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HANDBOOK OF ZOOLOGY

Günter Purschke, Markus Böggemann, Wilfried Westheide (Eds.)

ANNELIDA

Günter Purschke, Markus Böggemann, Wilfried Westheide (Eds.)

PLEISTOANNELIDA, SEDENTARIA III AND ERRANTIA I

VOLUME 3

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Handbook of Zoology
Annelida

Volume 3:
Sedentaria III, Errantia I

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Handbook of Zoology

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Annelida

Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

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Foreword

Annelida, the segmented worms, comprise one of the most important taxa of invertebrates occurring in marine, fresh water and terrestrial environments. Especially the marine forms, commonly called polychaetes, are one of the most widespread, abundant and diverse elements of the world benthic marine fauna. Although only comprising somewhat around 21,000 described species, annelids show a remarkable diversity in form and function. This diversity mirrors the plasticity of their bauplan or, more precisely, their segmentation constituting prostomium, followed by a number of primarily identical segments, and the pygidium. The prostomium usually includes the brain and the most important sensory structures, the segments are equipped with lateral appendages, the parapodia, and the pygidium characterized by a pre-pygidial budding zone. In the parapodia, generally used for locomotion, another annelid key-character may be found, the chaetae, made up of β–chitin. New segments may be formed through the entire life span and consequently their number vary around a mean in adults or may be fixed. Species are usually of median size and do not exceed a few cm in length. However, their range is much wider; some interstitial annelids belong of the smallest adult metazoans known while others reach body lengths of more than 3 m. The number of segments varies accordingly from less than ten to several hundred. Deviations from this sketched plan of organization are legendary and may comprise all parts of the body including segmentation and chaetae. The marine forms often show broadcast spawning and primarily their life cycle comprises an acoelomate planktonic larva, the trochophore, and a coelomate benthic adult. Others show internal fertilization and direct development. Annelids use a wide range of food sources and feeding habits range from microphagous suspension feeding to predation as well as to a few cases of mutualism with endosymbiotic bacteria, parasitism or parenteral nourishment. Besides plasticity of segmentation, their reproductive and feeding biology are most likely the main reasons for the diversity observed in annelids. Consequently, several annelid groups have not even been recognized as members of this group and were treated as separate phyla in the past.

Annelida is an ancient group and its evolutionary origin can be traced back to the Cambrian. Together with its diversity this ancient origin made it extremely difficult to clarify their evolutionary history. The traditional classification and subdivision of Annelida into Polychaeta, Oligochaeta and Hirudinea – the later united as Clitellata – does not reflect their phylogenetic systematization. After a scientific debate lasting for several decades, the first robust phylogenetic hypotheses, using phylogenomic data, were published just about 10 years ago. These and follow-up studies confirmed that polychaetes constitute nothing else but a paraphyletic assemblage of the more or less plesiomorphic Annelida. The same applies for the oligochaetes representing a basal grade of Clitellata. Therefore, polychaetes are now seen as those annelids that do not possess a clitellum. The annelid phylogenetic tree possesses a so-called basal radiation consisting of a few taxa and two major branches including the vast majority of Annelida, Errantia and Sedentaria, united as Pleistoannelida. In a highly derived position Sedentaria now also comprise Clitellata. Thus, phylogenomic analyses led to resurrection of two traditional taxa albeit with somewhat different taxon composition. Ironically, exactly these two groups were thought not representing monophyletic units during the last decades. In addition, some taxa which were regarded to represent separate phyla turned out to be nothing else but true Annelida, although being morphologically highly derived especially with respect to one of the so-called key characters, segmentation. These taxa are Sipuncula, Myzostoma, Pogonophora and Echiura, which are now placed in different positions in the phylogenetic tree of Annelida. Most recently another even more aberrant group of unknown affinities was shown to be part of the annelid tree as well: Orthonectida. This fact impressively demonstrates the adaptive capacity and potential of the annelid bauplan. It is hoped that these former phyla will be reduced in rank to family level; this happened to Pogonophora now known as Siboglinidae and next are Echiura which in the future may be found as Thalassematidae.

The vast majority of polychaete species is marine; here they are dominant members of the epi- and endobenthos but there are also a few holopelagic species. Polychaetes comprise one of the most important groups of invertebrates in the marine food webs where they can be found in almost every habitat, often in high abundances. In addition, a few polychaete species managed to colonize even freshwater and terrestrial realms. Other polychaetes occur in comparatively extreme environments from hydrothermal vents at the ocean floor spreading centres to the terrestrial ground water. In contrast to polychaetes, the mainly limnetic and terrestrial clitellate oligochaetes are structurally uniform; nevertheless, Clitellata is a comparatively speciose and ecologically very important group.

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With global human activities and climate change distribution patterns of many species are subjected to dramatic changes. As a consequence certain introduced species turned out to become pests with often fatal impact for the original ecosystems.

The Annelid volume of the first edition of the Handbook of Zoology appeared in the years between 1928 and 1934, edited by W. Kükenthal and T. Krumbach. Especially the anatomical part still serves as a valuable resource of knowledge. However, since then our knowledge on annelids broadly increased. Although several reviews on annelids have been published, they usually cover only special topics. So around the year 2010 the idea was born that a new edition of this very successful work would be urgently needed. Very soon it turned out to be impossible to write a handbook in its strict sense treating morphology, anatomy, reproduction, development, ecology, phylogeny and taxonomy on this group of animals in a single volume. Even more than in former times today such a task could not be achieved by a single person or just by a few authorities and so we began looking for authors who could contribute to such a big effort. Unfortunately, we had to learn that for many annelid groups specialists did not exist in the scientific zoological community or were not available for various reasons. Therefore, it took much longer than originally planned to compile the manuscripts and in spite of our efforts there will remain a few gaps of missing chapters. This is the reason why currently only the polychaetes will be treated in the handbook. It was a great advantage that each chapter ready for publication was published electronically as Zoology Online so that the chapters are available for the scientific community quite soon after acceptance. All contributions were peer-reviewed and revised prior to publication.

Finally in the beginning of 2019 it was possible to publish the first volume on annelids (Basal groups and Sedentaria I) followed by the second volume covering Sedentaria II in the same year. Now about one year later the third out of four planned volumes can be published. Since we try to keep as up-to-date as possible with scientific progress, we roughly follow the new phylogeny in arrangement of the taxa treated in the various chapters, each of which is generally devoted to a single family. We are well aware of the fact that such a phylogeny is nothing else but a hypothesis which, on our current knowledge, best explains the phylogeny or evolution of a certain group. There are more than 100 families of annelids and the systematic position has not been solved for every taxon resulting in many open phylogenetic questions. Some taxa may now appear in a position that might be suspected to future changes, which, however, does not interfere with the information content of such a chapter.

This third volume covers the third part of Sedentaria completing the Sabellida/Spionida clade and containing the clade Terebellida/Arenicolida. These are followed by two taxa under discussion and here classified as *incertae sedis*: Diurodrilidae and Nerillidae. The volume continues with the first part of Errantia: Myzostoma, Protodriliformia and Eunicida I. The fourth and last volume will complete the cade Errantia with the remaining Eunicida and Phyllodocida.

Although currently the Corona pandemic also casts a heavy cloud over scientific life and workflow, all people involved managed to publish this volume with only slight delay from the originally designed deadline. At this place, we would again like to thank all authors that have contributed to this volume of the Handbook of Zoology; they have done an excellent job. The work of the various reviewers is gratefully acknowledged; reviewing scientific manuscripts always takes a considerable amount of working time, especially because some chapters on larger groups are voluminous. Nonetheless their helpful suggestions for improvements helped keeping the scientific standard as high as possible. Last not least we thank the lectors and employees of our publisher DeGruyter for their endless help and fruitful discussions during the publishing process.

Günter Purschke, Wilfried Westheide,
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Osnabrück, Wallenhorst and Vechta, Germany,
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Andreas Bick

7.4 Sedentaria: Spionida/Sabellida

7.4.8 Fabriciidae Rioja, 1923

Introduction

Fabriciidae Rioja, 1923 consists of semisedentary, tube-dwelling polychaetes that inhabit different types of substrates in brackish, marine, and even freshwater environments. Most species occur in intertidal and subtidal areas, although one species is known from the continental shelf and at least two not-yet-described species are known from the deep sea of the southwest Atlantic Ocean. Approximately 80 nominal species have been described and classified into 17 genera (WoRMS 2020). Only a few diagnostic characters exist at the generic and specific levels, making identification difficult.

Fabriciidae constitutes a monophyletic clade within Sabellida. Fabriciid fan worms were initially placed within Sabellidae until Kupriyanova and Rouse (2008) showed that assignment would mean that Sabellidae is paraphyletic. Consequently, they were removed from Sabellidae, and Fabriciidae is regarded as a sister taxon of Serpulidae (Capa et al. 2011, Huang et al. 2011, Struck 2011) or, more recently, as sister taxon of a Sabellidae/Serpulidae clade (Tilic et al. 2020).

Like all members of Sabellida, Fabriciidae possesses a radiolar crown that extends outside of its tubes and is used for feeding, tube construction, and respiration. The body has a distinct thoracic region and an abdominal region indicated by chaetal inversion; i.e., different types of capillary chaetae are present on the thoracic notopodia and abdominal neuropodia, and a range of uncini exist on the thoracic neuropodia and abdominal notopodia. In contrast to the great disparity within Sabellidae and Serpulidae, that within Fabriciidae is rather low. Fabriciids usually have three pairs of radioles and a constant number of eight thoracic and three (two or four in exceptional cases) abdominal chaetigers. The thoracic uncini always exhibit a long handle with a rostrum or main fang, and the abdominal uncini exhibit a short handle without a rostrum.

The tubes of Fabriciidae consist of simple secretions and can be abandoned quickly and regularly. Individuals are able to move within the substrate or even swim. They usually crawl with the posterior end in front, whereas the tentacular crown is folded up and dragged behind. Their pygidial eyes (present in most species) are then used for optical orientation.

These worms employ their radiolar crown to filter particles from the water or sweep the sediment surface (Lewis 1968a). All fabriciids are gonochoristic and intratubular brooders with direct larval development (e.g., Leidy 1883, Forsman 1956, Lewis 1961, Muus 1967, Rassmussen 1973, Bell 1982, Nausch 1988, Bick 1996, Nishi 1996, Rouse and Fitzhugh 1994).

Some species are dominant or subdominant members of benthic communities and may form dense populations with more than 1 million individuals per square meter (Lewis 1968b, Light 1969, Bagheri and McLusky 1982). Brood protection reduces the dispersal and mortality of the larvae and thus increases the probability of settling in a suitable habitat. This is one major reason for the high abundances of these species in addition to the availability of a rich food supply.

The comprehensive work on this group consists of a series of taxonomic papers by Banse (1956, 1957, 1959a, b) and particularly by Fitzhugh (e.g., Fitzhugh 1983, 1989, 1990a, b, c, d, e, 1991a, b, 1992a, b, 1993, 1995a, b, 1996, 1998, 2001, 2002, Fitzhugh et al. 1994).

The present review of Fabriciidae includes information on the morphology, biology, ecology, and distribution of this group compiled from relevant literature and new unpublished observations. The current taxonomic status of its genera and species is mainly derived from the World Register of Marine Species (WoRMS), complemented by own unpublished data.

Morphology

External morphology

Most fabriciids are shorter than 5 mm (Fig. 7.4.8.1). The largest species are *Manayunkia godlewskii* Nusbaum, 1901 and *Pseudofabriciola capensis* (Monro, 1937), with lengths of approximately 16 and 10 mm, respectively (Nusbaum 1901a, Fitzhugh 1991a). The smallest species is *Fabriciola minuta* Rouse, 1996, with a length of less than 1 mm.

Radiolar crown. Fabriciidae species possess a radiolar crown, also referred to as the branchial or tentacular crown, with three pairs of radioles (Figs. 7.4.8.1, 7.4.8.2). The development of the radiolar crown during ontogenesis usually starts with three pairs of radioles in many members of Sabellidae and Serpulidae, which may represent the plesiomorphic character state within Sabellida, and ontogenesis could recapitulate phylogeny in this case. The crown is a residue of the largely reduced prostomium. It originates from two branchial lobes that are clearly separated from each other (also observed in Serpulidae; but fused in Sabellidae). The radiolar crown is homologous to the prostomial palps of other polychaetes

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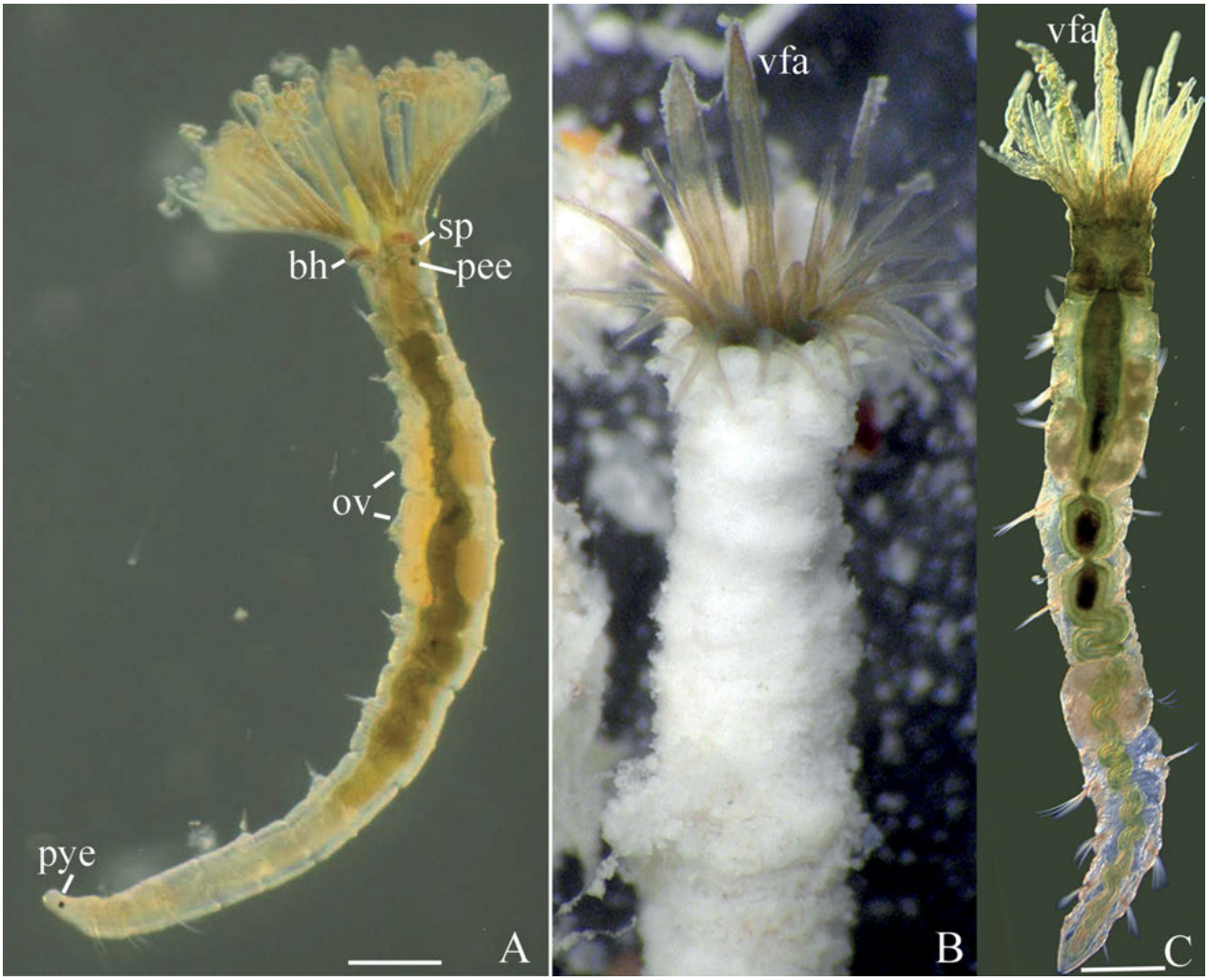


Fig. 7.4.8.1: Micrographs of live specimens. A, *Fabricia stellaris* (Müller, 1774) from the Baltic Sea; B, C, *Manayunkia athalassia* Hutchings, Deckker & Geddes, 1981 from South Australia. Micrographs by A. Dietrich (A) and G. Rouse (B, C). bh, branchial hearts; ov, oocyte-bearing chaetigers; pee, peristomial eyes; pye, pygidial eyes; sp, spermatheca; vfa, ventral filamentous appendages. Scale bars: A = 200 µm, C = 500 µm.

(Orrhage 1980). Secondary branches, usually referred to as pinnules, are present on the radioles of Sabellida. Randel and Bick (2012) have shown that the "pinnules" of Fabriciidae are completely different structures in comparison to those of Sabellidae and Serpulidae. The branches of the radioles of Fabriciidae are formed by the successive longitudinal splitting of the radioles (Figs. 7.4.8.2A, B, D, 7.4.8.3A–D). As a result, the width of the radioles decreases from proximal to distal. All branches terminate approximately at the height of the main branch, which means that the basal branches are distinctly longer than the distal branches. The symmetrical branching of the radioles leads to bipectinated radioles, as found in most genera of Fabriciidae (Figs. 7.4.8.2D, 7.4.8.3C, D, 7.4.8.4F), whereas pectinated radioles are the result of asymmetrical branching, as observed in *Manayunkia* (Figs. 7.4.8.2A–C, 7.4.8.3A, B, 7.4.8.4A–E). The ultrastructure of the two types of radioles is also different (see Internal morphology section). In contrast, the radioles of Sabellidae and Serpulidae do not split along their length (Fig. 7.4.8.3E–G). Therefore, the width of the radioles is only slightly different from the proximal to distal regions. The pinnules on the radioles of Serpulidae and Sabellidae could be an evolutionary novelty (Fig. 7.4.8.3E–G). They exhibit approximately the same length along the respective radioles. The length of the radioles usually exceeds that of the pinnules. Although the pinnules exhibit a similar function in Sabellida, this term should not be used for Fabriciidae because of their different origin and convergent development within Sabellida.

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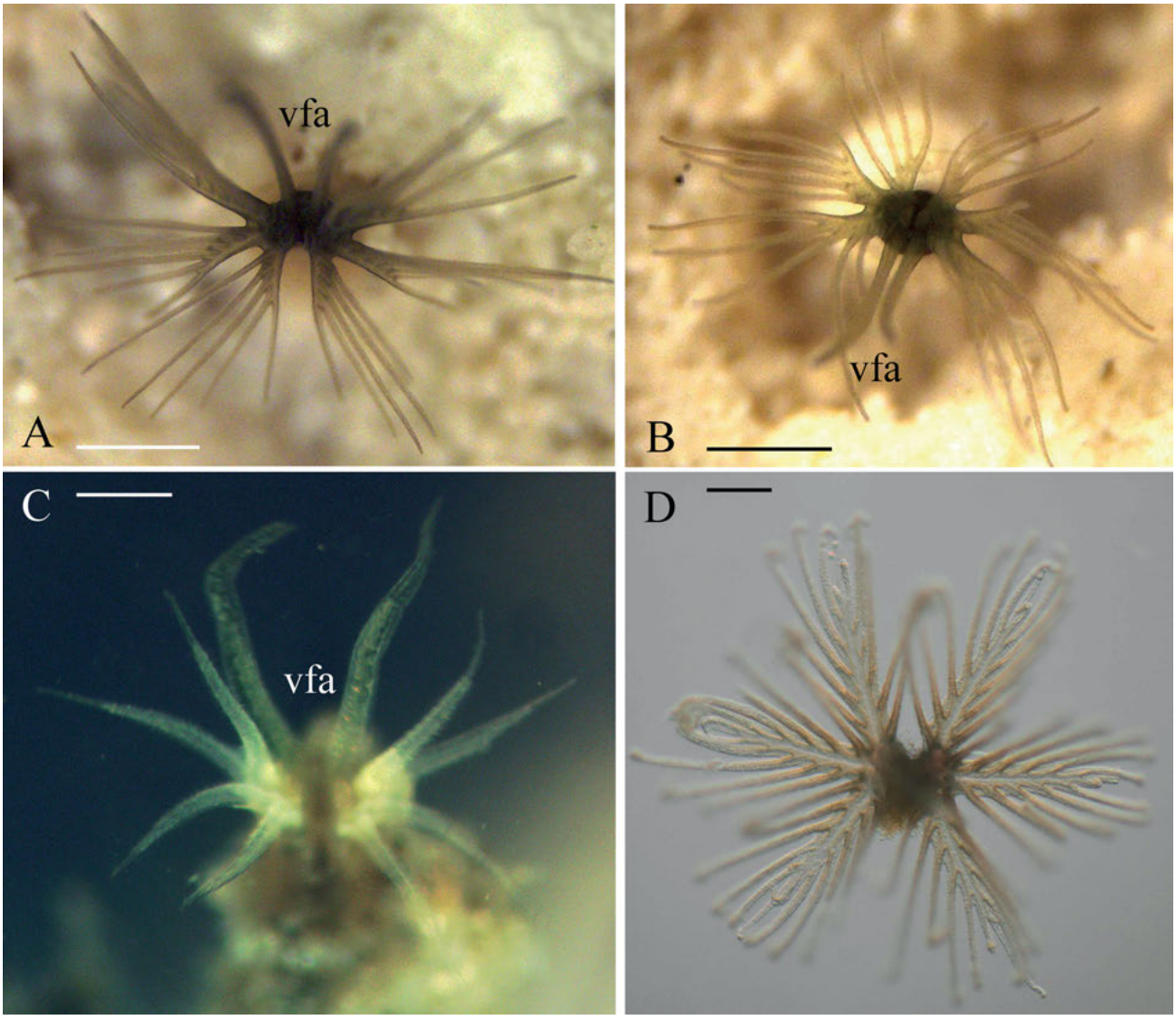
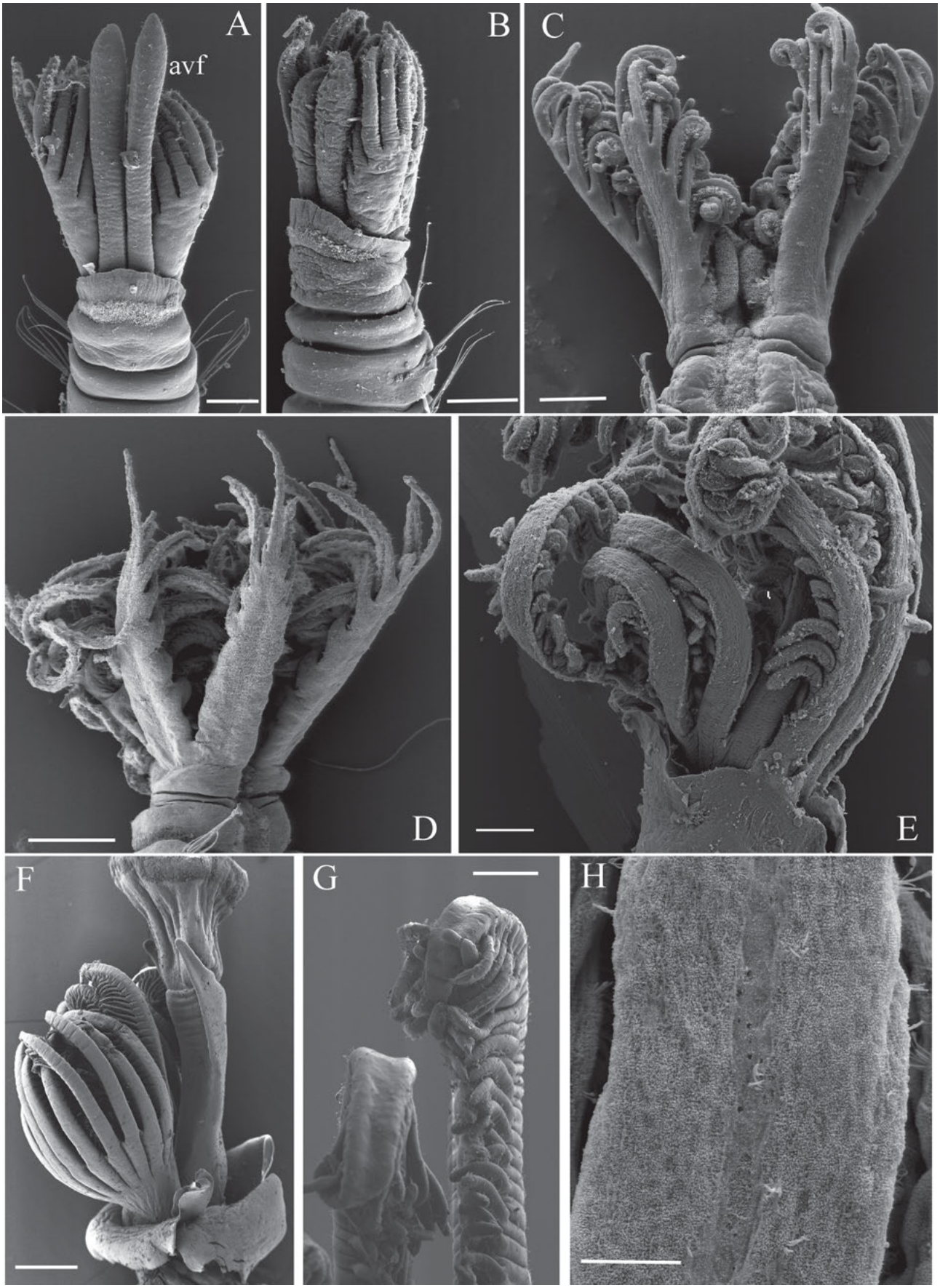


Fig. 7.4.8.2: Radiolar crown morphology of Fabriciidae (micrographs of live specimens). A, B, Asymmetrical branching and pectinate radioles in *Manayunkia athalassia* Hutchings, Deckker & Geddes, 1981; C, Asymmetrical branching and pectinate radioles in *Manayunkia aestuarina* (Bourne, 1883); D, Symmetrical branching and bipectinate radioles in *Fabricia stellaris* (Müller, 1774). vfa ventral filamentous appendages. Micrographs by G. Christie (A, B), M. Wagner (C), and A. Dietrich (D). Scale bars: A, B = 200 µm, C = 100 µm, D = 200 µm.

