubble-like proboscis with the opening in the middle of the bubble (Maldanidae, Paraonidae) (Tzetlin & Purschke 2005); (2) a lobed axial proboscis as in the Orbiniidae (Anderson 1959) and Scalibregmatidae (Ashworth 1902); and (3) eversible ciliated oral tentacles as in *Armandia leptocirrus* (Tampi 1958) and *Ophelina gaucha* (Elias et al. 2003). It is still not known whether the tentacles (type 3) are a modification of a soft axial non-muscular proboscis or another type, perhaps similar to the mouth tentacles found in many polychaetes (Ampharetidae, Terebellidae, Cossuridae, etc., Tzetlin & Purschke 2005). The distribution of different types of these modifications across families with a soft axial proboscis is not clear. This is especially true for Opheliidae, Scalibregmatidae, and Orbiniidae, while other families like Maldanidae, Arenicolidae, Capitellidae, and Paraonidae are better studied (Tzetlin 1991). The present paper is devoted to the investigation of the structure of the proboscis in a number of species of Opheliidae, Scalibregmatidae, and Orbiniidae in order to understand its morphology and taxonomic value.

Materials and methods

Material studied (Table 1) included 16 species of Opheliidae, Scalibregmatidae, and Orbiniidae from the collections in the National Museum of Natural History (NMNH), Smithsonian Institution, USA. Observations, dissections, and photographs were made using a Wild stereomicroscope equipped with a Nikon digital camera or a Sony DSC717 digital camera. For SEM investigation, specimens were dehydrated by a graded ethanol series, critical-point dried using CO₂, mounted on aluminum stubs, coated with gold, and examined with an Amray 1810, Hitachi 400A. Later, examined specimens were removed from SEM stubs and redeposited in their original tubes with alcohol.

TABLE 1. Material studied.

Abbreviations: NMNH, Smithsonian Institution, National Museum of Natural History; WSBS, Nikolai Pertsov White Sea Biological Station of Moscow State University (*specimens deposited at the WSBS do not have collection numbers).

| Species | Sampling area | Place of storage, lot number* | No. specimens studied |
|---|--|-------------------------------|-----------------------|
| Opheliidae Malmgren 1867 | | | |
| <i>Armandia maculata</i> (Webster, 1884) | Andros Isl., Bahamas, Caribbean Sea | NMNH 43077 | 5 |
| <i>Armandia brevis</i> (Moore, 1906) | San Juan Isl., Friday Harbor, Washington, North Pacific | NMNH 43868, 43872, 43866 | 3 |
| <i>Ophelina acuminata</i> Oersted 1843 | Georges Bank, North Atlantic Ocean | NMNH 168207, 168208 | 6 |
| <i>Ophelina nematoides</i> (Ehlers, 1913) | 51°25'S, 62°45'W, Antarctic Ocean | NMNH 56115 | 5 |
| <i>Polyopthalmus pictus</i> (Dujardin, 1839) | Magdalena Bay, S California, Pacific Ocean | NMNH 20497 | 8 |
| <i>Ophelia verrilli</i> Riser, 1987 | Sheepscot Bay, Maine, North Atlantic Ocean | NMNH 043927 | 2 |
| <i>Ophelia limacina</i> (Rathke, 1843) | White Sea, Arctic Ocean | WSBS | 2 |
| <i>Euzonus micronata</i> (Treadwell, 1814) | Long Bay, Gulf of Alaska, B.C. | NMNH 40729 | 2 |
| <i>Travisia pupa</i> Moore, 1906 | Chesapeake Bay, North Atlantic Ocean | NMNH 43894 | 4 |
| <i>Travisia glandulosa</i> McIntosh, 1879 | Weddell Sea, 61°38'05S, 34°35'W, Antarctic Ocean | NMNH 56367 | 1 |
| <i>Travisia gravieri</i> McIntosh, 1908 | Off New Jersey, North Atlantic Ocean | NMNH 1017302 | 2 |
| <i>Travisia forbesii</i> Johnston 1840 | White Sea | WSBS | 4 |
| Scalibregmatidae Malmgren 1867 | | | |
| <i>Polyphysia crassa</i> (Oersted, 1843) | Gullmar Fjord, Sweden, North Sea | NMNH 074689, 4989 | 4 |
| <i>Scalibregma inflatum</i> Rathke 1843 | Carr Inlet, Washington, USA North Pacific Ocean White Sea, Arctic Ocean Russia | NMNH, 43837 WSBS | 7 |
| <i>Sclerocheilus antarcticus</i> Ashworth, 1915 | South Shetland Island | NMNH 56629 | 5 |
| <i>Sclerobregma branchiata</i> Hartman, 1965 | 40°05'05N, 67°29'10W, Lydonia Canyon, North Atlantic Ocean | NMNH 1018827 | 3 |
| Orbiniidae Hartman 1942 | | | |
| <i>Nainereis setosa</i> (Verrill, 1900) | Tampa Bay, Florida, Atlantic Ocean | NMNH 45612 | 2 |
| <i>Phylo ornata</i> (Verrill, 1873) | Nantucket Sound, Massachusetts, North Atlantic Ocean | NMNH 33872 | 2 |
| <i>Scoloplos armiger</i> (Müller, 1776) | White Sea, Arctic Ocean | WSBS | 3 |