The radioles of most fabriciids contain an acellular supporting tissue that is interpreted as a radiolar skeleton. A distinct supporting structure is absent in *Manayunkia* (see Internal morphology section). The radioles and ventral filamentous appendages in this genus are clearly wrinkled (Figs. 7.4.8.1C, 7.4.8.3B) in contrast to the situation in all other fabriciid genera (Figs. 7.4.8.1A, 7.4.8.3C, D) (Bick 2004).

Two other structures associated with the radiolar crown are the dorsal lips and the ventral filamentous appendages (Fig. 7.4.8.5A, B). The dorsal lips extend from the inner dorsal margin of the branchial lobe and terminate dorsal to the mouth. They are ciliated and used for sorting particles to be used as food or for tube construction. The dorsal lips can be described as low, narrow ridges or well-developed triangular or rounded lobes. However, they are poorly developed in some cases (e.g., in *Novafabricia infratorquata* (Fitzhugh, 1973)) and even absent among some species of *Fabricinuda* (Bick 2004, Fitzhugh 2010). Ventral filamentous appendages originate from the dorsal margin of the dorsal lips. These appendages contain either narrow or wide blood vessels and have been described as nonvascularized (e.g., in all species of *Fabriciola* and *Rubifabriciola*) or vascularized (Fig. 7.4.8.5B) (e.g., in all species of *Augeneriella*, *Echinofabricia*, *Mananayunkia*, and *Pseudoaugeneriella*). Only

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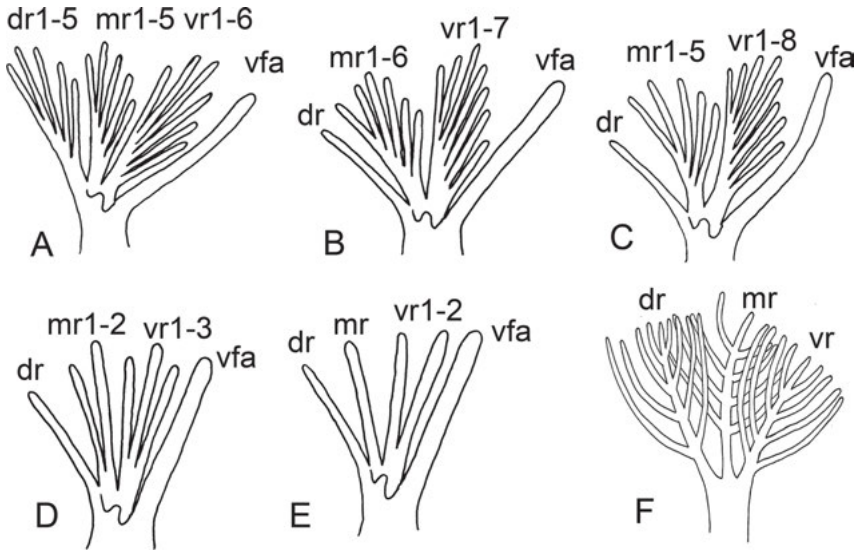


Fig. 7.4.8.4: Schematic view branching of the radiolar crown in *Manayunkia* species and *Fabricia stellaris* (Müller, 1774). A–E, Asymmetrical branching and pectinate radioles; A, *M. athalassia* Hutchings, Deckker & Geddes, 1981; B, *M. caspica* Annenkova, 1928; C, *M. zenkewitschii* Sitnikova, Shcherbakov & Kharchenko, 1997; D, *M. mizu* Rouse, 1996; E, *M. aestuarina* (Bourne, 1883); F, Symmetrical branching and bipectinate radioles; *F. stellaris*. dr, dorsal radiole; mr, median radiole; vfa, ventral filamentous appendage; vr, ventral radiole. Numbers indicate the number of branches. Original.

among species of *Augeneriella* are the ventral filamentous appendages branched.

Prostomium and peristomium. The prostomium and the peristomium are fused. The peristomium is divided into an anterior ring and a posterior ring. The anterior peristomial ring is usually wider than it is long or as wide as it is long. It is usually distinctly shorter than the posterior ring or of equal length in most species of *Augeneriella*, and it is even longer in *Fabricinuda* spp. The anterior extension of the anterior peristomial ring forms as a collar. This anterior peristomial ring collar usually encircles the anterior peristomial margin distinctly. This collar is reduced to a low ridge only among species of *Fabricinuda*. The collar forms a triangular, widely rounded, or rectangular ventral lobe. A midventral ciliated patch (in most fabriciids) or a ciliated band located ventrally on the posterior margin of the anterior peristomial ring (among members of *Manayunkia*) is always developed on the ventral lobe (Fig. 7.4.8.3A, B). The collar usually exhibits a middorsal separation as a continuation of the fecal groove (Fig. 7.4.8.3C), but this separation is absent among species of *Pseudofabriciola*. Peristomial eyes are developed in most species of Fabriciidae (Fig. 7.4.8.1A), but pigmented eyes are not found in deep-sea species (Baumhaker 2012). The eyes are black in most fabriciids or red as in *Echinofabricia* and *Rubifabriciola*.

Thorax and Abdomen. The body is divided into a thoracic region and an abdominal region (Figs. 7.4.8.1A, C, 7.4.8.6A). Fabriciids have eight thoracic and usually three abdominal chaetigers. However, *Brandtika* spp., *Fabriciola minuta*, and *Monroika africana* (Monro, 1939) have two abdominal chaetigers, and *Echinofabricia* spp. has four. The boundary between the thorax and the abdomen is distinct because of the chaetal inversion and the shift in the position of the fecal groove (Fig. 7.4.8.7F). The chaetal inversion refers to the changes in the position of the capillary chaetae from the thoracic notopodia to the abdominal neuropodia and that of the uncini from the thoracic neuropodia to the abdominal notopodia. The fecal groove, an epidermal region covered with dense cilia from the anal opening to the middorsal collar, is shifted from the ventral midline on the abdomen to the dorsal midline on the thorax (Fig. 7.4.8.7F).

Parapodia and chaetae. The parapodia are biramous, except for the first chaetiger, which only exhibits notopodial capillaries (Fig. 7.4.8.6A). There are four types of chaetae among species of Fabriciidae: narrowly hooded, pseudospatulate, pinhead, and transitional (=pilose, after Jones 1974) chaetae (Figs. 7.4.8.6B, D, G, 7.4.8.8B–D). The chaetae on the first chaetiger and superior thoracic notochaetae are usually elongated, narrowly hooded capillaries (Fig. 7.4.8.6B). The inferior thoracic notochaetae

◂ **Fig. 7.4.8.3**: Pattern of the radiolar crown branching in Sabellida (SEM micrographs). A, B, Asymmetrical branching and pectinate radioles in *Manayunkia athalassia* Hutchings, Deckker & Geddes, 1981 (Fabriciidae); C, D, Symmetrical branching and bipectinate radioles in *Fabricia stellaris* (Müller, 1774) (Fabriciidae); E, Radioles with pinnules in *Laonome xeprovala* Bick and Bastrop in Bick et al. 2018 (Sabellidae); F, G, Radioles with pinnules in *Spirobranchus triqueter* (Linnaeus, 1758) (Serpulidae); H, Cilia on the aboral radiole side in *F. stellaris*. avf, ventral filamentous appendages. Scale bars: A–E, G = 100 µm, F = 500 µm, H = 10 µm. Original.

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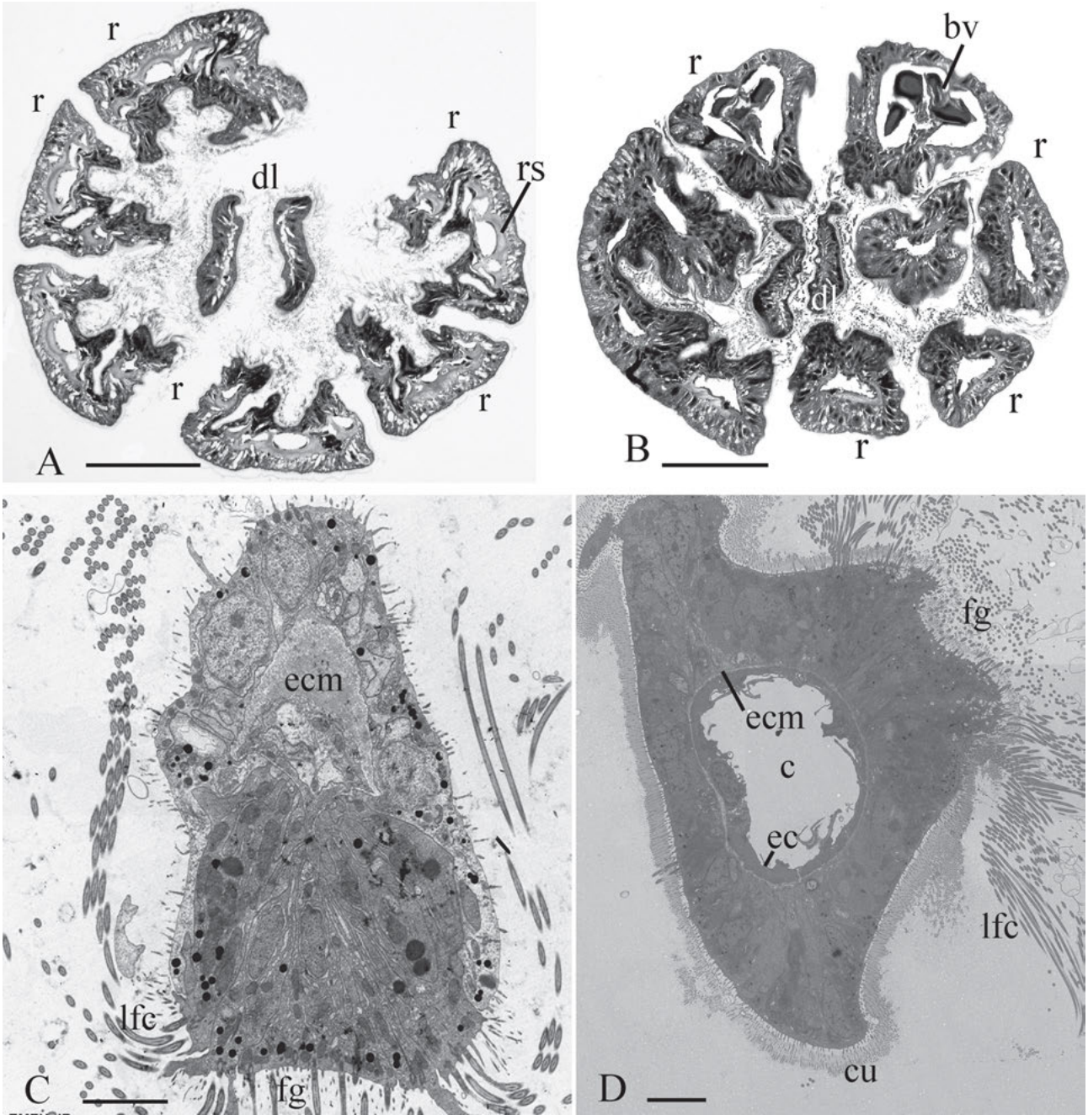


Fig. 7.4.8.5: Transverse section of the radiolar crown and radioles of *Fabricia stellaris* (Müller, 1774) and *Manayunkia aestuarina* (Bourne, 1883). A, Semithick section of the radiolar crown of *F. stellaris*; B, Semithick section of the radiolar crown of *M. aestuarina*; C, Ultrathin section of a tip of a radiole of *F. stellaris*; D, Ultrathin section of a radiole of *M. aestuarina*. bv, blood vessel; c, coelomic cavity; cu, cuticle; dl, dorsal lip; ec, epithelial cell; ecm, extracellular matrix; fg, food groove; lfc, laterofrontal cilia; r, radiole; rs, radiolar skeleton. Scale bars: A, B = 50 µm, C = 3 µm, D = 5 µm.

are also elongated and narrowly hooded but are usually shorter than the superior notochaetae and slightly bent (Figs. 7.4.8.7G, 7.4.8.8), or they are pseudospatulate (Figs. 7.4.8.6G, 7.4.8.7G). The distribution of the pseudospatulate chaetae is not consistent within the genera of fabriciids. They occur on chaetigers 2 to 5 or 2 to 8 and on chaetigers 3 to 5, 3 to 6, 3 to 7, or 3 to 8. The abdominal neurochaetae are also narrowly hooded capillaries. The number of abdominal neurochaetae is, in general, lower than the number of thoracic notochaetae. In addition, some or even all species of *Rubifabriciola* have pinhead chaetae on the abdominal neuropodia (Fig. 7.4.8.6D).

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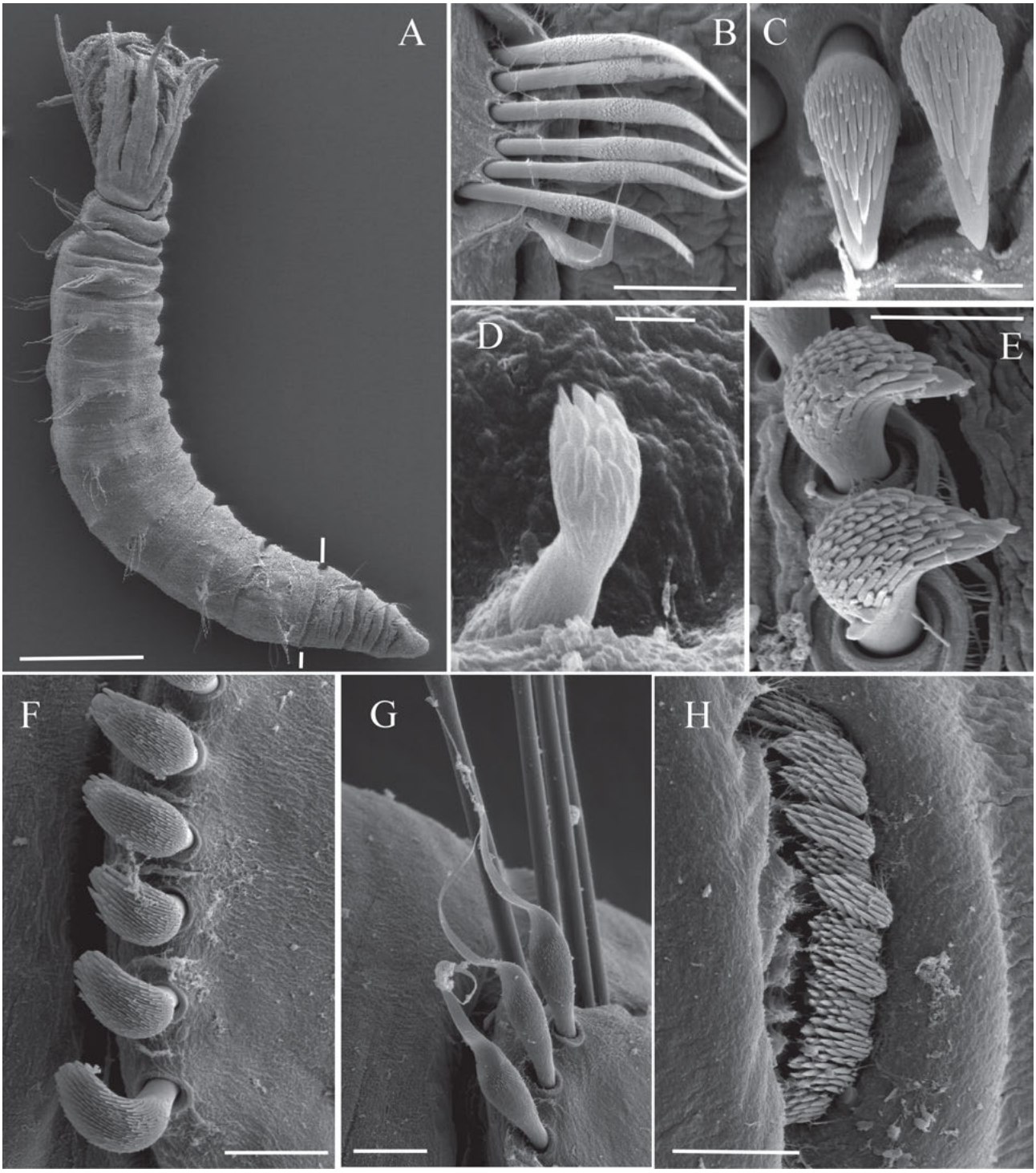


Fig. 7.4.8.6: Chaetae and uncini of Fabriciidae (SEM micrographs). A–C, *Fabricia stellaris* (Müller, 1774); A, Lateral view with thoracic and abdominal regions; B, Six narrowly hooded and one pseudospatulate chaetae of thoracic region; C, Thoracic uncini with a single larger tooth above the main fang; D, *Rubifabriciola tonerella* (Banse, 1959), pinhead chaetae of first abdominal chaetiger; E, *Manyunkia aestuarina* (Bourne, 1883),Thoracic uncini without a large tooth above the main fang but with several rows of small apical teeth; F, G, *Manayunkia athalassia* Hutchings, Deckker & Geddes, 1981; F, Thoracic uncini with several rows of small apical teeth; G, Three pseudospatulate capillaries of thoracic region; H, Dentate region of abdominal uncini. Scale bars: A = 200 µm, B, F–H = 10 µm, C, E = 5 µm, D = 1 µm. Original.

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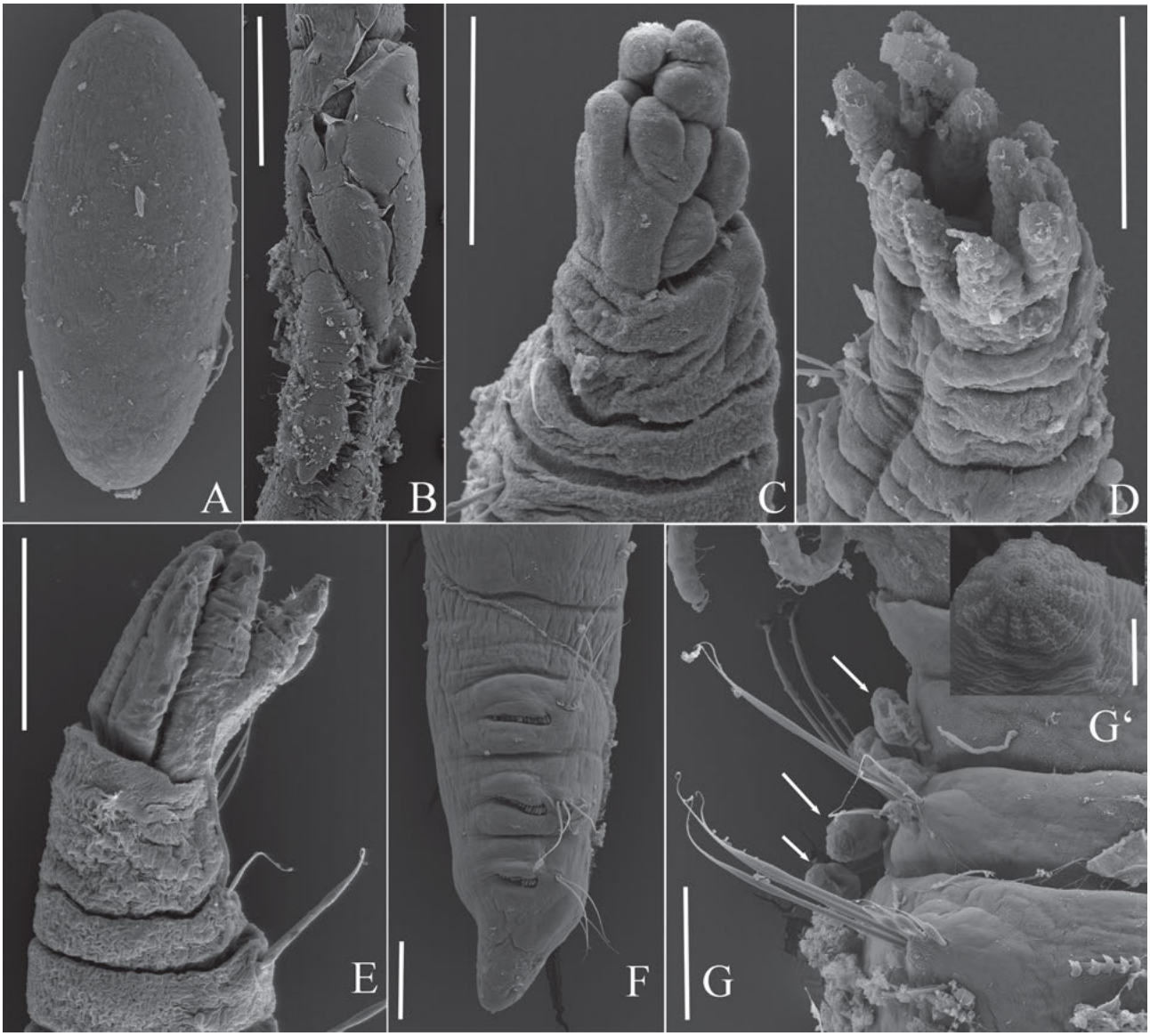


Fig. 7.4.8.7: Larval development and epibiosis in *Manayunkia aestuarina* (Bourne, 1883) (SEM micrographs). A, Egg; B, Clutch from a tube with several larvae; C, D, Larvae with three pairs of radioles and short ventral filamentous appendages; E, Larva with completely developed radiolar crown and first uncini in anterior thoracic chaetigers; F, Abdomen of adult specimen with shift in the position of the fecal groove; G, Peritrichous ciliates on anterior chaetigers. Scale bars: A, C–G = 50 µm, B = 200 µm, G′ = 5 µm. Original.

These chaetae have a blunt tip and exhibit several small teeth apically. They are not always clearly visible, as they protrude only slightly or not at all. The transitional chaetae at the position of the thoracic uncini are especially remarkable. They occur on the last thoracic chaetigers (chaetigers 6–8) of *Brandtika* spp., *Manayunkia godlewskii*, and *Manayunkia zenkewitschii* Sitnikova, Shcherbakov & Kharchenko, 1997 (Fig. 7.4.8.8B–D). They represent a link between the capillary chaetae and the thoracic uncini. The shortening of the capillaries and an increase in curvature to form a right angle between the shaft and the rostrum and the enlargement of the microvilli, which are responsible for the tooth-like edge, occur, leading to the uncini. It is not clear whether this is a plesiomorphic character state or an evolutionary novelty that supports locomotion outside the tube.

The thoracic and abdominal uncini are aligned in transverse rows (Figs. 7.4.8.6F, H, 7.4.8.7F, G). The thoracic uncini are formed at the dorsal edge of the neuropodial rim, whereas the abdominal uncini are formed at the ventral edge of the notopodial chaetal formation site (Bartolomaeus 2002). The thoracic uncini are characterized by

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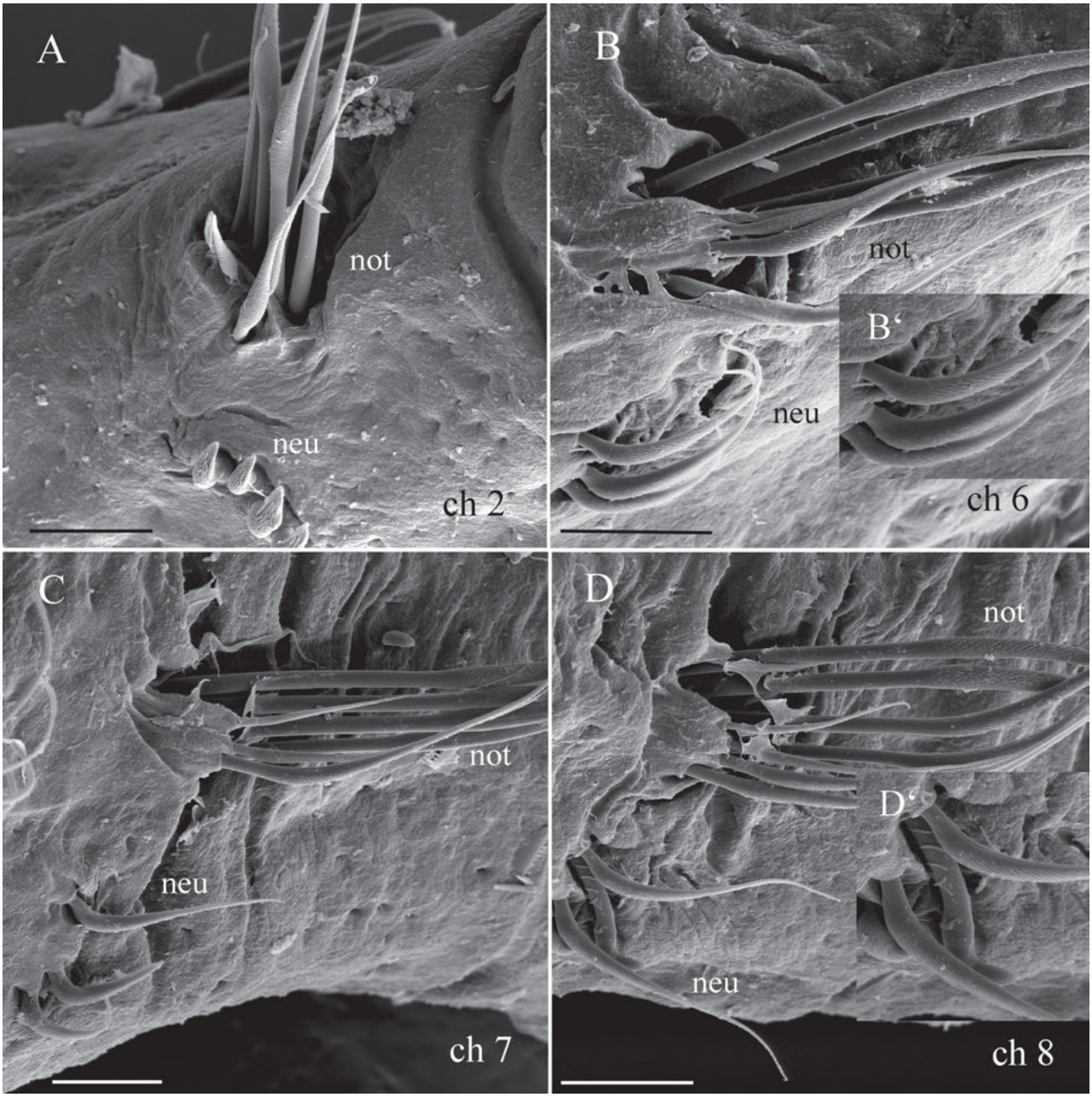


Fig. 7.4.8.8: Pattern of thoracic neuropodial chaetae in *Manayunkia zenkewitschii* Sitnikova, Shcherbakov & Kharchenko, 1997 (SEM micrographs). A, Chaetiger 2, normal shape of neuropodial thoracic uncini (also present on chaetigers 3–5); B, Chaetiger 6 with three strongly bent neuropodial narrowly hooded chaetae; C, Chaetiger 7 with one strongly bent neuropodial narrowly hooded chaetae and two transitional chaetae; D, Chaetiger 8 with two strongly bent neuropodial narrowly hooded chaetae and two transitional uncini-like chaetae. ch, chaetiger; neu, neuropodium; not, notopodium. Scale bars: A–D = 20 µm. Original.

a long manubrium and a main fang surmounted by a series of smaller teeth (Fig. 7.4.8.6C, E, F). A slightly offset medium-sized tooth occurs between the large main fang and the smaller apical teeth in several genera (Fig. 7.4.8.6C) (e.g., in *Augeneriella*, *Fabricia*, *Fabricinuda*, *Monroika*, *Novafabricia*, and *Pseudoaugeneriella*). The apical teeth can also exhibit about the same size (Fig. 7.4.8.6F) (e.g., in *Echinofabricia* species) or may gradually decrease in size away from the main fang (Fig. 7.4.8.6E). A layer of less electron-dense material on the adrostral side that appears translucent has usually been referred to as a hood. The dentate distal end is bent toward the manubrium. The abdominal uncini are arranged side by side in a torus. Their dentate region is anteriorly directed (Figs. 7.4.8.6H,

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7.4.8.7F). They usually exhibit multiple rows of equal-sized teeth. Only *Novafabricia chilensis* (Hartmann-Schröder, 1962) and *Novafabricia gerdi* (Hartmann-Schröder, 1974) are known to have a single row of teeth. The length of the manubrium is as long as the dentate region or up to two to three times longer.

Pygidium. The pygidium is broadly or gently tapered and triangular or bluntly rounded posteriorly (Figs. 7.4.8.1A, C, 7.4.8.6A, 7.4.8.7F). The anus is a depressed midventral longitudinal slit located at the anterior margin of the pygidium or between the last chaetiger and pygidium. Only in exceptional cases is the anus located in a broad, ventral depression (e.g., in *Pseudofabriciola analis* Fitzhugh Giangrande & Simboura, 1994). The entire surface of the pygidium is glandular (and therefore darkly stained with methyl green). A pair of black, dark brown, or red rounded eyes is present in most species of Fabriciidae (Fig. 7.4.8.1A). They are located in the posterior part of the pygidium. Pygidial eyes are absent in all species of *Manayunkia*, *Monroika*, *Fabriciola parvus* Rouse, 1993, and two undescribed deep-sea species (Baumhaker 2012).

Spicules. Emergent spicules are present in the epithelium of *Echinofabricia* spp. (Huang et al. 2011). They are 25 to 30 µm long and 3 µm in diameter. They are secreted by a single cell and remain in the epidermis, with the highest concentration on the abdomen. They contain high concentrations of calcium and phosphor. These spicules are unique to Fabriciidae and even Annelida. Otherwise, the epithelium of the fabriciids is glandular, with the highest concentration of glandular cells on the ventrum of the peristomial rings, the midventral anterior margin of chaetiger 1, the ventrum of the anterior thoracic chaetigers and all abdominal chaetigers, and especially the pygidium (blue or dark blue using methyl green staining).

Internal morphology

Radiolar crown. The radiolar crown consists of primary (radioles) and secondary branches (see External morphology section), between which no morphological or ultrastructural differences can be found (Randel and Bick 2012, own unpublished data). The primary and secondary branches of most fabriciids are supported by an acellular skeleton consisting of a solid extracellular matrix (ECM) and myoepithelial cells (Fig. 7.4.8.5C, D) (Bick 2004, Randel and Bick 2012). They may function as antagonists in the opening and folding of the radiolar crown, in which the ECM may be responsible for extension and myofibrils for contraction. Adjacent to the ECM and myoepithelial cells, there are several intraepithelial adoral and aboral nerves. The epidermis of the radioles consists of nonciliated and ciliated cells. Approximately five ciliated cells shape the concave food groove, with the two outer cells forming the long laterofrontal cilia and the three middle cells forming the short cilia (Fig. 7.4.8.5C, D). Interestingly, the food grooves of Sabellidae and Serpulidae are also composed of five ciliated cells with the same pattern of ciliation (Nicol 1930, Evenkamp 1931, Thomas 1940, Hanson 1949, Fitzsimons 1965). Aboral ciliated cells have been observed only sporadically (Fig. 7.4.8.3H). Some species (e.g., *Novafabricia chilensis*, *Novafabricia infratorquata*, and *Rubifabriciola tonerella*) possess median radioles with one distinct blood vessel (Bick 2004). This situation probably exists in additional species. However, corresponding investigations are still pending.

The above-described scheme can probably be generalized to most Fabriciidae but not to *Manayunkia*. Most strikingly, the center of the radioles of *M. aestuarina* consists of a large cavity (potentially a continuation of the coelomic cavity?) surrounded by epithelial cells and a narrow ring-shaped ECM (Fig. 7.4.8.5D). The lack of a solid ECM is probably responsible for the wrinkled surface of the radioles and ventral filamentous appendages after fixation. The epidermal cells of the radioles have a cuticle that is 1 to 2 µm thick (Fig. 7.4.8.5D). Approximately 8 to 10 ciliated cells constitute the shallow or even convex food groove, with the outer cells forming the long laterofrontal cilia and the middle cells forming the short cilia. Aboral ciliated cells occur only sporadically. Myofibrils are located in the aboral nonciliated epithelial cells. Several intraepithelial adoral and aboral nerves are also present. It is possible that the central cavity present in *Manayunkia* has been completely displaced by an increase in the ECM and the proportion of myofibrils in myoepithelial cells in the remaining Fabriciidae. The radiolar crown of *Manayunkia* could present the most ancestral character state within Fabriciidae and Sabellida.

Epidermis. The columnar epithelium of the body region is covered with a thin cuticle. The epithelium is glandular, with the highest concentration of glandular cells on the ventrum and the whole pygidium. Emergent spicules are present in the epithelium of *Echinofabricia* (Huang et al. 2011).

Musculature. There is a thin layer of ring muscle fibers as well as a thicker layer of longitudinal muscle fibers beneath the epidermis, which are interrupted only at the dorsal and ventral midline and laterally. Thus, four longitudinal muscles are formed (Zenkevitsch 1925).

Digestive system. The digestive system of Fabriciidae consists of a simple straight gut with a narrow ectodermal

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foregut without a buccal organ, a larger endodermal midgut, and a narrow ectodermal hindgut. No intestinal loops or blind sacks are present (Nusbaum 1901a). The digestive tract is ciliated along its whole length (Meehean 1929).

Circulatory system. The circulatory system is closed. There are large dorsal and ventral longitudinal blood vessels. The intestine is surrounded by a vascular blood sinus. Branchial hearts are present. They pump blood into the vessels of the ventral filamentous appendages or specialized radioles of the radiolar crown. From there, the blood flows back into the body within vessels adjacent to the oesophagus. These vessels lead into the ventral longitudinal vessel. At the posterior end, the blood flows through pairs of loops to the contractile dorsal vessel. The blood is red or green (e.g., Leidy 1883, Foulke 1884, Zenkevitsch 1925, Meehean 1929, Pettibone 1953, Lewis 1968a).

Nephridia. Metanephridia with podocytes are located in the peristomium and the first chaetiger. They consist of a nephrostome at the dissepiment between the peristomium and the first chaetiger and pigmented, twisted paired tubes that unite to form an unpaired duct. This duct opens between the radiolar lobes on the dorsal side (Zenkevitsch 1925, Nusbaum 1901a, Bartolomaeus and Quast 2005).

Nervous system. The cerebral ganglion is located in the peristomium due to the reduction of the prostomium. The innervation of the radiolar crown is equivalent to the palps of other taxa of polychaetes and is considered to be homologous (Orrhage 1980, Orrhage and Müller 2005). A ventral nerve cord is present, but detailed information on this structure is absent. Fabriciidae possesses several sensory structures, including radioles, two pairs of both peristomial and pygidial eyes, and a nuchal organ. There are sensory ciliated cells with an unknown function on the aboral side of the radioles (Fig. 7.4.8.3H) (Randel and Bick 2012). The nuchal organ presents an anomalous position probably due to the development of the radiolar crown (Purschke 2005). It is located next to the esophagus and consists of two nuchal pouches arising from the dorsal epithelium of the esophagus. Each of the pouches exhibits an olfactory chamber and sensory cells (Purschke 1997). The peristomial or cerebral eyes of fabriciids have never been examined in detail but those of the Sabellidae. Based on the examination of *Chone ecaudata* (Moore, 1923) (Sabellidae), these eyes consist of rhabdomeric photoreceptor cells and supportive cells forming a pigmented cup that encloses the microvilli of the photosensory cells (Ermak and Eakin 1976). Nusbaum (1901a) provided drawings of cross-sections of the anterior region of *Manayunkia baicalensis* Nusbaum, 1901. The peristomial eyes are embedded in the brain. The pygidial eyes are simple plaques of columnar epidermal cells, each of which consists of several photoreceptor cells and pigmented supportive cells. The photoreceptor cells are regarded as rhabdomeric; however, the microvilli are twisting, and their density is low (Purschke et al. 2006). The peristomial eyes are most likely more complex and more light sensitive than the simpler pygidial eyes in Sabellidae. This is most likely also true for Fabriciidae.

Genital organs and gametes. All fabriciids are gonochoric. They lack distinct gonads. The development of the gametes begins at the coelomic epithelium and is completed in certain thoracic segments (see Reproduction and development section). Males have a dorsal sperm duct that runs along the thoracic region below the fecal groove and opens behind the radiolar crown. However, it is not yet known how the eggs are released in females. Fabriciid species possess either prostomial (e.g., in *Bansella*, *Fabricia*, and *Manayunkia*) or peristomial (e.g., in *Echinofabricia*) spermathecae. The structure of the spermathecae is simple in most Fabriciidae but more complex in others. It exhibits three distinct regions: an opening leading to an atrium that is heavily ciliated, a connecting piece that has a narrow or a wide duct, and a pigmented sperm-storage region without cilia. Such complex spermathecae have been described in *Fabricia stellaris*, *Novafabricia tenuiseta* Fitzhugh, 1990, and *Parafabricia ventricingulata* Fitzhugh, 1992 (Rouse 1992, 1995a, 1996b). Sperm can also be stored in epidermal cells in the prostomial radiolar crown in some species of *Augeneriella* or in the peristomium (e.g., in *Novafabricia* or *Pseudofabriciola*) (Huang et al. 2011).

Reproduction and development

All fabriciids are gonochoric, intratubular brooders with direct larval development. There are a variety of data on the reproductive organs and gametogenesis of Fabriciidae (e.g., Zenkevitsch 1925, Kahmann 1984, Nausch 1988, Rouse 1992, 1993, 1995a, b, 1996a, b, 1999, 2005, Rouse and Fitzhugh 1994, Huang et al. 2011). However, information on reproduction and larval development is only available for certain species. Most such information is available for *Fabricia stellaris*, *Fabricinuda trilobata* Fitzhugh, 1983, *Manayunkia aestuarina* (Bourne, 1883), *Manayunkia baicalensis*, and *Manayunkia speciosa* Leidy, 1858 (Zenkevitsch 1925, Forsman 1956, Lewis 1961, Schütz 1965, Muus 1967, Rassmussen 1973, Brehm 1978, Bell 1982, Knight-Jones and Bowden 1984, Nausch 1988, Rouse and Fitzhugh 1994, Bick 1996).

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Spermiogenesis only occurs in the thoracic chaetigers in all species (an apomorphy for Fabriciidae). The number of chaetigers with sperm stages varies mainly between genera. Spermiogenesis occurs on chaetigers 3 to 8 in *Bansella*, *Fabricia*, and *Pseudofabricia*, chaetigers 4 to 8 in *Augeneriella*, *Brifacia*, *Fabricinuda*, and *Pseudofabriciola*, and chaetigers 6 to 8 in *Manayunkia* and *Raficiba*. Spermiogenesis varies only among species of *Echinofabricia*, *Fabriciola*, *Novafabricia*, and *Rubifabriciola* (occurring on chaetigers 3–8 or 4–8) and is still unknown in *Brandtika*, *Monroika*, *Parafabricia*, and *Pseudoaugeneriella*. Sperm develop in large clusters of spermatids attached to a central cytophore (Rouse and Fitzhugh 1994, Rouse 1995b, Huang et al. 2011). A single dorsal sperm duct that runs below the fecal groove from chaetiger 8 is present in all male fabriciids. Both characters are apomorphies of Fabriciidae. Three sperm characters are also apomorphies of Fabriciidae. For further details, see Rouse (1993, 1995b) and Huang et al. (2011) and the Taxonomic history section in this chapter. The opening of the sperm duct lies immediately behind the common pore of the anterior pair of nephridia (Rouse 1995b, Huang et al. 2011). In this way, sperm can be released into seawater via the flow of water produced by the cilia of the fecal groove.

The position of egg development in female Fabriciidae varies. It takes place on chaetigers 3 and 4 in *Bansella*, *Fabricia* (Fig. 7.4.8.1A), and *Fabriciola*, chaetigers 3 to 6 in *Monroika* (Jones 1974), chaetiger 4 in *Manayunkia*, *Fabricinuda*, *Pseudofabriciola*, and *Raficiba*, and chaetigers 4 and 5 in *Manayunkia mizu* Rouse, 1996 (e.g., Annenkova 1929, Pettibone 1953, Nausch 1988, Bick 1996, Fitzhugh 1996, 2001, 2002, Rouse 1996a). It has been assumed that eggs are discharged via rupture of the body wall (Bourne 1883, Kahmann 1984) or through short canals in oocyte-bearing chaetigers (Holmquist 1973). However, it also seems possible that the oviducts may be very small and have been overlooked so far (Rouse 1995b).

It is not yet known how females obtain sperm to fertilize the eggs spawned into their tubes. Pseudocopulation was suggested to occur in *Manayunkia baicalensis* by Zenkevitsch (1925) and *Fabricia stellaris* by Franzén (1956). According to Zenkevitsch (1925), the transfer of sperm from the male to the female in *M. baicalensis* takes place when the ventral side of the female is in direct contact with the dorsal side of the male (pseudocopulation). Thus, the openings of the spermathecae of the female come into contact with the single dorsal sperm duct of the male. However, Kahmann (1984) also showed that the transfer of sperm from males to females in *Fabricia stellaris* does not require direct contact between the sexes. According to Kahmann (1984), the position of the spermathecae in the radiolar crown dorsolateral to the buccal opening suggests that sperm released into the water may enter the spermathecae. This implies the recognition and discrimination of sperm from other particles that are collected by the radiolar crown. It is also possible that the transfer of sperm varies between species. In any case, the high abundances of most species may favor the transfer of sperm.

The brooding of larvae requires sperm storage by the female. Fabriciidae possesses prostomial or peristomial spermathecae (see Internal morphology section). The spermatozoa occur freely in the lumen. Sperm can also be stored in epidermal cells in the prostomial radiolar crown or the peristomium (Huang et al. 2011).