Four additional species were collected in the vicinity of the White Sea Biological Station of Moscow State University (Table 1). Living specimens of *Scalibregma inflatum*, *Ophelia limacina*, *Travisia forbesii*, and *Scoloplos armiger* were examined with a stereomicroscope and photographed with a Canon 400D digital camera; the specimens were later fixed in 4% formaldehyde solution and transferred to ethanol.

Results

Orbiniidae Hartman 1942

All studied specimens have a typical soft axial ciliated proboscis with the opening situated in the center of the everted proboscis. In *Phylo ornata* (Fig. 1A–B) and *Scoloplos armiger* (Fig. 6D) the everted proboscis is greatly folded and multilobed, whereas in *Nainereis setosa* (Fig. 1 C–D) the proboscis surface is more-or-less smooth and flat. No sign of a ventral bulb was found in the mouth apparatus of adult *P. ornata* or *N. setosa*.

Scalibregmatidae Malmgren 1867

All four studied species (*Polyphysia crassa*, *Scalibregma inflatum* (Figs. 1E–G, 6 C) *Sclerocheilus antarcticus*, and *Sclerobregma branchiata*) have a typical soft axial proboscis with the opening situated in the center of the everted proboscis. The proboscis is multilobed, with a clear border between proximal (unciliated) and distal (ciliated) parts (Fig. 1F).

Opheliidae Malmgren 1867

Twelve species of Opheliidae from six genera and all three subfamilies according to Hartman-Schroeder (1971) were investigated (Table 1).

Ophelia. In both *O. verrilli* (Fig. 2A, B) and *O. limacina* (Fig. 2C, D) the protracted proboscis is represented by an axial symmetrical bubble-like structure with a smooth ciliated surface. In living specimens of *O. limacina*, the proboscis was bright red (Fig. 6B).

Euzonus. *E. micronata* also has a symmetrical proboscis with the opening in the center, but its surface is more ornate and had a few lobes (Fig. 2E–F).

Travisia. The proboscis is ciliated, symmetrical, with the opening in the center when everted, folded, and multi-lobed in all four studied species: *T. pupa* (Fig. 3D), *T. grandulosa* (Fig. 3C), *T. gravieri*, and *T. forbesii* (Fig. 3A, B, 6A). The surface of the protracted proboscis is much more ornate than in *Ophelia* and *Euzonus*.

Ophelina. In both *O. acuminata* (Fig. 4A) and *O. nematoides* (Fig. 4D, E) the everted proboscis is a lobed structure covered with cilia. The ventral surface of the proboscis has a median groove, which is well developed in *O. acuminata* and less so in *O. nematoides*. In contrast to the pharynges of *Ophelia* and *Euzonus*, that of *Ophelina* has no opening. The whole structure looks like a tongue pulled out from the mouth. While the appearance of this tongue-like structure is rather different from the symmetrical proboscides of *Ophelia*, *Euzonus*, and *Travisia*, morphologically it is quite similar, being asymmetrical in the sagittal plane. The anterior-dorsal side of the non-muscular proboscis is much larger than the ventral one. The ventral face is very short, so only the dorsal part is in practice eversible. The pharyngeal opening, or mouth, is situated ventrally when proboscis is everted.

Polyophthalmus. *P. pictus* has an asymmetrical proboscis similar to the one found in *Ophelina*, with a flattened ventral surface and a ventral median groove (Fig. 4B). When the proboscis is inverted the pharyngeal organ is located dorsal to the pharyngeal cavity and esophageal lumen (Fig. 4C).