Limited observations on reproduction and larval development are available within fabriciids. *Fabricia stellaris* females harbor approximately 6 to 9 eggs per egg-bearing chaetiger (Fig. 7.4.8.1A) (Forsman 1956, Rassmussen 1973). The ovaries are located on the coelomic epithelium near the ventral blood vessel. At a length of approximately 10 to 20 µm, oocytes are released into the coelom before the onset of vitellogenesis, where they grow to a size of approximately 0.2 mm (Rassmussen 1973, Berrill 1977, Kahmann 1984, Nausch 1988). The gonads are active year-round, but their activity is inhibited during winter months (Nausch 1988). According to Rassmussen (1973), egg laying in *F. stellaris* takes place year-round, with a reduced intensity during winter and an increased intensity during summer in Isefjord, Denmark. Forsman (1956) and Nausch (1988) found mature specimens only during summer, and Muus (1967) observed larvae in spring (from February to April). Every 4 to 6 days, a new clutch of eggs is deposited into the tube. The eggs are most likely shed through dorsolateral apertures between the chaetae. As described above, no genital ducts and no gonopores have been found in these species. Approximately 8 to 24 eggs and developing larvae have been simultaneously found in a female tube in the Baltic Sea (Nausch 1988). Lewis (1961) observed a maximum of 10 clutches of eggs per tube, with one to seven individuals per clutch on the southern coast of Northumberland, North Sea, and Rassmussen (1973) observed two to nine eggs in each clutch. The clutches, which are covered with a mucus envelope, are distributed along the length of the tube, and all stages of development from egg to preadult are simultaneously present (Lewis 1961). The period from egg laying to hatching is less than 2 weeks at approximately 20°C (Rassmussen 1973). *F. stellaris* reproduces only at salinities between 5 and 35 psu (Nausch 1988). However, at 35 psu, many eggs no longer develop. The greatest numbers of eggs have been observed at approximately 10 psu in the southern Baltic Sea (Nausch 1988). The development of larvae within the

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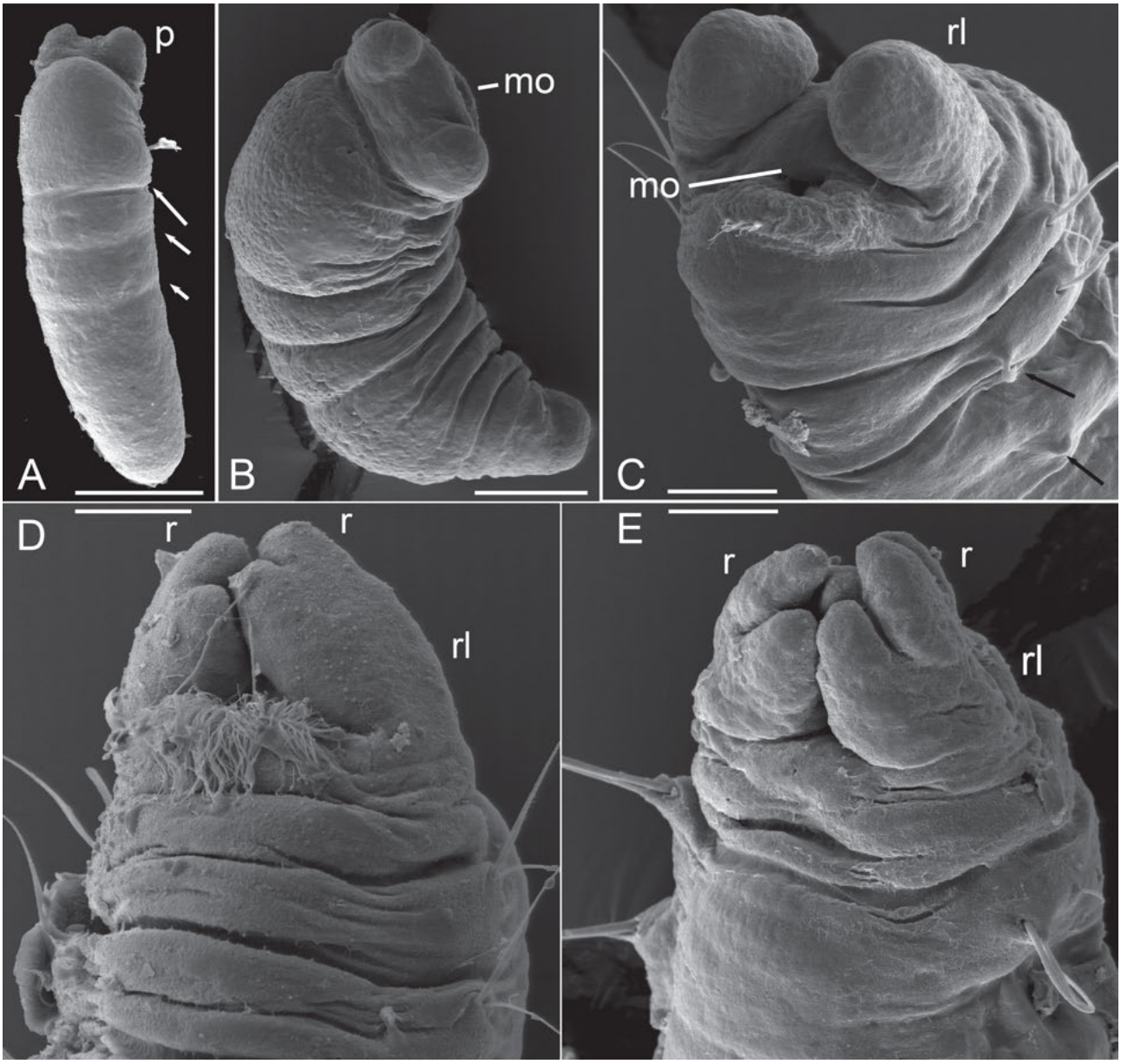


Fig. 7.4.8.9: Larval stages of *Fabricia stellaris* (Müller, 1774) (SEM micrographs). A, Barely segmented (arrows) juvenile with protuberances on anterior end; B, Juvenile with mouth opening, eight thoracic segments and one capillary on chaetigers 1 to 3 each; C, Anterior end of a six-chaetiger juvenile with radiolar lobes and one uncinus on chaetigers 1 and 2 each (arrow), mouth opening slightly anteriorly shifted; D, Anterior end of an eight-chaetiger juvenile with first appearance of radioles, mouth opening located between radiolar lobes; E, Anterior end of juvenile with three pairs of radioles. mo, mouth opening; p, protuberance; r, radiole; rl, radiolar lobe. Scale bars: A = 60 µm, B = 40 µm, C–E = 20 µm. Original.

tubes of females was described by Randel and Bick (2012). Before the initiation of segmentation, a pair of protuberances appears at the anterior end, which represents the branchial lobes of the radiolar crown (Fig. 7.4.8.9A). Thereafter, three thoracic segments are formed. On the first chaetiger, one narrowly hooded notochaetae develops. One of the next stages is characterized by the existence of eight thoracic segments with one narrowly hooded chaeta on each of the first three segments, whereas the mouth opening is still located ventrally, and abdominal chaetigers are still absent (Fig. 7.4.8.9B). In the next stage, there are two narrowly hooded notochaetae on the first six thoracic chaetigers and one uncinus on the second and third chaetigers (Fig. 7.4.8.9C). The mouth opening is displaced more terminally; a patch of cilia is located ventral to the mouth. Three pairs of short, unbranched radioles

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are present on larvae with eight thoracic chaetigers (Fig. 7.4.8.9D, E). The mouth opening is now located between the branchial lobes. Only at this stage do abdominal chaetigers appear. In the final stages of larval development, characterized by the presence of eight thoracic and one to three abdominal chaetigers and an incompletely developed radiolar crown, the larvae leave the maternal tube, crawl on the surface for a short time, and construct their own tubes adjacent to the maternal tube (Randel and Bick 2012). The resultant sex ratio is 1 male to 4 to 5 females (Forsman 1956).

The maximum number of larvae observed in a single tube of *Fabricinuda trilobata* was 18, with an average of approximately 6 (Rouse and Fitzhugh 1994). The number of clutches and the number of eggs in a single clutch seem to be size related, i.e., larger females may have more eggs and clutches in their tubes. The development is similar to that above described for *Fabricia stellaris*. This concerns the pattern of segmentation, the formation of radiolar crown, the thoracic capillaries, and the thoracic uncini. However, the dentition of uncini among juveniles and adults differs slightly. Subsequent to the formation of all thoracic chaetigers, abdominal chaetigers with chaetae and uncini begin to develop. Juveniles are able to feed immediately after they have crawled out of the tube (Rouse and Fitzhugh 1994).

According to Forsman (1956) and Schütz (1965), *Manayunkia aestuarina* females are three to five times as numerous as males, but Bick (1996) found a sex ratio of approximately 1:1 in the southern Baltic Sea. *M. aestuarina* females exhibit between two and four eggs on chaetiger 4. The reproduction of *M. aestuarina* is discontinuous, as neither embryo nor juvenile recruitment has been observed during winter months (from November to March) in a South Carolina salt marsh (Bell 1982). Reproduction also starts at the end of March or beginning of April in the southern Baltic Sea but is completed by the end of August, as no eggs or larvae are found in the female tubes this time onward (Schütz 1965, Bick 1996). Males reach reproductive maturity before females in the Baltic Sea (Bick 1996). Males with sperm and females with eggs have been observed in autumn and winter in the North Sea (Schütz 1965). On average, 4 eggs of approximately 0.2 to 0.3 mm long (Fig. 7.4.8.7A) and developing larvae are simultaneously found within a tube, with a maximum number of 16 eggs occurring in the middle of the reproductive period (Fig. 7.4.8.7B). Bell (1982) observed 8 to 12 larvae per tube, each of which

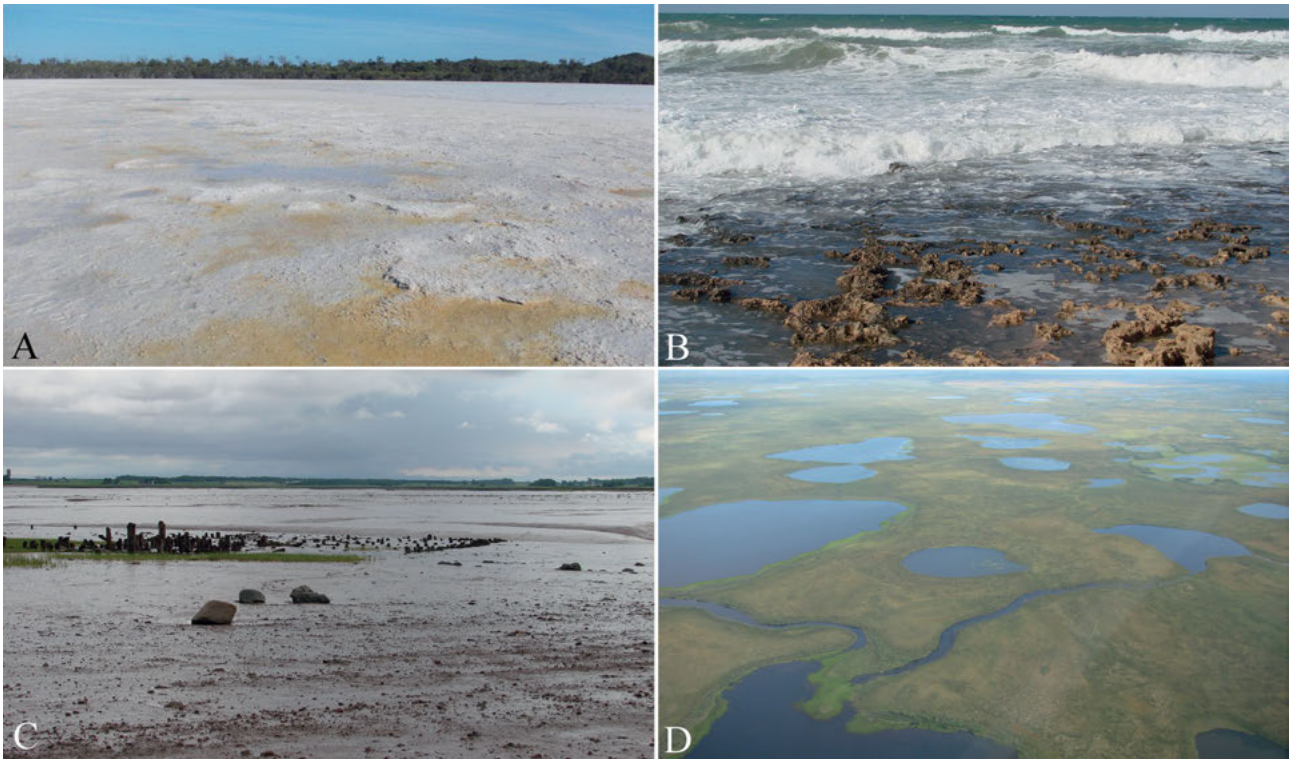


Fig. 7.4.8.10: Characteristic habitats of Fabriciidae species. A, Hypersaline salt lakes (Yalgorup Lake System, Swan Pond, Western Australia); B, Marine intertidal and subtidal hard bottoms (Mediterranean Sea); C, Mudflat areas (northeast America); D, Freshwater lakes (Canadian Arctic). Images by G. Christie (A) and Andreas Bick (B–D).

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in a different stage of development. The youngest stages generally occupy the anterior part of the tube, with the more advanced larvae behind them. All larvae face the tube mouth, and all stages are joined by a mucous coating. The development of larvae may take 2 weeks (Forsman 1956), from 2 to 4 weeks (Bell 1982), or 8 weeks (Bick 1996). Low temperatures delay the development time. The larvae leave the tube at a size of 0.6 to 0.7 mm (Fig. 7.4.8.7C–E) (Bick 1996). They do not crawl far from the female tube. The survival rate of juveniles is approximately 15% to 20%, and the average age of this species is approximately 1 year (Bick 1996).

Schloesser et al. (2016) described the abundance, reproduction, and recruitment of *Manayunkia speciosa* in Lake Erie. Mature specimens have been found in the lake from April to October. The sex ratio is approximately 1:1 on average but with a higher proportion of males (72%) in April and a higher proportion of females in October (80%). This means that males become sexually mature earlier than females and that females remain mature longer than males. Reproduction is continuous from May to September, but a first peak recruitment occurs between late June and mid-July and a second peak occurs in early September. The mean number of larvae found in the tubes of females is approximately 5, and the maximum number is 20. The greatest number of larvae that has been found simultaneously in the tube of a female is 35; under laboratory conditions, a total of 36 larvae have been recorded over the course of a season (Wilson et al. 2010). Schloesser et al. (2016) assumed a minimum lifespan of approximately 10 months for *M. speciosa*.

Sitnikova et al. (1997) described the morphology, distribution, and reproduction of three *Manayunkia* species found in Lake Baikal. The mature eggs of the smallest species, *M. zenkewitschii*, are approximately 0.23 to 0.29 mm long. The maximum number of developmental stages in the tube of the females is 18, but eggs are observed within the females simultaneously. The reproductive season in Lake Baikal is probably limited to spring and summer, with a peak during June. The eggs of *M. baicalensis* are 0.28 to 0.33 mm long, and the maximum number of larvae in the tubes of females is 36. The reproduction of this species takes place mainly in July and August. The eggs of the largest species, *M. godlewskii*, are approximately 0.35 to 0.43 mm long. Up to 48 larvae have been observed in the tubes of *M. godlewskii* females, and the breeding season is from September to October (extending to December in some cases).

Nishi (1996) found one to four larvae simultaneously in the tubes of adult females of *Fabricinuda bikinii* (Hartman, 1954). The smallest stage is approximately 20 µm long, and the largest, with developing branchial lobes, is approximately 60 µm long.

Distribution, ecology, and biology

Distribution and ecology

Species of Fabriciidae are distributed in marine, brackish, and freshwater benthic ecosystems worldwide (Fig. 7.4.8.10). They appear to be adapted to environmental stress, so their abundances are very high in unfavorable zones with low biodiversity. However, they have been found to be rapidly displaced by interspecific competition with other suspension feeders (see Phylogeny section), and they disappear rapidly from substrates that are displaced by flow-mediated disturbance.

Several species are also common in freshwater and hypersaline salt lakes, which is unusual among polychaetes (e.g., Leidy 1858, Nusbaum 1901a, b, Monro 1939, Banse 1957, Gitay 1970, Holmquist 1973, Jones 1974, Hutchings et al. 1981, Glasby et al. 2009).

It is notable that species of genus *Manayunkia* occur in marine, brackish, and freshwater habitats as well as in hypersaline or athalassic saline lakes (Leidy 1858, Banse 1956, Hutchings et al. 1981, Bick 1996, Rouse 1996a), whereas species of the genera *Monroika* and *Brandtika* occur exclusively in freshwater (Jones 1974). The last two genera are associated with gastropods and bivalve mollusks, although *Monroika africana* is not confined to shells and valves and is also found on incrustations on stones (Hartman 1951, Jones 1974). Holmquist (1973) concluded from the distribution pattern of *Manyunkia speciosa* that she observed in North America that this species must be an ancient freshwater inhabitant (Fig. 7.4.8.10D). It is believed that this species is a freshwater relic that has been separated from a marine ancestor by geological and climatic events in the past (Schloesser et al. 2016).

This is certainly true for *Manayunkia*, which is a genus that inhabits Lake Baikal. Lake Baikal originated from a deep trench formed 80 million years ago by movements of the Earth's crust. Approximately 25 million years ago, the trench was slowly filled with freshwater. Three species of the genus currently occupy different substrates. *M. zenkewitschii* is mainly found on hard bottoms with or without cover of algae and freshwater sponges at depths of 3 to 20 m (rarely 30 m), whereas *M. baicalensis* occurs on sandy bottoms and *M. godlewskii* occurs on muddy bottoms at depths of 0.8 and 80 and 3.5 to 80 m, respectively (Sitnikova et al. 1997). The occurrence of three species of this genus in an old freshwater lake may be result of speciation by niche specialization. The three species are best

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adapted to the specific characteristics of their particular habitats.

Another *Manayunkia* species, *M. athalassia* Hutchings, Deckker & Geddes, 1981, may persist in the sediment of dried-out saline lakes in South Australia (Figs. 7.4.8.1B, 7.4.8.9A). It has been assumed that some moisture may be trapped by hygroscopic salt crystals and cover of dead plants and algae (Hutchings et al. 1981). However, the temperature may simultaneously exceed 40°C. If distilled water is added to the mud of the dry lakes, active adult specimens can be observed within 1 day at a wide range of salinities, between 27 and 95 psu. It has also been found that specimens could survive a salinity of 82 psu for several months (Hutchings et al. 1981).

Augeneriella hummelincki Banse, 1957 and *Augeneriella lagunari* Gitay, 1970 have also been found in hypersaline salt lakes in the Caribbean and Mediterranean seas (Banse 1957, Gitay 1970).

Giangrande et al. (2014) identified five fabriciid species in a coastal system off the island of Ischia in the Mediterranean Sea, which is naturally acidified by carbon dioxide vent emissions. Among these species, two, *Parafabricia mazzellae* Giangrande, Gambi, Micheli & Kroeker, 2014 and *Brifacia aragonensis* Giangrande, Gambi, Micheli & Kroeker, 2014, are the most abundant even in the extremely low pH zone (pH 6.6–7.2).

The actual distribution of most species appears to be largely unknown possibly due to the small size of the species. More than two-thirds of all described species are only known from the type locality or locations near the type locality. However, it is notable that most genera in this group are found worldwide. Members of the most species-rich genera, *Novafabricia* and *Pseudofabriciola*, which include 11 and 12 species, respectively, are known from the Atlantic, Indian, and Pacific oceans and Caribbean and Mediterranean seas.

However, there are a few exceptions to this pattern. *Fabricia stellaris* seems to be very common in the north Atlantic Ocean, White Sea, Caspian Sea, Mediterranean Sea, and Arctic Ocean probably also due to its high tolerance to abiotic factors, including exposure, temperature, and salinity. This species is split into subspecies, which is rather unusual within polychaetes; three geographically separated subspecies are currently accepted (Fitzhugh 1990d). However, molecular studies have not yet confirmed the correctness of this classification. *F. stellaris stellaris* is the most widely distributed subspecies, being found in the northeast Pacific Ocean (doubtful), north Atlantic Ocean, Mediterranean Sea, White Sea, and Arctic Ocean (e.g., Verrill 1873, Ditlevsen 1929, Wesenberg-Lund 1950, Forsman 1956, Banse 1979, Gillandt 1979, Cardell 1990, Weslawski et al. 1997, Berger et al. 2001, Cacabelos et al. 2008), whereas *F. stellaris caspica* and *F. stellaris adriatica* only occur in the Caspian Sea (Zenkevitsch 1922) and Adriatic Sea (Banse 1956, Cantone 2003), respectively, as well as in the Black Sea (Cinar and Gönlügür-Demirci 2005).

Another species, *Manayunkia aestuarina*, is an important component of the benthic communities of shallow sheltered waters, especially in European and North American boreal brackish regions (Fig. 7.4.8.10C) (Muus 1967, Kendall 1979, Bell 1982, Bishop 1984, Junoy and Viéitez 1990, Bick 1996), and is also found on the Pacific coast of North America (Light 1969, Eckman 1979).

Another example of a wide but disjunct distribution of a Fabriciidae species is that of *Novafabricia infratorquata*. This species was first found along the coast of Belize and was later reported from the Mediterranean Sea (Fitzhugh 1983, Bick 2005, Licciano and Giangrande 2006). However, this still needs to be verified.

Most Fabriciidae species occur in shallow waters. Only certain *Pseudofabriciola* species (e.g., *Pseudofabriciola californica* Fitzhugh, 1991, *Pseudofabriciola filamentosa* (Day, 1963), *Pseudofabriciola filaris* Fitzhugh, 2002, and *Pseudofabriciola longipyga* Fitzhugh, Giangrande & Simboura, 1994), *Fabricinuda longilabrum* Fitzhugh, 2002, and *Raficiba barryi* Fitzhugh, 2001 are known to occur between depths of 50 and 335 m (Day 1963, Fitzhugh 1991a, b, 2001, 2002). In the deep-sea basins of the southwest Atlantic Ocean, two species have been found at a depth of approximately 5,000 m, which have been provisionally assigned to the genera *Novafabricia* and *Fabriciola* (Fig. 7.4.8.10) (Baumhaker 2012). However, a description of these species is not yet available.

Fabriciidae species are usually found in sheltered areas on sandy, muddy, or hard bottoms, in mangroves, on red and green algal mats, and in seagrass beds, always where there is a large amount of fine particulate matter present in the water column (Fig. 7.4.8.10B) (e.g., Muus 1967, Lewis 1968b, Bick 1996). Some species do not show a preference for a particular substrate type. *Fabricia stellaris* is known from hard (Gillandt 1979), sandy (Sicinski 1982), and soft (Berger et al. 2001, Cacabelos et al. 2008) bottoms in addition to occurring among algae (Weslawski et al. 2010), as an epizoan on algae (Muus 1967), and on corallines (Southern 1914) and forming tubes within sponges and *Lithothamnion* (Southern 1914). Two other species, *Rubifabriciola tonerella* and *Novafabricia infratorquata*, are found on the shells of *Stramonita haemastoma* inhabited by hermit crabs in the Mediterranean Sea. Both species have been characterized as facultative symbionts of *Calcinus tubularis* (Linnaeus, 1767) (see Bick 2006). They use the cavities

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formed by boring species in the encrusting calcareous algae that cover the shells. *R. tonerella* was first described from submarine caves in the Mediterranean Sea (Banse 1956, 1959b) but has since been found in infralittoral polychaete assemblages associated with the brown algae *Cystoseira amentacea* and with Demospongiae (Bick 2006). *N. infratorquata* was first found in mats of green algae and *Caulerpa verticillata* as well as rootmats of *Rhizophora mangle* from Belize (Fitzhugh 1983) and later identified on photophilic algae in the Adriatic Sea (Licciano and Giangrande 2006).

The highest abundances of fabriciid species (e.g., *Fabricia stellaris* and *Manayunkia aestuarina*), of more than 1 million individuals per square meter, have been reported in potentially physiologically stressful conditions, including protected areas with a high organic matter content of sediment and brackish waters with highly variable salinities (Schütz 1965, Lewis 1968b, Light 1969, Bagheri and McLusky 1982). The maximum densities of *Manayunkia speciosa* also occur in lentic habitats among benthic algae where there are high levels of detritus and exposure is therefore reduced (Schloesser et al. 2016). The availability of a rich food supply, the protection of the brood in the female tube, and the ability to colonize the habitat quickly seem to be the most important factors leading to such high abundances. *F. stellaris* and *M. aestuarina* may also form large mixed populations containing up to several hundred thousand individuals, as they are not in direct competition for food (e.g., Zenkevitsch 1935, Lewis 1968b). *F. stellaris* feeds on suspended material, whereas *M. aestuarina* is primarily a deposit feeder (Lewis 1968b). *F. stellaris* and *Fabriciola baltica* Friedrich, 1939 form mixed dense populations in the littoral and sublittoral zones of the White Sea (Fateev 1997). Both species have been also found sympatrically in the Barents Sea in the Arctic (Fateev 1999).

It may be presumed that the habitats of fabriciids are located in areas of low exposure, as it appears that they are readily transported with substrates that are displaced by disturbances. The abundance of *Fabricia stellaris* in sandy sediments is correlated with physical and biological parameters (Strelzov and Guverich 1978). The authors who reported this finding stated that both the accumulation and the erosion of sediment decrease the abundance of the species. Wave action increases the erosion of sediment but also increases the quantity of suspended organic matter, which has a positive effect on suspension feeders. *Manayunkia aestuarina* displays a positive response to increased nutrient enrichment, suggesting that this species is sensitive to pollution (Mitwally and Fleeger 2013). Changes in the organic content of the sediment lead to changes in the abundance of *M. aestuarina* in the Baltic Sea. A reduction in organic matter content from approximately 1.8% to 1.0% has been found to be followed by a reduction in abundance from approximately 16,000 to 6,000 individuals per square meter (Bick 1996). It is also assumed that nutrient reduction based on a pollution control program in Lake Erie could have caused a decline in the abundance of *Manayunkia speciosa* (Schloesser et al. 2016). Thus, it has been assumed that this species is an indicator of moderate organic pollution but is intolerant of severe pollution (Mackie and Qadri 1971). *M. speciosa* cannot be found in anoxic sediments (Stocking and Bartholomew 2007).