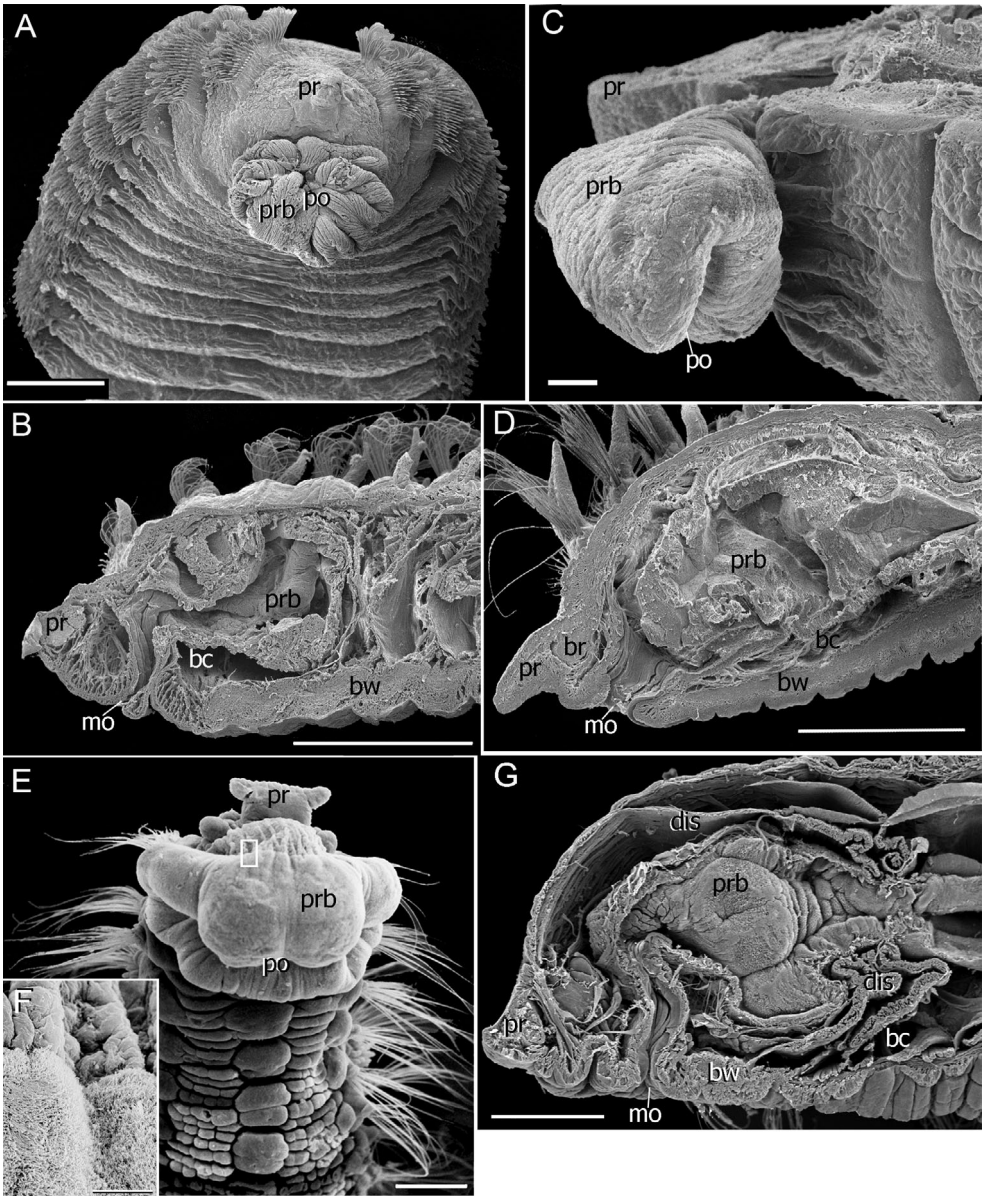


FIGURE 1. SEM. A–B, *Phyllo ornata*. A, anterior-ventral view with proboscis everted; B, sagittal section with inverted proboscis; C–D, *Nainereis setosa*, ventral view of sagittal section with proboscis everted; D, sagittal section with inverted proboscis; E–G, *Scalibregma inflatum*. E, ventral view with proboscis everted, rectangular frame is an area shown on F; F, border between ciliated and unciliated part of the proboscis; G, sagittal section with inverted proboscis. Scale: A, B, D = 1 mm; C = 100 μ m; E = 300 μ m; F = 30 μ m; G = 400 μ m. Abbreviations: bc, body cavity; bw, body wall; br, brain; dis, anterior dissepiments (septa); mo, mouth opening; po, proboscis opening; pr, prostomium; prb, proboscis.