Tube building

Fabriciidae species produce flexible tubes consisting of the finest sediment particles stabilized by mucus. Detritus is deposited on the outside of the tubes. The tubes are usually significantly longer than the worms themselves, but they are sometimes approximately the same length as the worms (e.g., Muus 1967, Fitzhugh 1990a, b, e, 1992b, 2002, Rouse 1996). The tubes of juvenile worms lie flat on the substrate, but the tubes of adults are usually vertically oriented. Tube building was described in detail for *Fabricia stellaris* and *Manayunkia aestuarina* by Lewis (1968a).

On hard bottoms or algae, *Fabricia stellaris* forms tubes by the secretion of mucus, in which a cylinder is formed by crawling with the pygidium at the front. The mucous cells are located around the pygidium and on the ventral surface of the worms. Rolling motions of the worm support the collection and attachment of particles to the primary mucus tube.

On soft bottoms, *Fabricia stellaris* bores into the substrate through rotating movements with the pygidium positioned at the front. The rotating motions result in the lining of the inner wall of the tube with mucus. The upper margin of the tube above the level of the surrounding substrate is extended by the ventral lobe of the anterior peristomial ring, which exhibits glandular cells and cilia that collect particles from the surface of the substrate and fix them to the tube. Thereafter, medium-sized particles of 5 to 30 μm in diameter are collected and presorted by the radiolar crown and deposited on the top edge of the tube. This is done with the aid of the ventral lobe of the anterior peristomial ring. In very sheltered areas, the tubes project approximately 5 mm or more above the level of the substrate, whereas, in exposed areas, they do not rise above the surface (Lewis 1968a).

Similar to *Fabricia stellaris*, *Manayunkia aestuarina* bores into the substrate via rotating movements conducted in a posterior end-first orientation. As the ventral

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lobe of the anterior peristomial ring collar is rectangular, weakly ciliated, and not very mobile, this species does not collect particles from the surface of the substrate, as observed in species such as *F. stellaris* and other fabriciids with a rounded or triangular lobe of the anterior peristomial ring (Bick 2004). In muddy or sandy sediment, a tube is built by the worm by stretching and bending backward until particles stick to its radiolar crown. The particles are stripped off at the upper edge of the tube, and adhering particles are removed (Lewis 1968a). Medium-sized particles are also sorted out by the tentacle crown, transported to the ventral lobe of the peristomial rings, coated with mucus, and placed on the upper edge of the tube. The openings of the tubes protrude from the substrate by a maximum of 2 mm, which permits the radiolar crown to be placed on the substrate to feed on the upper sediment layer (deposit feeding). Chain-like bales of feces are found near the tube. After damage caused by larger benthic species, the worms quickly rebuild their tubes at a rate of 5 mm per approximately 1.5 hours (Muus 1967).

Manayunkia athalassia has been found in translucent gelatinous tubes in soft clayey carbonate sediments (Fig. 7.4.8.1B). This species sometimes lives in colonies of up to 20 individuals (Hutchings et al. 1981). According to Leidy (1883), most of the tubes of *M. speciosa* occur as single tubes, but two to five tubes connected together have been found in some cases. The tubes of *P. capensis* are fused together along most of their length and thereby form large clusters (Fitzhugh 1991a).

The tube material of *Augeneriella*, *Fabricinuda*, *Novafabricia*, and *Pseudofabriciola* species consists of mucus with detritus, fine mud or silt, and calcium or quartz sand grains. At least some species (e.g., *Rubifabriciola tonerella* and *Novafabricia infratorquata*) use the empty holes of species boring in calcareous substrates, such as *Cliona* spp. (Demospongiae), polydorids (Spionidae), and *Dodecaceria concharum* Örsted, 1843 (Cirratulidae) (Bick 2006).

Biology and behavior

Fabriciids are small tube-dwelling polychaetes that can voluntarily leave their tubes and travel with their posterior end in front. Mechanical disturbances caused by large benthic species and a lack of oxygen in the sediment result in the rapid exit of these species from their tube or deep withdrawal into their tubes. However, Wilson et al. (2010) observed that mature females with larvae in their tubes left the tubes less often than males or nonbreeding females. When they left the tubes, they often forced juveniles out as well. Schloesser et al. (2016) concluded from their observations of *Manayunkia speciosa* from western Lake Erie that a large proportion of individuals occur outside of their tubes most of the time during warmer months and that their tubes are not maintained in colder months.

High temperatures, a lack of oxygen, and other unfavorable parameters cause *Manayunkia aestuarina* to extend the posterior end out of the tube and perform circular movements. Frequently, the radiolar crown is then thrown off (Schütz 1965). Outside of the tubes, the worm encases itself in mucus and shows great chaetal activity in search for a suitable substratum (Knight-Jones 1981).

Fabriciids feed on suspended material. In addition to detritus, they ingest bacteria, heterotrophic protozoa, cyanophyceans, and, above all, diatoms. However, they can also exhibit deposit feeding. This feeding type has been described in *Manayunkia aestuarina* by Lewis (1968a). To perform this type of feeding, two pairs of radioles are placed on the substrate with the adoral side on the surface of the substrate. The cilia of the radioles promote the collection of food particles from the substrate and their transport to the mouth opening.

The ability to sort suitable particles for food intake and tube construction has been described in *Fabricia stellaris* and *Manayunkia aestuarina*, and it is assumed to exist in all Fabriciidae species (Lewis 1968a). The sizes of the ingested particles are usually approximately 1 to 2 µm, less frequently between 2 and 7 µm, and occasionally may be up to 20 µm (Lewis 1968a).

Fecal pellets leave the subterminal anus and travel upward in the fecal groove up to the incised dorsal part of the anterior peristomial ring. The pellets are carried by the cilia of the fecal groove and the main current of the radiolar crown, which eventually carries the pellets clear of the radiolar crown (Lewis 1968a).

Symbiosis

Symbiosis is used in its broader sense in the following text. Here, it includes commensalism and parasitism.

The freshwater species *Brandtika asiatica* Jones, 1974 is a commensal species of mollusks. It is not a shell burrower, but it attaches its tubes on the shells of viviparid gastropods and unionid bivalves in Southeast Asian rivers (Jones 1974). The relationships between these taxa are not yet known. Another freshwater species, *Monroika africana*, has been found at the apical end of *Hydrobia plena* freshwater snails in the Congo River, West Africa. This species is not confined to shells and also found in incrustations on stones (Hartman 1951, Jones 1974). Thus, this species is at least a facultative symbiont. Two marine species, *Rubifabriciola tonerella* and *Novafabricia infratorquata*, have been found on shells of the red-mouthed rock shell

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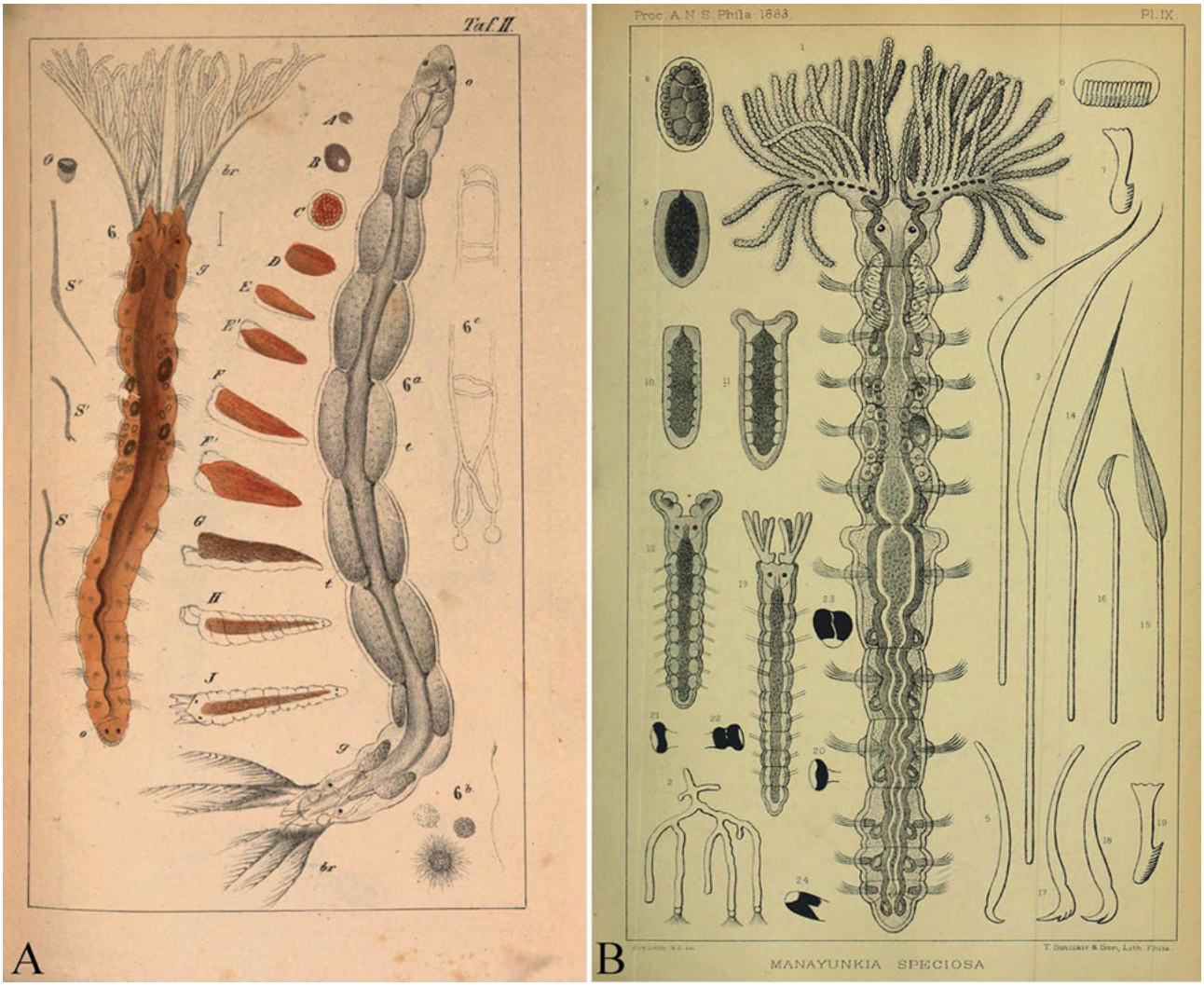


Fig. 7.4.8.11: Original plates of the morphology and development of the first described species of Fabriciidae from the nineteenth century. A, B, figures 14–24, *Fabricia stellaris* (Müller, 1774); B, figures 1–13, *Manayunkia speciosa* Leidy, 1858. Both original plates show the external and internal morphologies in great detail, particularly the blood vessel (*M. speciosa*), the nephridia, several stages of the development of gametes and larvae, and the tubes (*M. speciosa*). Original from Schmidt (1848) and Leidy (1883).

Stramonita haemastoma (Linnaeus, 1767) inhabited by hermit crabs in the Mediterranean Sea (see Distribution and ecology section). Both species have been characterized as facultative symbionts of *Calcinus tubularis* (see Bick 2006). Jensen and Bender (1973) observed *Fabricia stellaris* on the shells of different gastropods inhabited by *Pagurus bernhardus* Linnaeus, 1758 in Denmark and Sweden. It is assumed in these cases that Fabriciidae inhabit the shells of freshwater and marine mollusks, as they are not covered by algae and sponges, and there is little competition with other species, especially with other suspension feeders. Shells are regarded as a mobile substratum for fabriciid species showing low competition. Their abundances are also very high in other benthic habitats with low diversity and competition (see Distribution and ecology section).

Another example of commensalism is the occurrence of peritrichous ciliates on anterior chaetigers in *Manayunkia aestuarina* (Fig. 7.4.8.7G, G′). Several examples of epibiosis between polychaetes and ciliates exist (Mikac et al. 2019), but this is the first record of epibiosis between Peritrichia and Fabriciidae. It has been assumed that several advantages and disadvantages for both partners exist. However, it is not known whether these relationships are species specific.

Manayunkia speciosa is an obligate invertebrate host of the myxozoan parasites *Ceratonova shasta* Noble, 1950 and *Parvicapsula minibicornis* Kent, Whitaker & Dawe, 1997, which cause ceratomyxosis in salmon and trout in North America (Bartholomew et al. 2006, Alexander et al. 2014). *C. shasta* is responsible for necrosis that may be accompanied

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Fig. 7.4.8.12: Deep-sea Fabriciidae from the southwest Atlantic Ocean. A, Anterior end from lateral; B, Complete specimen; C, Thoracic uncinus; D, Abdominal uncini. Scale bars: A = 50 µm, B = 200 µm, C, D = 2 µm.

by a severe inflammatory reaction and subsequent death of its salmonid hosts (Alexander et al. 2014). Internally, infection with *C. shasta* affects the entire digestive tract, liver, gall bladder, spleen, gonad, kidneys, heart, gills, and muscle tissues. Infection with *C. shasta* in adult Chinook salmon causes mortality through intestinal perforations and cooccurring bacterial infections (Bartholomew 1998). Approximately 70% to 100% of juvenile Chinook salmons are infected by the parasites during early summer when these fish migrate to the ocean. They can cause mortality rates of approximately 40% in *Oncorhynchus* spp. (Schloesser et al. 2016). *P. minibicornis* is found in the kidneys of juvenile Chinook salmon, but the effect of the infection is not yet clear because it is often present concurrently with *C. shasta*. Management actions such as flow manipulations to increase the mortality of the host *M. speciosa* and disturb its habitat have been implemented (Alexander et al. 2014).

Phylogeny and taxonomy

Taxonomic history

The first species of Fabriciidae was identified in 1774, when *Tubularia stellaris* was first described from the Baltic Sea in Denmark by O.F. Müller (1774). Thus, this very small species is one of the earliest described polychaete species (Fig. 7.4.8.11A, B, figures 14–24). The same species was later described as *Tubularia fabricia* from the west coast of Greenland by Fabricius (1780), as *Othonia fabricii* from the Scottish coast by Johnston (1835), as *Amphicora sabella* from Helgoland by Ehrenberg (1836) and the Faroe Islands by Schmidt (1848), and as *Fabricia leidyi* and *Haplobranchus atlanticus* from the east coast of North America by Verrill (1873) and Treadwell (1932), respectively. Thus, the distribution of this species, which is known today as *Fabricia stellaris*, is quite well characterized (Fitzhugh 1990d).

The second described species of Fabriciidae is *Manayunkia speciosa* Leidy, 1858 (Fig. 7.4.8.11B, figures 1–13). It is notable that this is a small freshwater species. The genus name was derived from the Indian name of the Schuylkill River at Fairmont, within which it was first discovered. Subsequently, additional species of the genera *Brandtika*, *Manayunkia*, and *Monroika* have been described from freshwater lakes and rivers.

All fabriciid species have long been included within Sabellidae Latreille, 1825 based on the shared presence of a radiolar crown on a reduced prostomium, a thorax

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region with notopodial chaetae and neuropodial uncini, and an abdominal region with neuropodial chaetae and notopodia uncini. The tube of fabriciids is usually formed from mucus combined with mud or sand, as also observed in all Sabellidae, whereas nearly all species of Serpulidae, the sister taxon, inhabit calcareous tubes. Rioja (1923) established the subfamily Fabriciinae based on the presence of thoracic acicular uncini in several genera of Sabellidae.

As a result of a morphology-based cladistic analysis of Sabellidae, Fitzhugh (1989) transferred genera with thoracic acicular uncini as well as a radiolar skeleton consisting of vacuolated cells to Sabellinae. The radiolar skeleton and the dorsally fused radiolar lobes are considered as apomorphic characters of Sabellinae. The monophyly of Fabriciinae is based on the absence of ventral lips, the modification of the abdominal uncini into an elongated manubrium, and the presence of branchial hearts (Fitzhugh 1991b, Huang et al. 2011).

Whereas the monophyly of Fabriciinae and Sabellinae is well supported based on morphological characters, this is not the case for Sabellidae. Kupriyanova and Rouse (2008) proposed a molecular-based phylogeny of Sabellida, suggesting that Fabriciinae, Sabellinae, and Serpulidae are monophyletic, whereas Fabriciinae forms a clade with Serpulidae, and Sabellinae is their sister group. Consequently, Fabriciinae has been separated from Sabellinae and was regarded as the sister taxon, Fabriciidae, of Serpulidae (Kupriyanova and Rouse 2008, Huang et al. 2011). Recently, Tilic et al. (2020) conducted a large-scale phylogenomic analysis with 3 species of Fabriciidae, 2 species of Serpulidae and 15 species of Sabellidae. Their results support the position of Fabriciidae as sister taxon to a Sabellidae and Serpulidae clade. Rouse (1990, 1992, 1993, 1995a, b, 1996a, b, 1999, 2005) and Rouse and Fitzhugh (1994) showed that sperm morphology and the reproductive system are also useful for phylogenetic reconstruction in Fabriciidae. They found six unambiguous synapomorphies that complemented the three abovementioned morphological characters (Huang et al. 2011): spermiogenesis in the thorax with a large cluster of spermatids associated with a central cytophore and the presence of a single, dorsal sperm duct, sperm nuclear projection, sperm nuclear membrane thickening, and an extra-axonemal sheath.

More than half of all the species and genera that are considered valid today have not been described until 1990. The comprehensive examination of characters by Fitzhugh (see References), who identified structures of the radiolar crown and the anterior end as essential diagnostic characters, significantly contributed to progress in the taxonomy of Fabriciidae. The discovery of two Fabriciidae species in deep-sea basins of the southwest Atlantic Ocean shows that members of this taxon also occur in the deep sea (Fig. 7.4.8.12) (Baumhaker 2012). Future studies of the deep-sea fauna may therefore increase the number of known species significantly.

The identification of species remains difficult, as only a few diagnostic characters exist. Additionally, some important diagnostic characters are size dependent and vary with sex or individually (Holmquist 1967, Bick 1995, 2007). This is the case, for example, for the number of abdominal chaetigers in *Echinofabricia* (see Rouse 1990) and *Fabricia* (see Rassmussen 1973), the radiolar crown-to-body length ratio in *Fabriciola* (see Bick 2005), the extent of the branching of the radioles in *Fabricia* (see Knight-Jones and Bowden 1984), and the ventral filament appendages in *Augeneriella* (see Gitay 1970, Fitzhugh 1990e) as well as the number and dentition of the uncini in *Augeneriella* (see Gitay 1970), *Fabricinuda* (see Rouse and Fitzhugh 1994), and *Novafabricia* (see Bick 2005).

Fitzhugh and Simboura (1995) observed a range of variation in the anterior end and the pygidium of *P. longipyga*. They concluded that the observed differences are most likely due to different degrees of contraction as a consequence of fixation. Such artifacts, which certainly occur in other fabriciids as well, further complicate the identification of these small worms based on only a few diagnostic characters.

Phylogeny

Fossils of fabriciids are unknown, and hypotheses about their phylogeny have thus been based on extant species, their development, their character states, and their distribution. Based on the investigation of reproductive characters, Rouse and Fitzhugh (1994) suggested that ancestral sabellids are small, gonochoristic species and brooders of larvae with direct development. Within Sabellida, these characters are distinctly present only in Fabriciidae. Other possible plesiomorphic characters include the presence of only three pairs of radioles, the ability to leave the tubes voluntarily, and the ability to switch between suspension and deposit feeding, whereas the related Serpulidae and Sabellidae are sessile and exhibit highly specialized radiolar crowns, usually with more than three pairs of radioles and pinnules for filter feeding (see External morphology section). Most species of Sabellidae and Serpulidae also begin their ontogenetic development with three pairs of radioles, which could represent the plesiomorphic character state within Sabellida (e.g., Segrove 1941, Okuda 1946, Berrill 1977, McEuen et al. 1983, Yun and Kikuchi

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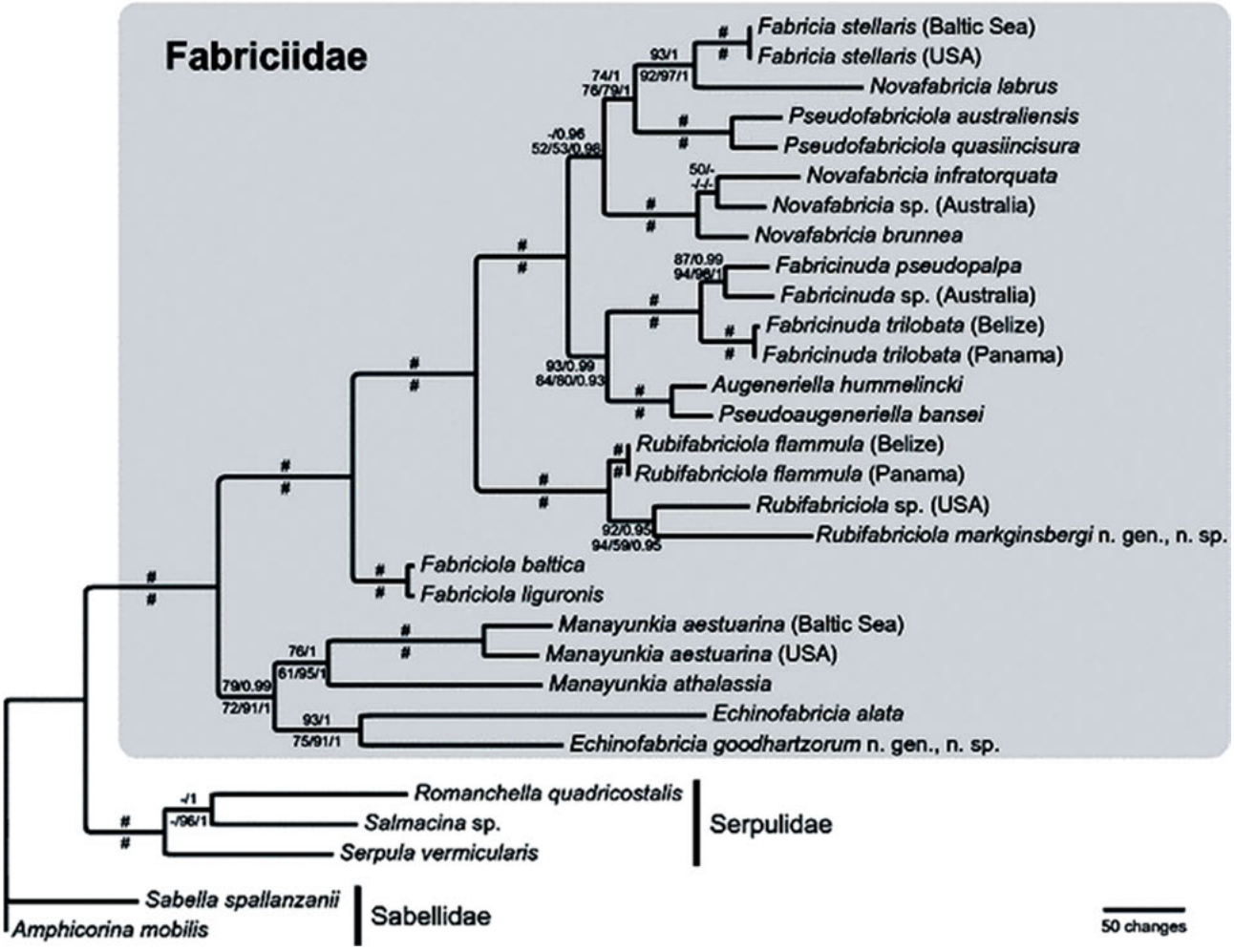


Fig. 7.4.8.13: Most parsimonious (MP) tree from analysis of combined molecular and morphological data. Numbers adjacent to branches are support values from various analyses. Those above are from the combined data analyses (MP jack-knife ≥50 followed by Bayesian posterior probability ≥0.9), whereas the numbers below are from the analyses of molecular data only (MP jack-knife ≥50 followed by maximum likelihood bootstrap ≥50 and Bayesian posterior probability ≥0.9). #, jack-knife/bootstrap values of 100 and posterior probability of 1. (Reprint from Huang et al. 2011, fig. 1, with permission from John Wiley & Sons. See reference list for full citation.)

1991, Nishi and Yamasu 1992, Rouse and Fitzhugh 1994, Del Pasqua et al. 2017).

Fabriciids exhibit a worldwide distribution (see Distribution and ecology section). Even the species of monophyletic genera are distributed worldwide. This is remarkable in regard to their rather limited dispersal capacities because of brood protection and direct development.

Fitzhugh (2002) suggested that intertidal occurrence might be plesiomorphic. This assumption is based on the mapping of depth distributions onto the consensus tree of a cladistic analysis. Most species of Fabriciidae actually occur in the tidal and shallow subtidal zone. It has been suggested that adaptation to stressful conditions might be a common trait within Fabriciidae (Giangrande et al. 2014).

Based on the abovementioned characters, along with efforts such as the reevaluation of the ultrastructure of the radiolar crown and the splitting of the radioles (Fig. 7.4.8.4) (see External morphology and Internal morphology sections), it is suggested here that Fabriciidae could be the basal taxon within Sabellida or at least the taxon with the greatest number of plesiomorphies. Based on morphological studies, Smith (1991) suggested that Sabellinae forms a clade with Serpulidae and that Fabriciinae is the sister group of that clade. Tilic et al. (2020) also postulated this relationship based on a phylogenomic analysis.

In any case, the distribution of species and genera suggests that Fabriciidae is a very ancient polychaete taxon widespread in the oceans of the Palaeozoic or Mesozoic at least 250 to 200 million years b.p. [However, fossils attributed to spirorbids (Serpulidae) are known from as early as the Ordovician (505–438 million years b.p.) (Knight-Jones 1981).] With the development of the branchial crown with

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radioles and pinnules in Sabellidae and Serpulidae (see External morphology section), highly specialized filter feeders developed, which displaced the less specialized and less competitive fabriciids. At present, fabriciids are mainly found in habitats with low species numbers. Therefore, their occurrence in tidal zones under different stress conditions may not be a common character within Fabriciidae but may be the result of low competitiveness.

The adaptability of Fabriciidae and the distribution of certain species can be demonstrated using the example of *Manayunkia* (see Distribution and ecology section). The nine extant *Manayunkia* species occur worldwide in marine, brackish, and freshwater habitats as well as in hypersaline lakes. Their common ancestor was most likely already present in marine habitats worldwide. From those environments, different species were displaced into habitats that are normally unfavorable to marine species. For example, the marine ancestors of *Manayunkia* species found in Lake Baikal originated from the northern Mesozoic ocean, which stretched southward to the center of Siberia and then retreated slowly. The remaining lake is located in a shallow depression but deepened and grew larger due to movements of the Earth and became colder. Thereafter, it is no longer possible to migrate back and forth between Lake Baikal and the surrounding shallow lakes because the living conditions are too different. The ancestor of *Manayunkia* in Lake Baikal has adapted to its unique conditions. The great age of the lake has allowed the speciation of *Manayunkia* and the niche differentiation of the three species currently living in Lake Baikal.

Holmquist (1973) concluded from the distribution pattern of *Manayunkia speciosa* in North America that this species must also be a very old freshwater inhabitant that has been separated from a marine ancestor by geological and climatic events in the past.

Based on molecular sequence data, Kupriyanova and Rouse (2008) found that Fabriciinae is closer to Serpulidae than to Sabellinae. They proposed that Fabriciinae should be removed from Sabellidae and be referred to as Fabriciidae, leaving the revised Sabellidae. A common character of Fabriciidae and Serpulidae is the presence of well-separated radiolar lobes and acellular radiolar skeletons in contrast to the dorsally fused radial lobes and the skeleton formed by large vacuolated cells in Sabellidae. However, it is not clear if these characters are truly apomorphies of Fabriciidae/Serpulidae clade or plesiomorphic characters.

An analysis of phylogenetic relationships within Fabriciidae using molecular and morphological data was presented by Huang et al. (2011) (Fig. 7.4.8.13). They found nine apomorphies for Fabriciidae (see Taxonomic history section). *Echinofabricia* and *Manayunkia* are identified as sister groups, and this clade is considered as the sister to the remaining genera. At least *Manayunkia* is characterized by plesiomorphic characters, such as the structure of the radiolar crown without significant supporting structures, the asymmetrical branching of the radioles, and the presence of transitional chaetae (see External morphology section) on the posterior thoracic chaetigers (which, however, are positioned more anteriorly during crawling with the posterior end in front). *Fabricia*, *Fabricinuda*, *Fabriciola*, *Pseudofabriciola*, and *Rubifabriciola* form well-supported clades, whereas *Novafabricia* is not monophyletic. *Augeneriella* and *Pseudoaugeneriella* also form a well-supported clade, which is sister to *Fabricinuda*. *Monroika africana* forms a polytomy with *Manayunkia*; i.e., the relationship is not yet resolved. It has also been found that the apomorphic ventral filamentous appendages and pigmented spermathecae, which are apomorphies of Fabriciidae, have been lost several times within fabriciids. The anterior peristomial ring collar and the black peristomial eyes have also reverted to the outgroup conditions in some cases. However, in this paper, it is emphasized that the morphological characters may support a Fabriciidae/Serpulidae or Fabriciidae/Sabellidae clade. A possible sister group relationship of Fabriciidae with Sabellidae/Serpulidae is not discussed but is suggested here. Further studies are still needed to describe the phylogeny of these taxa and the relationships within Sabellida.

Fabriciidae Rioja, 1923

Type genus: *Fabricia* Blainville, 1828.

About 80 species.

Diagnosis: Small-bodied, hemisessil polychaetes with eight thoracic and three, exceptionally two or four, abdominal chaetigers. Three pairs of radioles; branchial lobes not fused together middorsally; radioles symmetrically or asymmetrically branched; ventral filamentous appendages present or absent; acellular radiolar skeleton absent or present; radiolar crown with branchial hearts; ventral lips absent. Anterior margin of anterior peristomial ring a low ridge dorsally and laterally; a triangular, rounded, or rectangular lobe ventrally. Thoracic uncini acicular, with main fang followed by smaller teeth. Abdominal uncini with elongated manubrium and dentate region; dentate region with multiple rows of equal-sized teeth. Spermiogenesis on thoracic chaetigers; spermatids in large cluster with central cytophore; single, dorsal sperm duct present. Sperm nuclear projection present; sperm nuclear membrane thickening; extra-axonemal sheath present.

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Remarks: The diagnosis of Fabriciidae is emended by the description of the branching patterns of the radiolar crown. The branches of the radioles are formed by successive longitudinal splitting. Pinnules, as present in Sabellidae and Serpulidae, are not developed. Symmetrical splitting leads to bipectinate radioles (present in most genera of Fabriciidae), and asymmetrical splitting to pectinated radioles (present in *Manayunkia*, *Monroika* (and probably also in *Brandtika*).
Distribution: Marine, brackish, and freshwater benthic ecosystems; from intertidal to deep sea; worldwide.

Augeneriella Banse, 1957

Type species: *Augeneriella hummelincki* Banse, 1957, by monotypy.
6 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages present, vascularized, dichotomously branched, nonciliated; dorsal lips erect, well developed. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a low ridge laterally and dorsally; a rounded, conical lobe ventrally; annulation between anterior and posterior peristomial rings distinct all around, except middorsally. Inferior thoracic notochaetae on chaetigers 2 and 8, sometimes on chaetiger 7, elongated, narrowly hooded and on chaetigers 3 to 7 or 3 to 6 pseudospatulate; thoracic uncini with single large tooth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same length and width as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.
Distribution: Caribbean Sea; Mediterranean Sea; Indian Ocean: Mozambique, Picard Island; South Australia (Day 1957, Gitay 1970, Hartmann-Schröder 1986, Fitzhugh 1990e, 1991a).

Bansella Fitzhugh, 2010

Type species: *Fabricia oregonica* Banse, 1956, by subsequent designation.
1 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips erect, triangular, rounded distally. Anterior peristomial ring distinctly wider than long but distinctly shorter than posterior ring; anterior margin of anterior peristomial ring a low ridge laterally and dorsally, with narrow middorsal separation; a wide, rectangular lobe ventrally; annulation between anterior and posterior peristomial rings distinct all around, except middorsally. Inferior thoracic notochaetae on chaetigers 2 to 8 narrowly hooded, distinctly shorter than superior notochaetae; thoracic uncini with single large tooth offset from midline of main fang followed by a series of smaller teeth; main fang slender; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same length as dentate region or longer. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8.
Distribution: Pacific Ocean: Oregon (Banse 1956, 1979, Hobson and Banse 1981, Fitzhugh 2010).

Brandtika Jones, 1974

Type species: *Brandtika asiatica* Jones, 1974, by original designation.
1 species (plus another undescribed species).
Diagnosis: Eight thoracic and two abdominal chaetigers. Anterior peristomial ring collar present; margin entire but with deep middorsal incision; annulation between anterior and posterior peristomial rings distinct. Inferior thoracic notochaetae on chaetigers 2 to 8 pseudospatulate; thoracic uncini on chaetigers 2 to 5 with single large tooth slightly offset over main fang followed by a series of smaller teeth; on chaetigers 6 to 8, short and geniculated (sharply bent) chaetae with pilose end (transitional chaetae) replaced the thoracic uncini; abdominal uncini with a single, proximal large central tooth surmounted distally by rows of equal-sized teeth.
Remarks: Characters of the radiolar crown are unknown due to the dried condition of the collected specimens (Jones 1974).
Distribution: Southeast Asia: Laos, Mekong River; Thailand, Salween River; Burma, Thoungyin River (Jones 1974).

Brifacia Fitzhugh, 1998

Type species: *Brifacia metastellaris* Fitzhugh, 1998, by original designation.
2 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips erect, well developed, elongated. Anterior margin of anterior peristomial ring a low ridge dorsally and laterally; ventrally a low, broadly triangular lobe; annulation between anterior and posterior peristomial rings distinct dorsally and ventrally. Inferior thoracic notochaetae on chaetigers 2 and 8 narrowly hooded and on chaetigers 3 to 7 pseudospatulate; thoracic uncini with a single large tooth slightly offset over main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same

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length as dentate region and wider than dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.
Distribution: Southeast Australia; Mediterranean Sea, Tyrrhenian Sea (Fitzhugh 1998, Giangrande et al. 2014).

Echinofabricia Huang, Fitzhugh & Rouse, 2011

Type species: *Echinofabricia goodhartzorum* Huang, Fitzhugh & Rouse, 2011, by original designation.
4 species.
Diagnosis: Eight thoracic and four abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; unbranched unvascularized ventral filamentous appendages present; dorsal lips as triangular ridges; radiolar lobes wide and short, with an even ventral margin. Epithelium with emergent spicules (upon fixation) that may splay out. Anterior peristomial ring dorsally shorter than posterior peristomial ring; anterior margin of anterior peristomial ring with wide ventral lobe; females with darkly pigmented spermathecae. Inferior thoracic notochaetae narrowly hooded; thoracic uncini with a series of uniformly small teeth above main fang; abdominal uncini with multiple rows of equal-sized teeth, manubrium 1.5 to 2.5 times longer and slightly wider than dentate region. Peristomial eyes red and disappear upon preservation. Spermiogenesis on chaetigers 3 to 8 or 4 to 8. Sperm nucleus with spiral ridge: spike-like nuclear projection; extra-axonemal sheath developed as simple sleeve; acrosome small and cap-like.
Remarks: Peristomial and pygidial eyes are not observed on fixed material of *E. alata*, *E. dubia*, and *E. rousei*. Spicules in the epithelium are not found in *E. rousei* probably due to bad preservation (Giangrande et al. 2013).
Distribution: Caribbean Sea: Belize; Australia; East Pacific, Hawaii; Mediterranean Sea (Hartmann-Schröder 1965, 1981, Rouse 1990, Huang et al. 2011, Giangrande et al. 2013).

Fabricia Blainville, 1828

Type species: *Tubularia stellaris* Müller, 1774, by monotypy.
1 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips erect, well developed; distal ends rounded. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a low ridge laterally and dorsally; a rounded, triangular lobe ventrally; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct dorsally. Inferior thoracic notochaetae on chaetigers 2 and 8 short, elongated, narrowly hooded and on chaetigers 3 to 7 with pseudospatulate chaetae; thoracic uncini with large tooth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium at least twice as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8.
Distribution: North Atlantic Ocean; Arctic Ocean; White Sea; Caspian Sea; Mediterranean Sea; Black Sea (Verrill 1873, Zenkevitsch 1922, Ditlevsen 1929, Wesenberg-Lund 1950, Banse 1956, Forsman 1956, Gillandt 1979, Cardell 1990, Weslawski et al. 1997, Fateev 1999, Berger et al. 2001, Cantone 2003, Cinar and Gönlügür-Demirci 2005, Cacabelos et al. 2008).

Fabricinuda Fitzhugh, 1990

Type species: *Fabricia limnicola* Hartman, 1951, by subsequent designation.
7 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages unbranched, slender and vascularized, or absent; dorsal lips present or absent. Anterior peristomial ring as long as or longer than posterior peristomial ring; anterior margin of anterior peristomial ring a low, even ridge all around or slightly oblique; rounded lobe present or absent on either side of dorsal midline; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct dorsally. Inferior thoracic notochaetae on chaetigers 2 and 8 narrowly hooded and on chaetigers 3 to 7 or 8 pseudospatulate; thoracic uncini with single large tooth slightly offset over main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.
Distribution: Pacific Ocean: California, Bikini Island, Gulf of Thailand; Caribbean Sea: Belize, Venezuela; Gulf of Mexico, Florida; Indian Ocean: Picard Island (Hartman 1954, Fitzhugh 1990a, 2002, Nishi 1996, López and Rodríguez 2008).

Fabriciola Friedrich, 1939

Type species: *Fabriciola baltica* Friedrich, 1939, by original designation.
6 species.
Diagnosis: Eight thoracic and three abdominal chaetigers (except *F. minuta* with two abdominal chaetigers). Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages

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nonvascularized, unbranched, slender; dorsal lips well developed, distal end rounded. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a low membranous collar, except for middorsal gap; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct dorsally. Inferior thoracic notochaetae on all chaetigers short, narrowly hooded; thoracic uncini with two or three larger teeth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium at least twice as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8 or 4 to 8.

Distribution: North Atlantic Ocean: Baltic Sea, Maine; White Sea; Barents Sea; Pacific Ocean: Commander Islands, Papua New Guinea; Caribbean Sea: Belize; India, Chilka Lake (Southern 1921, Annenkova 1934, Friedrich 1939, Fitzhugh 1990c, Rouse 1993, 1996a, Sarma et al. 1994, Fateev 1997, 1999).

Manayunkia Leidy, 1858

Type species: *Manayunkia speciosa* Leidy, 1858, by monotypy.

10 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles asymmetrically branched, slightly wrinkled; acellular radiolar skeleton absent; unbranched vascularized ventral filamentous appendages present, slightly wrinkled; dorsal lips erect, broadly rounded. Anterior margin of anterior peristomial ring developed as a membranous collar with rectangular ventral lobe, narrowly separated middorsally. Inferior thoracic notochaetae on chaetigers 5 to 8 or 6 to 8 elongated, narrowly hooded and on chaetigers 2 to 5 or 2 to 6 pseudospatulate; thoracic uncini with one or two larger teeth above main fang followed by a series of smaller teeth, sometimes with transitional chaetae on chaetigers 6 to 8; abdominal uncini with multiple rows of equal-sized teeth, manubrium longer than dentate region. Peristomial eyes present, pygidial eyes absent. Spermiogenesis on chaetigers 6 to 8.

Remarks: Based on the description of Annenkova (1938), *M. siaukhu* does not belong to this genus, as it has pygidial eyes. Already, Zenkevitsch (1935) and Hartman (1951) assumed a synonymy of *M. polaris* with *M. aestuarina*, and Banse (1956) assumed a synonymy of *M. balticus*, described as *Haplobranchus balticus* by Karling (1933), with *M. aestuarina*.

Distribution: North Atlantic Ocean: North America; North Sea; Baltic Sea; southwest Atlantic Ocean: Brazil; Pacific Ocean: Papua New Guinea; South Australia; Caspian Sea; Lake Baikal (Leidy 1858, Bourne 1883, Nusbaum 1901a, b, Annenkova 1929, Dybowski 1929, Zenkevitsch 1935, Banse 1956, Hutchings et al. 1981, Rouse 1996a, b, Sitnikova et al. 1997).

Monroika Hartman, 1951

Type species: *Manayunkia africana* Monro, 1939, by original designation.

1 species (plus another undescribed species).

Diagnosis: Eight thoracic and two abdominal chaetigers. Radioles asymmetrically branched; acellular radiolar skeleton absent; unbranched vascularized ventral filamentous appendages present; dorsal lips erect, broadly rounded. Anterior margin of anterior peristomial ring developed as a membranous collar with rectangular ventral lobe, narrowly separated middorsally. Inferior thoracic notochaetae on chaetigers 2 and 6 to 8 elongated, narrowly hooded and on chaetigers 2 to 5 pseudospatulate; thoracic uncini with one larger teeth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about twice as long as dentate region. Peristomial eyes black, pygidial eyes absent.

Remarks: A second *Monroika* species has been found in Uruguay River. This will be described elsewhere (Bick in preparation).

Distribution: West Africa, Congo River; South America, Uruguay River (Bick own unpublished data).

Novafabricia Fitzhugh, 1990

Type species: *Fabriciola chilensis* Hartmann-Schröder, 1962, by original designation.

11 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips reduced to low, narrow ridges. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring developed as low ridge laterally and dorsally and a rounded lobe ventrally; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct middorsally. Inferior thoracic notochaetae on chaetigers 2 and 6 to 8 or 7 to 8 narrowly hooded and on chaetigers 3 to 5 or 3 to 6 pseudospatulate chaetae; thoracic uncini with a single large tooth slightly offset over main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of one to several teeth per row, manubrium as long as dentate region or twice as long. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8 or 4 to 8.

Distribution: Atlantic Ocean: southwest Africa; Pacific Ocean: Australia, California, Chile, Papua New Guinea;

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Indian Ocean: Picard Island; Caribbean Sea: Belize, Mexico; Mediterranean Sea: Adriatic Sea, western Mediterranean, Tyrrhenian Sea (Day 1961, Hartmann-Schröder 1962, Fitzhugh 1990b, 1993, 1998, Martin and Giangrande 1991, Bick 2005, Licciano and Giangrande 2006).

Parafabricia Fitzhugh, 1992

Type species: *Parafabricia ventricingulata* Fitzhugh, 1992, by original designation.
2 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips well developed, triangular. Anterior and posterior peristomial rings wider than long; anterior margin of anterior peristomial ring developed ventrally as triangular, broad, distally rounded lobe, laterally and dorsally as rounded shelf; dorsolateral, lateral, and portion of ventral areas of anterior peristomial ring concealed by posterior peristomial ring; annulations between anterior and posterior rings only visible middorsally and ventrally. Inferior thoracic notochaetae on chaetigers 2 and 8 elongated, narrowly hooded and on chaetigers 3 to 7 pseudospatulate; thoracic uncini with one large tooth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same length as dentate region. Peristomial and pygidial eyes black.
Distribution: Pacific Ocean: northwest Australia; Mediterranean Sea, Tyrrhenian Sea (Fitzhugh 1992a, b, Giangrande et al. 2014).

Pseudoaugeneriella Fitzhugh, 1998

Type species: *Pseudoaugeneriella unirama* Fitzhugh, 1998, by original designation.
3 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; vascularized ventral filamentous present, slightly shorter than radioles, surface smooth or slightly wrinkled; dorsal lips low or slightly erect, broadly rounded distally or a low ridge, distinct from radioles. Anterior peristomial ring wider than long, shorter than posterior peristomial ring; anterior margin of anterior peristomial ring a low ridge laterally and dorsally; ventrally developed as an low, triangular lobe; annulation between anterior and posterior peristomial rings visible only ventrally. Inferior thoracic notochaetae on chaetigers 2 and 7 to 8 narrowly hooded and on chaetigers 3 to 6 each with two pseudospatulate chaetae; thoracic uncini with a large tooth slightly offset over main fang surmounted distally by progressively shorter teeth; abdominal uncini with multiple rows of equal-sized teeth; manubrium longer than dentate region, slightly expanded proximally. Peristomial and pygidial eyes black.
Distribution: Atlantic Ocean: Madeira, Canary, and Selvagem islands; Indian Ocean: Andaman Sea, Thailand; Pacific Ocean: Okinawa Island (Langerhans 1880, *Núñez* and Talavera 1995, Fitzhugh 1998, 1999, *Núñez* et al. 2001, Bick 2004).

Pseudofabricia Cantone, 1972

Type species: *Pseudofabricia aberrans* Cantone, 1972, by monotypy.
1 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; nonvascularized ventral filamentous present, very short; dorsal lips as triangular ridges. Anterior peristomial ring wider than long, shorter than posterior peristomial ring; anterior margin of anterior peristomial ring a ridge laterally and dorsally; ventrally developed as an elongated triangular tongue-like flattened lobe. Inferior thoracic notochaetae on chaetigers 2 to 8 elongated, narrowly hooded; thoracic uncini with a large tooth above the main fang surmounted distally by progressively shorter teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about twice as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8.
Distribution: Mediterranean Sea: Tyrrhenian and Adriatic seas (Cantone 1972, Giangrande and Cantone 1990, Fitzhugh 1995a, b).

Pseudofabriciola Fitzhugh, 1990

Type species: *Pseudofabriciola incisura* Fitzhugh, 1990, by original designation.
12 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages unbranched, slender and vascularized, or absent; dorsal lips erect, well developed, triangular or reduced to low, narrow ridges. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a well-developed, high, entire membranous collar; even high all around; middorsal region of collar not split along its entire length; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct middorsally. Inferior thoracic notochaetae on chaetigers 2 to 8 narrowly hooded; thoracic uncini with small subequal teeth above main fang; abdominal uncini with

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multiple rows of equal-sized teeth, manubrium as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.
Distribution: Mediterranean Sea: Adriatic Sea, Aegean Sea, Ionian Sea; Pacific Ocean: California, Gulf of Thailand, Papua New Guinea; South Africa; Caribbean Sea: Belize; Gulf of Mexico, Florida; Indian Ocean: Picard Island, Western Australia (Monro 1937, Day 1963, Hartmann-Schröder 1981, 1986, Giangrande and Castelli 1986, Simboura 1989, Fitzhugh 1990b, 1991a, 1996, Fitzhugh et al. 1994, 1995a, b, 2002).

Raficiba Fitzhugh, 2001

Type species: *Raficiba* Fitzhugh, 2001, by original designation.
1 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips erect, well developed; branchial lobes adjacent to ventral margin of each lip extended as distinct, thin, membranous flap; branchial lobes slightly narrower than peristomium. Anterior peristomial ring, excluding collar, wider than long; anterior margin of anterior peristomial ring a low ridge, dorsally and laterally; ventrally as very elongated, scoop-shaped lobe; annulations between anterior and posterior peristomial rings distinct dorsally and laterally. Inferior thoracic notochaetae on chaetigers 2 to 8 pseudospatulate; thoracic uncini with large tooth medially over main fang followed by four to five arching rows of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same length as dentate region; Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 6 to 8.
Distribution: Antarctica, Ross Sea (Fitzhugh 2001).