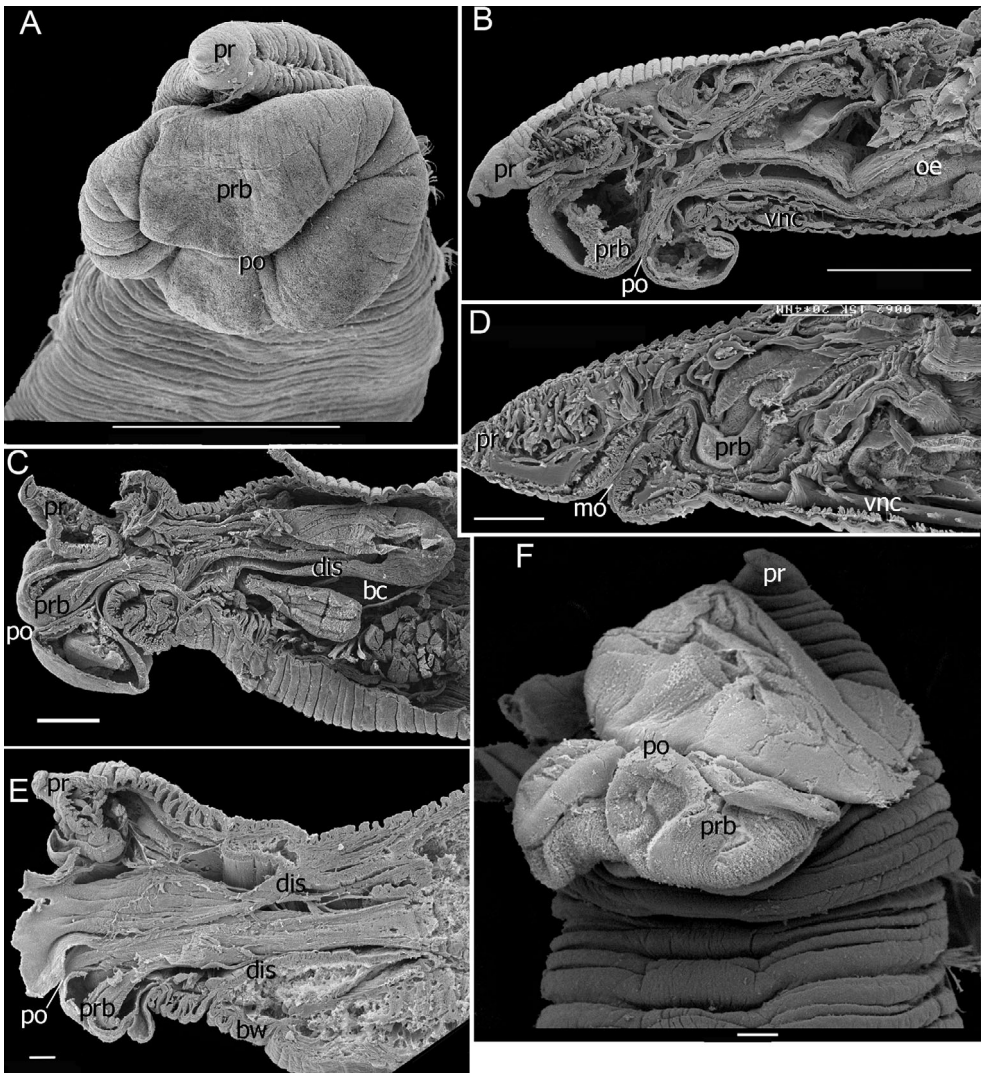


FIGURE 2. SEM. Opheliids with symmetrical bubble-like proboscis. A–B, *Ophelia verrilli*. A, ventral view with proboscis everted; B, sagittal section with proboscis everted; C–D, *O. limacina*. C, sagittal section with everted proboscis; D, sagittal section with inverted proboscis; E–F, *Euzonus micronata*. E, sagittal section with proboscis everted; F, ventral view with proboscis everted. Scale: A–B = 1 mm; C = 500 μ m; D = 200 μ m; E–F, 100 μ m. Abbreviations: bc, body cavity; bw, body wall; dis, anterior dissepiments (septa); mo, mouth opening, oe, esophagus; po, proboscis opening; pr, prostomium; prb, proboscis; vnc, ventral nerve cord.

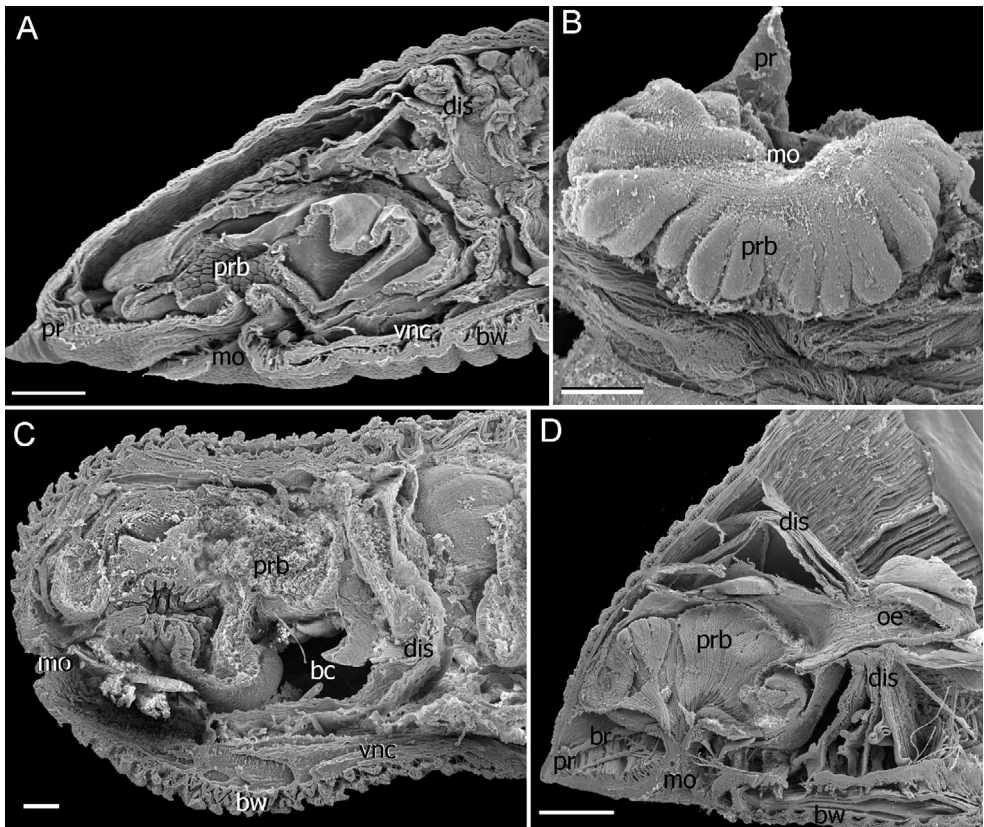


FIGURE 3. SEM. A–B, *Travisia forbesii*. A, sagittal section with inverted proboscis; B, dissection of anterior part, view of proboscis from the body cavity; C, *T. granulosa*, sagittal section with inverted proboscis; D, *T. pupa*, sagittal section with inverted proboscis. Scale: A = 300 μ m, B = 400 μ m, C = 100 μ m, D = 1 mm. Abbreviations: bc, body cavity; bw, body wall; br, brain; dis, anterior dissepiments (septa); mo, mouth opening; oe, esophagus; po, proboscis opening; pr, prostomium; prb, proboscis; vnc, ventral nerve cord.

Armandia. A. brevis has an asymmetrical lobed proboscis with a flattened ventral surface and well-developed median groove (Fig. 5 D, E), quite similar to that seen in *Ophelina* and *Polyopthalmus*.

In *A. maculata* the mouth parts are represented by a number (about 12) of ciliated tentacles rooted dorsally in the pharyngeal cavity. Muscles and vascular vessels were seen inside the tentacle cavity. Cilia are concentrated laterally along the tentacles, while the ventral and dorsal surfaces of the tentacles do not bear cilia. The tips of the tentacles are also ciliated (Fig. 5A–B). When protracted the tentacles are everted from the mouth opening. When retracted they are located inside the pharyngeal cavity dorsal to the mouth and esophageal opening (Fig. 5C).