Rubifabriciola Huang, Fitzhugh & Rouse, 2011

Type species: *Rubifabriciola markginsbergi* Huang, Fitzhugh & Rouse, 2011, by original designation.
10 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; unbranched unvascularized ventral filamentous appendages present; dorsal lips as triangular ridges; radiolar lobes wide and short, with an even ventral margin. Anterior peristomial ring wider than long, shorter than posterior peristomial ring; anterior margin of anterior peristomial ring a low membranous collar and with middorsal gap. Inferior thoracic notochaetae elongated, narrowly hooded; thoracic uncini with several rows of progressively shorter teeth above main fang; abdominal uncini with multiple rows of equal-sized teeth, proximal end of manubrium two or more times wider than dentate region; abdominal neuropodia with pinhead chaetae (in most species). Peristomial and pygidial eyes red (persisting after fixation). Spermiogenesis on chaetigers 3 to 8 or 4 to 8.
Distribution: Caribbean Sea, Belize; South Australia; Indian Ocean: Picard Island, Phuket Island; Pacific Ocean: California, Papua New Guinea, Okinawa Island; Red Sea; Mediterranean Sea, Adriatic Sea (Banse 1956, 1959a, Hartman 1969, Fitzhugh 1990c, 1992a, 1998, 1999, Rouse 1993, 1996a, b, Giangrande and Montanaro 1999, Huang et al. 2011).

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References

Alexander, J.D., Hallet, S.L., Stocking, R.W., Xue, L. & Bartholomew, J.L. (2014): Host and parasite populations after a ten year flood: *Manayunkia speciosa* and *Ceratonova* (syn *Ceratomyxa*) *shasta* in the Klamath River. *Northwest Science* 88: 219–233.

Annenkova, N.P. (1929): Über die pontokaspischen Polychaeten. II. Die Gattungen *Hypaniola*, *Parhypania*, *Fabricia* und *Manayunkia*. *Annuaire du Musee Zoologique de l'Académie des Sciences de l'URSS* 30: 13–20.

Annenkova, N.P. (1934): Kurze Übersicht der Polychaeten der Litoralzone der Bering-Insel (Kommandor-Inseln), nebst Beschreibung neuer Arten. *Zoologischer Anzeiger* 105: 322–331.

Annenkova, N.P. (1938): Polychaetes of the North Japan Sea and their horizontal and vertical distribution. USSR Hydrobiological Expedition in 1934 to the Japan Sea. *Akademiia Nauk (Leningrad)*: 81–230.

Bagheri, E.A. & McLusky, D.S. (1982): Population dynamics of oligochaetes and small polychaetes in the polluted Forth estuary ecosystem. *Netherlands Journal of Sea Research* 16: 55–66.

Banse, K. (1956): Beiträge zur Kenntnis der Gattungen *Fabricia*, *Manayunkia* und *Fabriciola* (Sabellidae, Polychaeta). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 84: 415–438.

Banse, K. (1957): Die Gattungen *Oriopsis*, *Desdemona* und *Augeneriella* (Sabellidae, Polychaeta). *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Köbenhavn* 119: 67–105.

Banse, K. (1959a): *Fabricia acuseta* n. sp., *Fabriciola ghardaqa* n. sp. und *Oriopsis armandi* (Claparède) aus dem Roten Meer (Sabellidae, Polychaeta). *Kieler Meeresforschungen* 15: 113–116.

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Banse, K. (1959b): Über die Polychaeten-Besiedlung einiger submariner Höhlen. Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952, Teil XII. *Pubblicazioni della Stazione Zoologica di Napoli* 30: 417–469.

Banse, K. (1979): Sabellidae (Polychaeta) from the northeast Pacific Ocean. *Journal of the Fisheries Research Board of Canada* 36: 869–882.

Bartholomew, J.L. (1998): Host resistance to infection by the myxosporean parasite *Ceratomyxa shasta*: a review. *Journal of Aquatic Animal Health* 10: 112–120.

Bartholomew, J.L., Atkinson, S.D., Hallet, S.L. (2006): Involvement of *Manayunkia speciosa* (Annelida: Polychaeta: Sabellidae) in the life cycle of *Parvicapsula minibicornis*, a myxozoan parasite of pacific salmon. *Journal of Parasitology* 92: 742–748.

Bartolomaeus, T. (2002): Structure and formation of thoracic and abdominal uncini in *Fabricia stellaris* (Müller, 1774) — implication for the evolution of Sabellida (Annelida). *Zoologischer Anzeiger* 241: 1–17.

Bartolomaeus, T. & Quast, B. (2005): Structure and development of nephridia in Annelida and related taxa. *Hydrobiologia* 535/536: 139–165.

Baumhaker, H. (2012): Taxonomische Untersuchungen an Sabellidae und Fabriciidae (Annelida: Polychaeta) der Tiefsee des Südwest-Atlantiks. *Masterarbeit, Universität Rostock*: 1–55.

Bell, S.S. (1982): On the population biology and meiofaunal characteristics of *Manayunkia aestuarina* (Polychaeta: Sabellidae: Fabriciinae) from a South Carolina salt marsh. *Estuarine, Coastal and Shelf Science* 14: 215–221.

Berger, V., Dahle, S., Galaktionov, K., Kosobokova, X., Naumov, A., Ratkova, T., Savinov, V. & Savinova, T. (2001): White Sea. Ecology and environment. *Derzavets Publisher, St. Petersburg, Tromsø*: 1–157.

Berrill, N.J. (1977): Functional morphology and development of segmental inversion in sabellid polychaetes. *The Biological Bulletin* 153: 453–467.

Bick, A. (1995): Entwicklungsbedingte Veränderungen von morphologischen Merkmalen bei *Marenzelleria viridis* (Verill), Spionidae) und *Manayunkia aestuarina* (Bourne), Sabellidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92: 41–53.

Bick, A. (1996): Reproduction and larval development of *Manayunkia aestuarina* (Bourne, 1883) (Polychaeta, Sabellidae) in a coastal region of the southern Baltic. *Helgoländer Meeresuntersuchungen* 50: 287–298.

Bick, A. (2004): Redescription of *Pseudoaugeneriella nigra* (Langerhans, 1880), new combination (Polychaeta: Sabellidae), with remarks on some characters of Fabriciinae. *Zoologischer Anzeiger* 243: 53–63.

Bick, A. (2005): Redescription of *Fabriciola tonerella* Banse, 1956, and a new record of *Novafabricia infratorquata* (Fitzhugh, 1983) from the Mediterranean Sea, with a key for the Fabriciinae of the Mediterranean Sea and the northeast Atlantic. *Zoologischer Anzeiger* 244: 137–152.

Bick, A. (2006): Polychaete communities associated with gastropod shells inhabited by the hermit crabs *Clibanarius erythropus* and *Calcinus tubularis* from Ibiza, Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 86: 83–92.

Bick, A. (2007): Die Bedeutung postlarvaler ontogenetischer Merkmalsvariationen für die Taxonomie der Spionidae und Sabellidae. *Habilitationschrift, Universität Rostock*: 1–106.

Bishop, T.D. (1984): A range extension for *Manayunkia aestuarina* (Bourne, 1883) (Polychaeta: Sabellidae) to the Gulf coast of the United States with a review of previous habitat information. *Gulf Research Reports* 7: 389–392.

Blainville, H.M.D de (1828): Mollusques, Vers et Zoophytes. In: *Dictionnaire des Sciences naturelles, dans lequel on traite methodiquement des differens etres de la nature, consideres soit en eux-memes. d'apres l'etat actuel de nos connais sciences, soit relativement a l'utilite qu'en peuvent retirer la medicine, l'agriculture, le commerce et les arts. Suive d'une biographie des plus celebres naturalists. F.G. Levrault, Strasbourg & Paris* 57: 536 pp.

Bourne, A.G. (1883): On *Haplobranchus*, a new genus of capitobranchiate annelids. *Quarterly Journal of Microscopical Science* 23: 168–179.

Brehm, W.T. (1978): First Gulf of Mexico record of *Manayunkia speciosa* (Polychaeta: Sabellidae). *Northeast Gulf Science* 2: 73–75.

Cacabelos, E., Moreira, J. & Troncoso, J.S. (2008): Distribution of Polychaeta in soft-bottoms of a Galician Ria (NW Spain). *Scientia Marina* 72: 655–667.

Cantone, G. (1972): *Pseudofabricia aberrans* n. gen. n. sp., un anellide polichete di incerta sede. *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania, ser. IV* 11: 1–7.

Cantone, G. (2003): Distribution of benthic polychaetous annelids in the Adriatic Sea with zoogeographic considerations. *Biogeografia* 24: 169–193.

Capa, M., Hutchings, P., Aguado, M.T. & Bott, N.J. (2011): Phylogeny of Sabellidae (Annelida) and relationships with other taxa inferred from morphology and multiple genes. *Cladistics* 27: 449–469.

Cardell, M.J. (1990): Ecological characteristics of a population of *Fabricia sabella* (Ehrenberg) (Polychaeta Sabellidae) in the "trottoirs" of *Lithophyllum tortuosum* Foslie. *Scientia Marina* 54: 305–310.

Cinar, M.E. & Gönlügür-Demirci, G. (2005): Polychaete assemblages on shallow-water benthic habitats along the Sinop Peninsula (Black Sea, Turkey). *Cahiers de Biologie Marine* 46: 253–263.

Day, J.H. (1957): The polychaete fauna of South Africa. Part 4. New species from Natal and Moçambique. *Annals of the Natal Museum* 14: 59–129.

Day, J.H. (1961): The polychaete fauna of South Africa. Part 6. Sedentary species dredged off Cape coasts with a few new records from the shore. *Journal of the Linnean Society of London* 44: 463–560.

Day, J.H. (1963): The polychaete fauna of South Africa Part 8: New species and records from grab samples and dredging. *Zoological Bulletin of the British Museum (Natural History)* 10: 383–445.

Del Pasqua, M., Lezzi, M., Licciano, M. & Giangrande, A. (2017): Larval development and post larval growth of *Branchiomma bairdi* (Annelida: Sabellidae) from a Mediterranean population. *Invertebrate Biology* 136: 207–216.

Ditlevsen, H.J. (1929): XVI. Polychaeta. In: Spärck, R. & Tuxen, S.L. (eds.) 1928–1971, *Zoology of the Faroes I(II)* 16: 1–83.

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Dybowski, B. (1929): Die Polychaeten des Baikalsees. *Bulletin de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles. Serie B. Sciences Naturelles (II)*: 441–486.

Eckman, J.E. (1979): Small-scale patterns and process in a soft substrate interstitial community. *Journal of Marine Research* 37: 437–457.

Ehrenberg, C.G. (1836): Über *Amphicora sabella*. *Mittheilungen aus den Verhandlungen der Gesellschaft naturforschender Freunde zu Berlin*: 1–5.

Ermak, T.H. & Eakin, R.M. (1976): Fine structure of the cerebral and pygidial ocelli in *Chone ecaudata* (Polychaeta: Sabellidae). *Journal of Ultrastructure Research* 54: 243–260.

Evenkamp, H. (1931): Morphologie, Histologie und Biologie der Sabellidenspecies *Laonome kroyeri* Malmgr. und *Euchone papillosa* M. Sars. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 53: 405–534.

Fabricius, O. (1780): Fauna Groenlandica, systematica sistens, Animalia Groenlandiae occidentalis hactenus indagata, quad nomen specificum, triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locom victum, generationem, mores, usum, capturamque singuli; prout detegendi occasion fuit, maximaque parti secundum proprias observations. Hafniae et Lipsiae, Ioannis Gottlob Rothe, Aulae atque Univers. Reg. Bibliopolae. Copenhagen & Leipzig: 1–452.

Fateev, A.E. (1997): Supplement to the fauna of Fabriciinae polychaetes (Polychaeta, Sabellidae) in the White Sea. *Zoologicheskii Zhurnal* 76: 28–35.

Fateev, A.E. (1999): On finding of *Fabriciola baltica* (Polychaeta, Sabellidae). *Zoologicheskii Zhurnal* 78: 751–754.

Fitzhugh, K. (1983): New species of *Fabriciola* and *Fabricia* (Polychaeta: Sabellidae) from Belize. *Proceedings of the Biological Society of Washington* 96: 276–290.

Fitzhugh, K. (1989): A systematic revision of the Sabellidae-Caobangiidae-Sabellongidae complex (Annelida: Polychaeta). *Bulletin of the American Museum of Natural History* 192: 1–104.

Fitzhugh, K. (1990a): *Fabricinuda*, a new genus of Fabriciinae (Polychaeta: Sabellidae). *Proceedings of the Biological Society of Washington* 103: 161–178.

Fitzhugh, K. (1990*b*): Two new genera of the subfamily Fabriciinae (Polychaeta: Sabellidae). *American Museum Novitates* 2967: 1–19.

Fitzhugh K. (1990c): Revision of the Fabriciinae genus *Fabriciola* Friedrich, 1939 (Polychaeta: Sabellidae). *Zoologica Scripta* 19: 153–164.

Fitzhugh, K. (1990*d*): A revision of the genus *Fabricia* Blainville, 1828 (Polychaeta: Sabellidae: Fabriciinae). *Sarsia* 75: 1–16.

Fitzhugh K. (1990e): Revision of the Fabriciinae genus *Augeneriella* Banse, 1957 (Polychaeta: Sabellidae). *Journal of Natural History* 24: 195–218.

Fitzhugh, K. (1991a): Systematics of several fabriciin fan worms (Polychaeta: Sabellidae: Fabriciinae) previously referred to *Fabricia* and *Fabriciola*. *Journal of Natural History* 25: 1101–1120.

Fitzhugh, K. (1991b): Further revisions of the Sabellidae subfamilies and cladistic relationships among the Fabriciinae (Annelida: Polychaeta). *Zoological Journal of the Linnean Society* 102: 305–332.

Fitzhugh K. (1992a): Species of *Fabriciola* Friedrich, 1939 (Polychaeta: Sabellidae: Fabriciinae), from the California coast. *Pacific Science* 46: 68–76.

Fitzhugh, K. (1992b): On the systematic position of *Monroika africana* (Monro) (Polychaeta: Sabellidae: Fabriciinae) and a description of a new fabriciin genus and species from Australia. *Proceedings of the Biological Society of Washington* 105: 116–131.

Fitzhugh, K. (1993): *Novafabricia brunnea* (Hartman, 1969), new combination, with an update on relationships among Fabriciinae taxa (Polychaeta: Sabellidae). *Contributions in Science, Natural History Museum of Los Angeles County* 438: 1–12.

Fitzhugh, K. (1995a): Additions to the description of the fanworm genus *Pseudofabricia* Cantone, 1972 (Polychaeta: Sabellidae: Fabriciinae). *Contributions in Science, Natural History Museum of Los Angeles County* 456: 1–6.

Fitzhugh, K. (1995b): An update on the systematic and occurrence of the fanworm genus *Pseudofabriciola* Fitzhigh, 1990 (Polychaeta: Sabellidae: Fabriciinae) in the Mediterranean. *Contributions in Science, Natural History Museum of Los Angeles County* 457: 1–10.

Fitzhugh, K. (1996): New fanworm species (Polychaeta: Sabellidae: Fabriciinae) in the genus *Pseudofabriciola* Fitzhugh. *Journal of Natural History* 30: 1267–1286.

Fitzhugh, K. (1998): New fan worm genera and species (Polychaeta, Sabellidae, Fabriciinae) from the western Pacific, and cladistic relationships among genera. *Zoologica Scripta* 27: 209–245.

Fitzhugh, K. (1999): New fanworm species (Polychaeta: Sabellidae: Fabriciinae) from Phuket, Thailand, with comments on *Fabriciola flammula* Rouse and *Fabriciola cri* Rouse. *Contributions in Science, Natural History Museum of Los Angeles County* 477: 1–17.

Fitzhugh, K. (2001): A new deep-water genus and species of Fabriciinae fanworm (Polychaeta: Sabellidae) from Antarctica. *Contributions in Science, Natural History Museum of Los Angeles County* 491: 1–8.

Fitzhugh, K. (2002): New species of *Fabricinuda* Fitzhugh and *Pseudofabriciola* Fitzhugh (Polychaeta: Sabellidae: Fabriciinae), with an emendation of *Pseudofabriciola australiensis* (Hartmann-Schröder). *Journal of Natural History* 36: 893–925.

Fitzhugh, K. (2010): Revised systematics of *Fabricia oregonica* Banse, 1956 (Polychaeta: Sabellidae: Fabriciinae): an example of the need for a uninomial nomenclatural system. *Zootaxa* 2647: 35–50.

Fitzhugh, K. & Simboura, N. (1995): An update on the systematic and occurrence of the fanworm genus *Pseudofabriciola* Fitzhugh, 1990 (Polychaeta: Sabellidae: Fabriciinae) in the Mediterranean. *Contributions in Science, Natural History Museum of Los Angeles County* 457: 1–10.

Fitzhugh, K., Giangrande, A. & Simboura, N. (1994): New species of *Pseudofabriciola* Fitzhugh, 1990 (Polychaeta: Sabellidae: Fabriciinae), from the Mediterranean Sea. *Zoological Journal of the Linnean Society* 110: 219–241.

Fitzsimons, G. (1965): Feeding and tube-building in *Sabellastarte magnifca* (Shaw) (Sabellidae: Polychaeta). *Bulletin of Marine Science* 15: 642–671.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Forsman, B. (1956): Notes on the invertebrate fauna of the Baltic. *Arkiv för Zoologi* 9: 389–419.

Foulke, S.G. (1884): *Manayunkia speciosa*. *Science* 3: 303–304.

Franzén, Å. (1956): On spermiogenesis, morphology of the spermatozoon and biology of fertilization among invertebrates. *Zoologiska Bidrag från Uppsala* 31: 355–482.

Friedrich, H. (1939): Polychaetenstudien. V–X. Zur Kenntnis einiger wenig bekannter oder neuer Polychaeten aus der westlichen Ostsee. *Kieler Meeresforschungen* 3: 362–373.

Giangrande, A. & Cantone, G. (1990): Redescription and systematic position of *Pseudofabricia aberrans* Cantone, 1972 (Polychaeta, Sabellidae, Fabriciinae). *Bollettino di Zoologia Italiana* 57: 361–364.

Giangrande, A. & Castelli, A. (1986): Occurrence of *Fabricia filamentosa* Day, 1963 (Polychaeta, Sabellidae, Fabriciinae) in the Mediterranean Sea. *Oebalia* 13: 119–122.

Giangrande, A. & Montanaro, P. (1999): Sabellidae (Polychaeta) del Mediterraneo: la distribuzione delle specie è fortemente correlate a quella degli specialist. *Biologia Marina Mediterranea* 6:1–10.

Giangrande, A., Licciano, M. & Castelli, A. (2013): The genus *Echinofabricia* (Annelida: Fabriciidae) in the Mediterranean Sea with the description of *E. rousei* sp. nov. *Journal of the Marine Biological Association of the United Kingdom* 93: 1773–1776.

Giangrande, A., Gambi, M.C., Micheli, F. & Kroeker, K.J. (2014): Fabriciidae (Annelida, Sabellia) from a naturally acidified coastal system (Italy) with description of two new species. *Journal of the Marine Biological Association of the United Kingdom* 94: 1417–1427.

Gillandt, L. (1979): Zur Systematik, Autökologie und Biologie der Polychaeten des Helgoländer Felslitorals. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 76: 19–73.

Gitay, A. (1970): A review of *Augeneriella* (Polychaeta: Sabellidae) and a new species from northern Sinai. *Israel Journal of Zoology* 19: 105–109.

Glasby, C.J., Timm, T., Muir, A.I. & Gil, J. (2009): Catalogue of non-marine Polychaeta (Annelida) of the world. *Zootaxa* 2070: 1–52.

Hanson, J. (1949): Observations on the branchial crown of the Serpulidae (Annelida, Polychaeta). *Quarterly Journal of Microscopical Science* 90: 221–233.

Hartman, O. (1951): Fabricinae (feather-duster polychaetous annelids) in the Pacific. *Pacific Science* 4: 379–391.

Hartman, O. (1954): Marine annelids from the northern Marshall Islands. *Professional Papers of the U.S. Geological Survey 260-Q*: 619–644.

Hartman, O. (1969): Atlas of sedentariate polychaetous annelids from California. *Allan Hancock Foundation, University of Southern California, Los Angeles*: 1–812.

Hartmann-Schröder, G. (1962): Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil II: Die Polychaeten des Eulitorals. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 60: 57–168.

Hartmann-Schröder, G. (1965): Zur Kenntnis der eulitoralen Polychaetenfauna von Hawaii, Palmyra und Samoa. *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, N.F. 9*: 81–161.

Hartmann-Schröder, G. (1981): Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 6. Die Polychaeten der tropisch-subtropischen Westküste Australiens (zwischen Exmouth im Norden und Cervantes im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 78: 19–96.

Hartmann-Schröder, G. (1986): Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 12. Die Polychaeten der antiborealen Südküste Australiens (zwischen Wallaroo im Westen und Port MacDonnel im Osten). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 83: 31–70.

Hobson, K.D. & Banse, K. (1981): Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences* 209: 1–144.

Holmquist, C. (1967): *Manayunkia speciosa* Leidy — A fresh-water polychaete found in northern Alaska. *Hydrobiologia* 29: 297–304.

Holmquist, C. (1973): Fresh-water polychaete worms of Alaska with notes on the anatomy of *Manayunkia speciosa* Leidy. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 100 (4): 497–516.

Huang, D., Fitzhugh, K. & Rouse, G.W. (2011): Inference of phylogenetic relationships within Fabriciidae (Sabellida, Annelida) using molecular and morphological data. *Cladistics* 27: 356–379.

Hutchings, P., Deckker de, P. & Geddes, M.C. (1981): A new species of *Manayunkia* (Polychaeta) from ephemeral lakes near the Coorong, South Australia. *Transactions of the Royal Society of South Australia* 105: 25–28.

Jensen, K. & Bender, K. (1973): Invertebrates associated with snail shells inhabited by *Pagurus bernhardus* (L.) (Decapoda). *Ophelia* 10: 185–192.

Johnston, G. (1835): Illustrations in British zoology. *Magazine of Natural History (London)* 8: 179–183.

Jones, M.L. (1974): *Brandtika asiatica* new genus, new species, from southeastern Asia and a redescription of *Monroika africana* (Monro) (Polychaeta: Sabellidae). *Proceedings of the Biological Society of Washington* 87: 217–230.

Junoy, J. & Viéitez, J.M. (1990): *Manayunkia aestuarina* (Bourne, 1883) (Polychaeta, Sabellidae), en la Ria de Foz (Galicia, *España*). *Boletin de la Real Sociedad Espanola de Historia Natural Seccion Biologica* 86: 83–94.

Kahmann, D. (1984): Preliminary investigations of the genital system and the mode of sperm transfer in the sedentary polychaete *Fabricia sabella* (Sabellidae). *Fortschritte der Zoologie* 29: 289–292.

Karling, T.G. (1933): *Haplobranchus balticus* n.sp., eine neue sedentäre Polychaete aus dem Finnischen Meerbusen. *Memoranda Societatis pro Fauna et Flora Fennica* 10: 242–245.

Kendall, M.A. (1979): The stability of the deposit feeding community of a mudflat in the River Tees. *Estuarine and Coastal Marine Science* 8: 15–22.

Knight-Jones, P. (1981): Behaviour, setal inversion and phylogeny of Sabellida (Polychaeta). *Zoologica Scripta* 10: 183–202.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Knight-Jones, P. & Bowden, N. (1984): Incubation and scissiparity in Sabellidae (Polychaeta). *Journal of the Marine Biological Association of the United Kingdom* 64: 809–818.