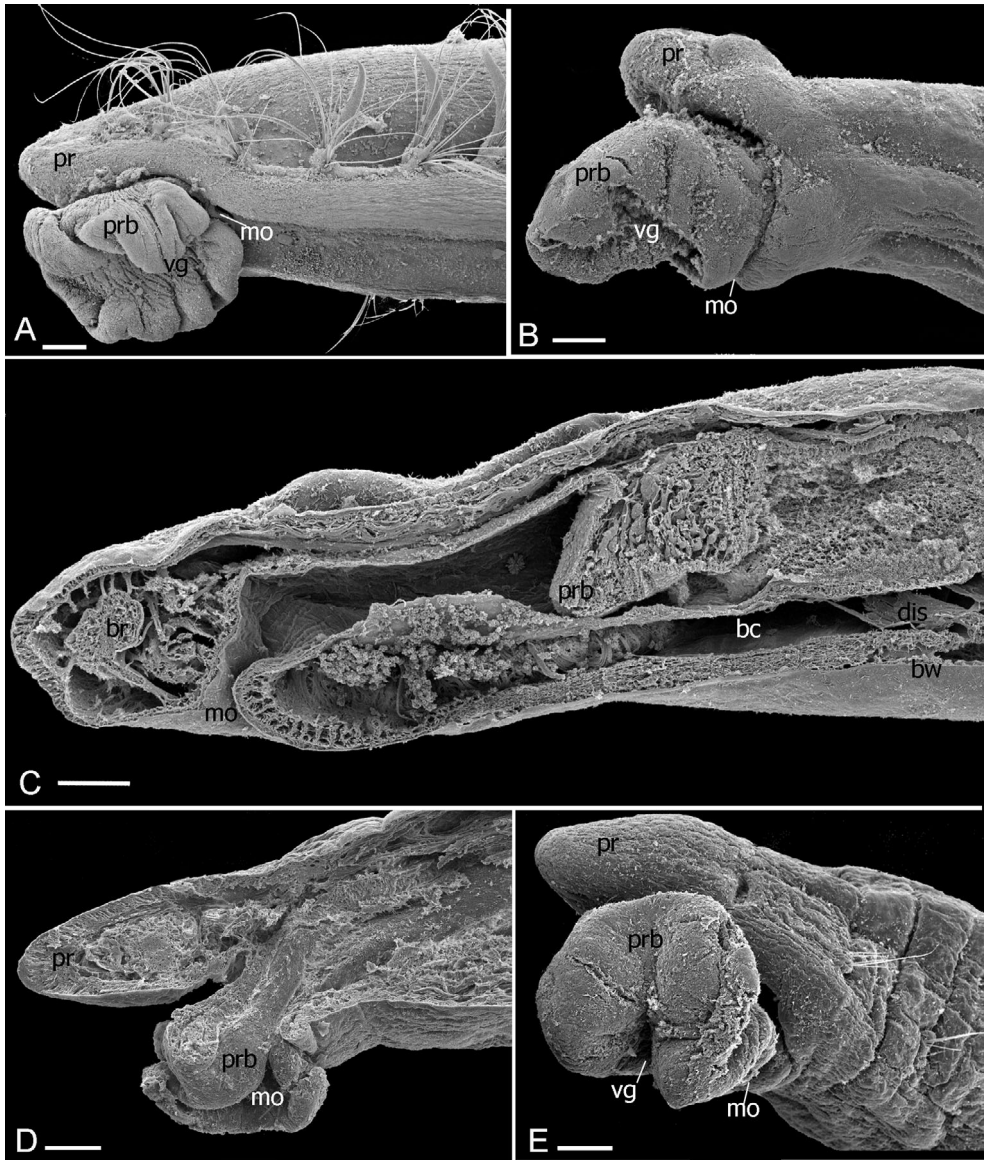


FIGURE 4. SEM. A, *Ophelina acuminata*, ventrolateral view with everted proboscis; B–C, *Polyophthalmus pictus*. B, ventrolateral view with everted proboscis; C, sagittal section with inverted proboscis; D–E, *Ophelina nematoides*. D, sagittal section with partially everted proboscis; E, ventrolateral view with everted proboscis. Scale: A = 200 μ m, B–E = 100 μ m. Abbreviations: bc, body cavity; bw, body wall; br, brain; dis, anterior dissepiments (septa); mo, mouth opening; oe, esophagus; po, proboscis opening; pr, prostomium; prb, proboscis; vg, proboscis ventral median groove.

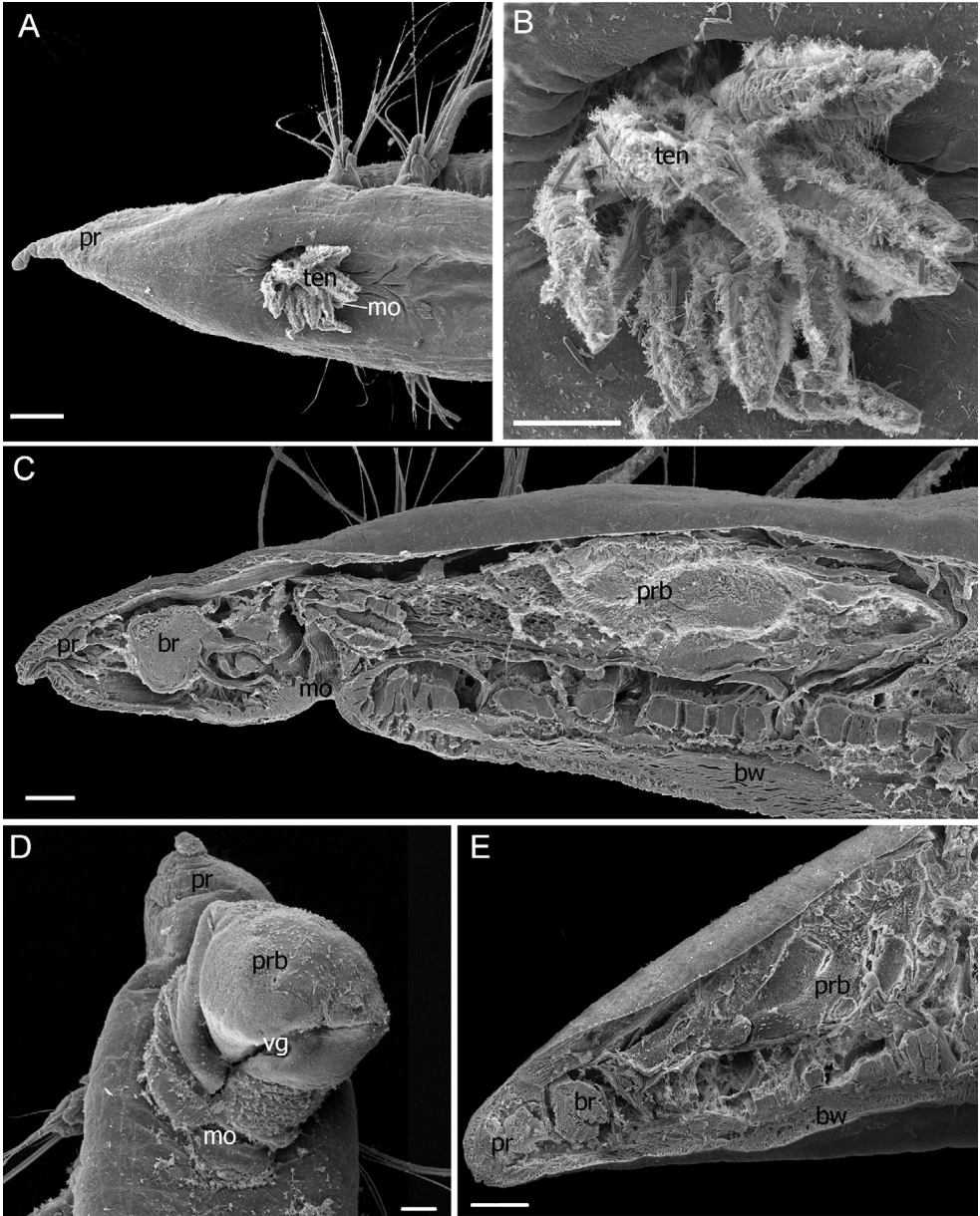


FIGURE 5. SEM. A–C, *Armandia maculata*. A, ventral view with everted tentacles; B, tentacles enlarged; C, sagittal section with inverted tentacles; D–E, *A. brevis*. D, ventral view with proboscis everted; E, sagittal section with inverted proboscis. Scale: A, E = 200 μ m, B–D = 100 μ m. Abbreviations: bw, body wall; br, brain; mo, mouth opening; ten, oral tentacles; pr, prostomium; prb, proboscis; vg, proboscis ventral median groove.

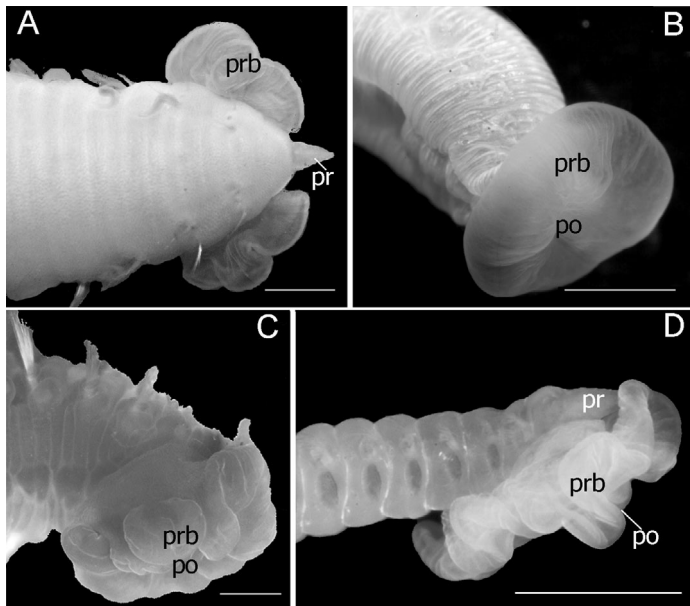


FIGURE 6. Live specimens with everted proboscis. A, *Travisia forbesii*, dorsal view; B, *Ophelia limacina*, lateral view; C, *Scalibregma inflatum*, lateral view; D, *Scoloplos armiger*, lateral view. Scale: A–D = 500 μ m. Abbreviations: pr, prostomium; po, proboscis opening; prb, proboscis.

Discussion

The fine structure of mouth parts was studied in 19 species from 13 genera belonging to the three families that have previously been described as taxa with soft non-muscular axial proboscides. These data demonstrate that in fact such taxa include a number of divergent proboscis types (Fig. 7).

1. A bubble-like symmetrical ciliated proboscis (Fig. 7A). This simplest type, which corresponds to the original image of a soft axial proboscis, was found in species of both *Ophelia* and *Euzonus*. Paraonidae, Capitellidae, and some Maldanidae have a similar mouth structure but without cilia (Tzetlin & Purschke 2005).

2. A folded symmetrical axial proboscis (Fig. 7B). This type is very similar to the first, but it has well-developed ciliated lobes, which form a very complicated structure with intricate patterns and motifs. Orbiniidae, Scalibregmatidae, and *Travisia* have this type.

3. An asymmetrical dorsal lobed proboscis (Fig. 7C). The plane of asymmetry is dorsoventral. This type was found in all studied species of *Ophelina*, *Polyophthalmus*, and *Armandia brevis*. It is a tongue-like lobed or flattened eversible structure. The mouth opening is situated ventrally and posteriorly relative to it. When inverted into the pharyngeal cavity the entire structure is rooted dorsally. Protraction of this structure is most probably achieved by changes in hydrostatic pressure in the pre-diaphragmal compartment of the body cavity. All studied representatives of Ophelininae—*Ophelina*, *Polyophthalmus*, and *Armandia*—have three well-developed muscular septae in the anterior part of the body at the posterior edges of segments 2, 3, and 4 (Tampi 1958; unpubl. data).

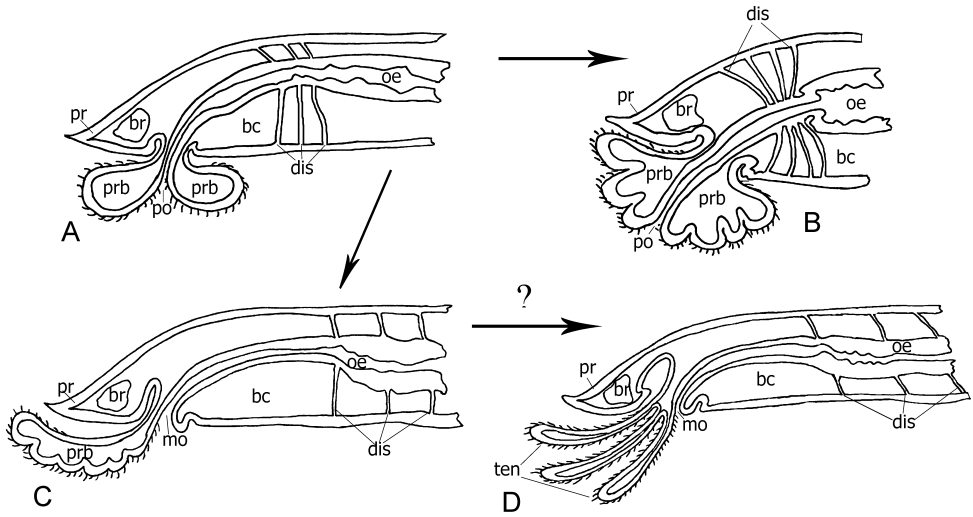


FIGURE 7. Scheme of transformation of axial non-muscular proboscis. A, bubble-like symmetrical ciliated proboscis; B, folded symmetrical axial proboscis; C, asymmetrical dorsal lobed proboscis; D, oral tentacles. Abbreviations: bc, body cavity; br, brain; dis, anterior dissepiments (septa); oe, esophagus; ten, oral tentacles; po, proboscis opening; pr, prostomium; prb, proboscis.

4. Oral tentacles (Fig. 7D). Originally these tentacles were described by Tampi (1958) in his detailed study of *Armandia leptocirrus*. Surprisingly his description was not used by any of the authors who worked on the taxonomy of Opheliidae. Until now we have not had any observations on how these tentacles work in the living organism. Based on their structure, the protraction of the oral tentacles from the mouth probably is accomplished by the extra hydraulic pressure in the pre-septum coelomic compartment, similar to that which takes place in proboscideal types 1–3. When retracted oral tentacles are situated dorsally in the pharyngeal cavity, similar to the folds of an asymmetrical lobed proboscis. Similarly, contractor muscles and vascular vessels are found inside the cavity of the tentacles. Thus, the suggestion that oral tentacles originate from the folds of asymmetrical dorsal lobed proboscis is the simplest hypothesis. Oral tentacles might be present in other Ophelininae. For example, Elias et al. (2003) described a lobed proboscis for *Ophelina gaucha*, but in their illustrations (fig. 2a, c), one can see both a tongue-like structure and oral tentacles.

A tentative scheme of transformation of a soft axial proboscis is presented in Fig 7. Three main trends of proboscis transformation can be noted: (1) enlargement of the ciliated surface of the proboscis by the development of numerous folds and intricate patterns, as seen in *Travisia*, Scalibregmatidae, and Orbiniidae; (2) appearance of an asymmetrical proboscis (Ophelininae); and (3) occurrence of the oral tentacles (a few species of *Armandia*, and at least one species of *Ophelina*). The origin of oral tentacles is still unclear, since they are found in two genera of Ophelininae, both genera that also include species with another type of proboscis (asymmetrical type). Furthermore this character could be used as a character in general diagnostic of Ophelininae.

The appearance of oral tentacles rooted on the posterior dorsal zone of the pharyngeal cavity in several species of Ophelininae is rather interesting in relation to the feeding apparatus of Cossuridae described by Tzetlin (1994). The last consists of about 15 buccal tentacles with long cilia. They are situated on the dorsal surface of the spacious buccal cavity, near the esophageal opening. Unlike the oral (buccal) tentacles in *Armandia*, the ones in *Cossura* have no large coelomic space inside, but are filled with muscle cells and their cytoplasmic extensions. There are no direct observations of the feeding behavior of *Cossura* (Dorgan et al. 2006) and we do not know the details of the mechanics of protraction of its oral tentacles. Indeed the general similarity of mouth structures in *Armandia* and *Cossura* is significant. Further investigation of ultrastructure of proboscides is required to clarify the interrelationships of Opheliidae and Cossuridae.

In contrast to the conclusions reached by Sene-Silva et al. (2007) based on a cladistic analysis of the external morphological characters of the Opheliidae, the study of mouth parts in Opheliidae supports the traditional system of Opheliidae with three subfamilies (Hartman-Schroeder 1971). Ophelinae are characterized by a soft axial bubble-like proboscis, Travisiniinae have a lobed axial proboscis, and Ophelininae have either an asymmetrical lobed proboscis or oral tentacles situated in the same way as lobed structures. Further anatomical studies with a wider sampling of taxa are definitely required to use these characters for phylogenetic analysis.

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