Kupriyanova, E.K. & Rouse, G.W. (2008): Yet another example of paraphyly in Annelida: Molecular evidence that Sabellidae contains Serpulidae. *Molecular Phylogenetics and Evolution* 46: 1174–1181.

Langerhans, P. (1880): Die Wurmfauna von Madeira. III. *Zeitschrift für wissenschaftliche Zoologie* 34: 87–143.

Latreille, P.A. (1825): Familles naturelles du règne animal, exposé succinctement et dans un ordre analytique avec l'indication de leurs genres. *J.-B. Baillière Paris*: 1–570.

Leidy, J. (1858): *Manayunkia speciosa. Proceedings of the Academy of Natural Sciences of Philadelphia* 10: 90.

Leidy, J. (1883): *Manayunkia speciosa. Proceedings of the Academy of Natural Sciences of Philadelphia* 35: 204–212.

Lewis, D.B. (1961): Development of the polychaete *Fabricia sabella* (Ehr.). *Nature* 192: 80–81.

Lewis, D.B. (1968a): Feeding and tube-building in the Fabriciinae (Annelida, Polychaeta). *Proceedings of the Linnean Society of London* 174: 37–49.

Lewis, D.B. (1968b): Some aspects of the ecology of *Fabricia sabella* (Ehr.) (Annelida, Polychaeta). *Zoological Journal of the Linnean Society* 47: 515–526.

Licciano, M. & Giangrande, A. (2006): The genus *Novafabricia* Fitzhugh, 1990 (Polychaeta: Sabellidae: Fabriciinae) along the Italian coast (Mediterranean Sea) with a description of *N. posidoniae* n.sp. *Scientia Marina* 70: 673–678.

Light, W.J. (1969): Extension of range for *Manayunkia aestuarina* (Polychaeta: Sabellidae) to British Columbia. *Journal of the Fisheries Research Board of Canada* 26: 3088–3091.

López, E. & Rodríguez, C.T. (2008): A new species of *Fabricinuda* Fitzhugh, 1990 (Fabriciinae: Sabellidae: Polychaeta) from the Caribbean, with an emendation of the genus. *Journal of Natural History* 42: 1937–1949.

Mackie, G.L. & Qadri, S.U. (1971): A polychaete, *Manayunki speciosa* from the Ottawa River, and its North American distribution. *Canadian Journal of Zoology* 49: 780–782.

Martin, D. & Giangrande, A. (1991): *Novafabricia bilobata* sp. nov. (Polychaeta, Sabellidae, Fabriciinae) from the Mediterranean. *Ophelia* 33: 113–120.

McEuen, F.S., Wu, B.L. & Chia, F.S. (1983): Reproduction and development of *Sabella media*, a sabellid polychaete with extratubular brooding. *Marine Biology* 76: 301–309.

Meehean, O.L. (1929): *Manayunkia speciosa* (Leidy) in the Duluth Harbor. *Science* 70: 479–480.

Mikac, B., Semprucci, F., Guidi, L., Ponti, M., Abbiari, M., Balsamo, M. & Dovgal, I. (2019): Newly discovered associations between peritrich ciliates (Ciliophora: Peritricha) and scale polychaetes (Annelida: Polynoidae and Sigalionidae) with a review of polychaete-peritrich epibiosis. *Zoological Journal of the Linnean Society* 20: 1–15.

Mitwally, H.M. & Fleeger, J.W. (2013): Long-term nutrient enrichment elicits a weak density response by saltmarsh meiofauna. *Hydrobiologia* 713: 97–114.

Monro, C.C.A. (1937): Note on a collection of Polychaeta from South Africa, with the description of a new species belonging to the family Sabellidae. *Annals and Magazine of Natural History, Series 10* 19: 366–370.

Monro, C.C.A. (1939): On a collection of Polychaeta from near the mouth of the River Congo. *Revue de Zoologie et de Botanique Africaines* 32: 213–225.

Müller, O.F. (1774): Vermium terrestrium et fluviatilium, seu, Animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia. *Havniae et Lipsiae*: 1–81.

Muus, B.J. (1967): The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. *Meddelelser fra Danmark Fiskeri- og Havundersøgelser, NY Series* 5: 1–316.

Nausch, M. (1988): Untersuchungen zur Reproduktion von *Fabricia sabella* (Ehrenberg). *Wissenschaftliche Zeitschrift der Wilhelm-Pieck-Universität Rostock, Mathematisch-naturwissenschaftliche Reihe* 37: 51–54.

Nicol, E.A.T. (1930): The feeding mechanism, formation of the tube, and the physiology of digestion in *Sabella pavonina*. *Transactions of the Royal Society of Edinburgh* 56: 537–600.

Nishi, E. (1996): A new record of *Fabricinuda bikinii* (Hartman) (Polychaeta: Sabellidae: Fabriciinae) from Okinawa, Japan. *Benthos Research* 51: 21–26.

Nishi, E. & Yamasu, T. (1992): Brooding and development of *Rhodopsis pusilla* Bush (Serpulidae, Polychaeta). *Bulletin of the College of Science, University of Ryukyus* 54: 93–100.

Núñez, J. & Talavera, J.A. (1995): Fauna of the polychaetous annelids from Madeira. *Boletim do Museu Municipal do Funchal, Suplemento* 4: 511–530.

Núñez, J. Riera, R., del Brito, M.C. & Pascual, M. (2001): Anélidos Poliquetos intersticiales recolectados en las Islas Savajes. *Vieraea* 29: 29–46.

Nusbaum, J. (1901a): *Dybowscella baicalensis* nov. gen. nov. spec. - Ein im Süßwasser lebender Polychaet. *Biologisches Centralblatt* 21: 6–9.

Nusbaum, J. (1901b): Noch ein Wort über *Dybowscella baicalensis* mihi und einige andere Süßwasserpolychaeten. *Biologisches Centralblatt* 21: 270–273.

Okuda, S. (1946): Studies on the development of Annelida Polychaeta I. *Journal of the Faculty of Science Hokkaido Imperial University, Series VI. Zoology* 9: 115–219.

Orrhage, L. (1980): On the structure and homologues of the anterior end of the polychaete families Sabellidae and Serpulidae. *Zoomorphology* 96: 113–168.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.

Pettibone, M.H. (1953): Fresh-water polychaetous annelid, *Manayunkia speciosa* Leidy, from Lake Erie. *The Biological Bulletin* 105: 149–153.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 535/536: 53–78.

Purschke, G. Arendt, D., Hausen, H. & Müller, M.C.M. (2006): Photoreceptor cells and eyes in Annelida. *Arthropod Structure and Development* 35: 211–230.

Randel, N. & Bick, A. (2012): Development, morphology and ultrastructure of the radiolar crown of *Fabricia stellaris* (Müller, 1774) (Polychaeta: Sabellida: Fabriciinae). *Acta Zoologica (Stockholm)* 93: 409–421.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Rassmussen, E. (1973): Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11: 1–507.

Rioja, E. (1923): Estudio sistemático de las Especies Ibéricas del suborden Sabelliformia. *Trabajos del Museo Nacional de Ciencias Naturales* 48: 5–144.

Rouse, G.W. (1990): New species of *Oriopsis* and a new record for *Augeneriella* cf. *dubia* Hartmann-Schröder, 1965 from eastern Australia. *Records of the Australian Museum* 42: 221–235.

Rouse, G.W. (1992): Ultrastructure of the spermathecae of *Parafabricia ventricingulata* and three species of *Oriopsis* (Polychaeta: Sabellidae). *Acta Zoologica* 73: 141–151.

Rouse, G.W. (1993): New *Fabriciola* species (Polychaeta, Sabellidae, Fabriciinae) from the eastern Atlantic, with a description of sperm and spermathecal ultrastructure. *Zoologica Scripta* 22: 249–261.

Rouse, G.W. (1995a): Spermathecae of *Fabricia* and *Manayunkia* (Sabellidae, Polychaeta). *Invertebrate Biology* 114: 248–255.

Rouse, G.W. (1995b): Is sperm ultrastructure useful in polychaete systematics? An example using 20 species of the Fabriciinae (Polychaeta: Sabellidae). *Acta Zoologica* 76: 57–74.

Rouse, G.W. (1996a): New *Fabriciola* and *Manayunkia* species (Fabriciinae: Sabellidae: Polychaeta) from Papua New Guinea. *Journal of Natural History* 30: 1761–1778.

Rouse, G.W. (1996b): Variability of sperm storage by females in the Sabellidae and Serpulidae (Polychaeta, Sabellida). *Zoomorphology* 116: 179–193.

Rouse, G.W. (1999): Polychaete sperm: Phylogenetic and functional considerations. *Hydrobiologia* 402: 215–224.

Rouse, G.W. (2005): Annelid sperm and fertilization biology. *Hydrobiologia* 535: 167–178.

Rouse, G. & Fitzhugh, K. (1994): Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. *Zoologica Scripta* 23: 271–312.

Sarma, A.L.N., Raju, K.R. & Wilsanand, V. (1994): Polychaetes of the genus *Manayunkia* Leidy (Polychaeta: Sabellidae) from east coast of India (Bay of Bengal). *Journal of the Bombay Natural History Society* 91: 420–426.

Schloesser, D.W., Malakauskas, D.M. & Malakauskas, S.J. (2016): Freshwater polychaetes (*Manayunkia speciosa*) near the Detroit River, western Lake Erie: Abundance and life-history characteristics. *Journal of Great Lakes Research* 42: 1070–1083.

Schmidt, E.O. (1848): Neue Beiträge zur Naturgeschichte der Würmer gesammelt auf einer Reise nach den Färör im Frühjahr 1848. *Friedrich Mauke Verlag, Jena*: 1–44.

Schütz, L. (1965): Über Verbreitung, Ökologie und Biologie des Brackwasserpolychaeten *Manayunkia aestuarina* (Bourne), insbesondere an den Küsten Schleswig-Holsteins. *Faunistisch-ökologische Mitteilungen aus Norddeutschland* 2: 226–234.

Segrove, F. (1941): The development of the serpulid *Pomatoceros triqueter*. *Quarterly Journal of Microscopical Science* 82: 467–540.

Simboura, N. (1989): *Fabricia filamentosa* Day, 1963 (Polychaeta, Sabellidae, Fabriciinae) a Lessepsian migrant in the Mediterranean Sea. *Oebalia* 16: 129–133.

Sitnikova, T.Y., Shcherbakov, D.Y. & Kharchenko, V.V. (1997): On taxonomic status of polychaetes (Sabellidae, Fabriciinae) from the open Lake Baikal. *Zoologicheskii Zhurnal* 76: 16–27.

Smith, R.S. (1991): Relationships within the order Sabellida (Polychaeta). *Ophelia Supplement* 5: 249–260.

Southern, R. (1914): Clare Island Survey. Archiannelida and Polychaeta. *Proceedings of the Royal Irish Academy* 31: 1–160.

Southern, R. (1921): Fauna of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Memoirs of the Indian Museum* 5: 563–659.

Stocking, R.W. & Bartholomew, J.L. (2007): Distribution and habitat characteristics of *Manayunkia speciosa* and infection prevalence with the parasite *Ceratomyxa shasta* in the Klamath River, Oregon-California. *Journal of Parasitology* 93: 78–88.

Strelzov, V.E. & Guverich, V.I. (1978): On the population ecology of the polychaete *Fabricia sabella* Ehrenberg (Polychaeta, Sabellidae) in the eastern Murmansk. *Oceanology* 18: 714–718.

Struck, T.H. (2011): Direction of evolution within Annelida and the definition of Pleistoannelida. *Journal of Zoological Systematic and Evolutionary Research* 49: 340–345.

Thomas, J.G. (1940): *Pomatoceros*, *Sabella* and *Amphitrite*. *L.M.B.C. Memoirs on Typical British Plants and Animals* 33: 1–89.

Tilic, E., Sayyari, E., Stiller, J., Mirarab, S. & Rouse, G.W. (2020): More is needed-thousands of loci are required to elucidate the relationships of the 'flowers of the sea' (Sabellida, Annelida). *Molecular Phylogenetics and Evolution* 151: 1–9.

Treadwell, A.L. (1932): *Haplobranchus atlanticus*, a new species of polychaetous annelid from St. Andrews, N.B. *Contributions to Canadian Biology, Toronto, New Series* 7: 277–281.

Verrill, A.E. (1873): Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Report of the United States Commissioner of Fisheries, 1871–1872*: 295–778.

Wesenberg-Lund, E. (1950): The Polychaeta of West Greenland, with special reference to the Fauna of Nordre Strømfjord, Kvane- and Bredefjord. *Meddelelser om Grønland* 151: 1–171.

Weslawski, J.M., Zajaczkowski, M., Wiktor, J. & Szymelfenig, M. (1997): Intertidal zone of Svalbard. 3. Littoral of a subarctic, oceanic island: Bjornoya. *Polar Biology* 18: 45–52.

Weslawski, J.M., Wiktor Jr., J. & Kotwicki, L. (2010): Increase in biodiversity in the Arctic rocky littoral, Sorkappland, Dvalbard, after 20 years of climate warming. *Marine Biodiversity* 40: 123–130.

Wilson, S.J., Wilzbach, M.A., Malakauskas, D.M. & Cummins, K.W. (2010): Lab rearing of a freshwater polychaete (*Manayunkia speciosa*, Sabellidae) host for salmon pathogens. *Northwest Science* 84: 183–191.

WoRMS (2020): Fabriciidae Rioja, 1923. In: Read, G. & Fauchald, K. (eds.): *World Polychaeta Database*. Fabriciidae Rioja, 1923. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=154918 (Accessed on 2020-01-10).

Yun, S.G. & Kikuchi, T. (1991): Larval development and settlement of *Chone duneri* Malmgren (Polychaeta Sabellidae). *Amakusa Marine Biological Laboratory, Kyushu University* 11: 31–42.

Zenkevitsch, L.A. (1922): *Fabricia sabella* subsp. *caspica*, subsp. nov. *Russische Hydrobiologische Zeitschrift* 1: 320–322.

Zenkevitsch, L.A. (1925): Biologie, Anatomie und Systematik der Süßwasserpolychäten des Baikalsees. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 50: 1–60.

Zenkevitsch, L.A. (1935): Über das Vorkommen der Brackwasserpolychaete *Manayunkia* (*M. polaris* n.sp.) an der Murmanküste. *Zoologischer Anzeiger* 109: 195–203.

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7.7 Sedentaria: Terebellida/ Arenicolida

Pat Hutchings, Orlemir Carrerette, and João Miguel de Matos Nogueira

7.7.1 Pectinariidae Quatrefages, 1866

Introduction

The family Pectinariidae is a small group of polychaetes that comprises the genera *Amphictene* Savigny, 1822, *Cistenides* Malmgren, 1866, *Lagis* Malmgren, 1866, *Pectinaria* Lamarck, 1818, and *Petta* Malmgren, 1866 and, according to Hutchings and Peart (2002), has more than 60 species. However, as discussed below, some authors have accepted some as subgenera (e.g., Day 1967, Holthe 1986a) of *Pectinaria*.

Pectinariids are easily recognized by their tube of cemented sand grains, which resembles an ice-cream cone (Fig. 7.7.1.1A). They also have a characteristic set of golden paleae at the margin of the operculum (Figs. 7.7.1.1B–D, F–I, 7.7.1.2A–I, K, 7.7.1.3A–D, 7.7.1.4A, E, 7.7.1.5A), which they use for digging in soft sediments. Pectinariids are free-living tubiculous animals and have been recorded from a wide variety of sediments, from fully marine habitats to protected waters where salinity drops briefly after heavy rain. Species are rarely found in large numbers, although one Australian species, *Pectinaria antipoda* Schmarda, 1861, is found in reasonably large numbers throughout the soft-bottom communities and in among seagrass beds along the east coast of Australia (Zhang and Hutchings 2019). Species range in size from a few to many millimeters in length. Some of the larger species appear to occur in warmer waters. *Amphictene favona* Hutchings & Peart, 2002, from Abrolhos Islands, Western Australia, is 35 to 97 mm long and 10 to 26 mm wide (Hutchings and Peart 2002), and *Pectinaria carnosa* Wong & Hutchings, 2015, from Lizard Island, Great Barrier Reef, Queensland, is 22.0 to 38.2 mm long and 8.0 to 12.8 mm wide.

No major revision of the family has been undertaken, although Fauvel (1927), Nilsson (1928), and Holthe (1986b) discussed the family in some detail. No subfamilies have been recognized. Pectinariids are among the first polychaetes described, with *Nereis cylindraria belgica* described by Pallas (1766), which was then, by subsequent designation, renamed as *Pectinaria belgica* (Pallas, 1766). One of the reasons that it was recognized so early is because of its distinctive characteristic tusk-shaped tube, made of a single layer of cemented sand grains, which is fragile and does not persist once the animal dies, and the golden opercular paleae. The tubes (Fig. 7.7.1.1A) are constructed by cementing individual sand grains together with proteinaceous glue (Watson 1928) and occur in the sediment upside down with the anterior end submerged below the sediment. The worms select shell fragments or sand grains that are carefully oriented and fitted together to form a smooth inner surface to the tube. It appears that once the worm dies the tube breaks down, as one rarely if ever finds an empty tube when sampling. As the animal grows, it uses larger sand grains, and the shape of the tube is similar regardless of the surrounding sediment composition (Busch and Loveland 1975). Species recorded from coral reef areas may incorporate foraminiferans into their tubes (Long 1973) or particles of coral sand. Species found adjacent to the outfall pipes of the sewage system of New York have been found to incorporate tomato seeds into their tubes (PH personal observation).

Lucas and Holthuis (1975) discussed the confused state of taxonomy in this family and presented evidence that the generic name *Pectinaria* and the two specific names *Pectinaria belgica* and *Pectinaria koreni* are not valid. Yet, these two European species have been commonly reported and widely studied in ecological and physiological studies. Lucas and Holthuis (1975) demonstrated that the type species of the genus (*N. cylindraria belgica*) is the senior synonym of *Lagis koreni* and that *Nereis pectinata* is a senior synonym of *Pectinaria sensu* Malmgren, 1866. Thus, although as *Lagis koreni* is technically valid, it is a subjective junior synonym of *P. belgica* according to Lucas and Holthuis (1975). Subsequently, Nielsen and Kirkegaard (1978) made an application to the International Commission of Zoological Nomenclature to preserve the names *P. belgica* and *Lagis koreni* under the Plenary Powers of the Commission, citing the many references to these common species in European waters and how confusing it would be if these names were not preserved. These arguments have been accepted by the Commission (ICZN 1982), so the names *Pectinaria belgica* Pallas, 1766 and *Lagis koreni* Malmgren, 1866 remain valid.

Pectinariids have always been considered related to terebellids (Savigny 1822, Grube 1850, Levinsen 1883, Fauvel 1927), although they do not closely resemble them externally, except for the presence of buccal tentacles and tori with uncini. Internally, however, they do share many morphological features.

Morphology

External morphology

Pectinariidae is one of a few polychaete families in which the number of segments is constant, 26 in all species. The body is divided into three regions: thorax, abdomen, and a posterior scaphe (Figs. 7.7.1.1B–K, 7.7.1.2A–K, 7.7.1.3A–D,

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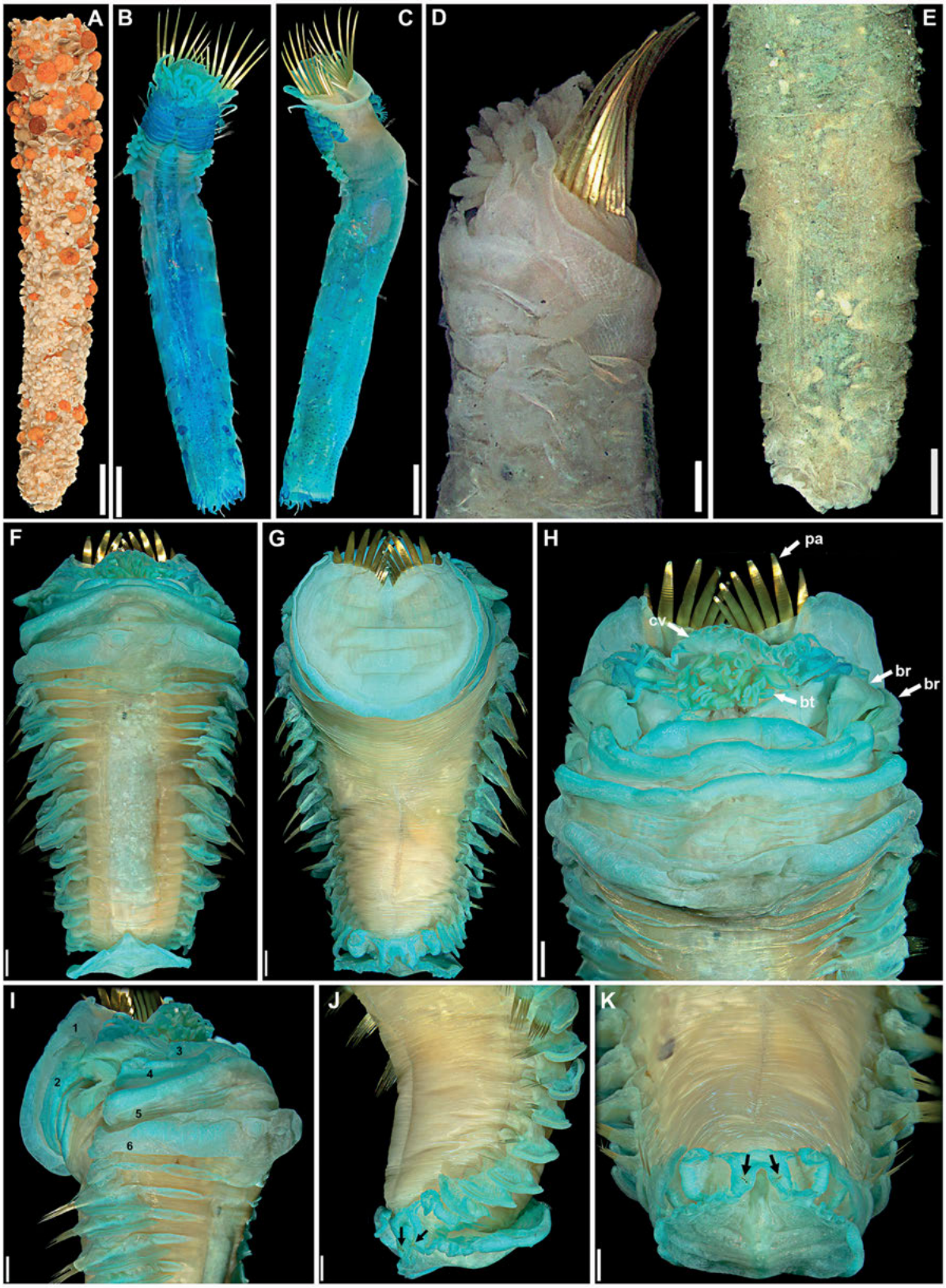


Fig. 7.7.1.1: *Petta investigatoris*: A, tube; B, C, entire worm, ventral and dorsal views, respectively, stained in methyl green. *Petta alissoni*: D, anterior end, left lateral view; E, posterior end, ventral view. *Pectinaria carnosa*, stained in methyl green: F, G, entire worm, ventral and dorsal views, respectively; H, I, anterior end, ventral and right lateral views, respectively; J, K, posterior end, left lateral and dorsal views, respectively. Arrows point to scaphal hooks. Numbers refer to segments. br, branchiae; bt, buccal tentacles; cv, cephalic veil; pa, paleae. Scale bars: A = 5 mm, B, C = 2 mm, D = 0.5 mm, E–K = 1 mm.

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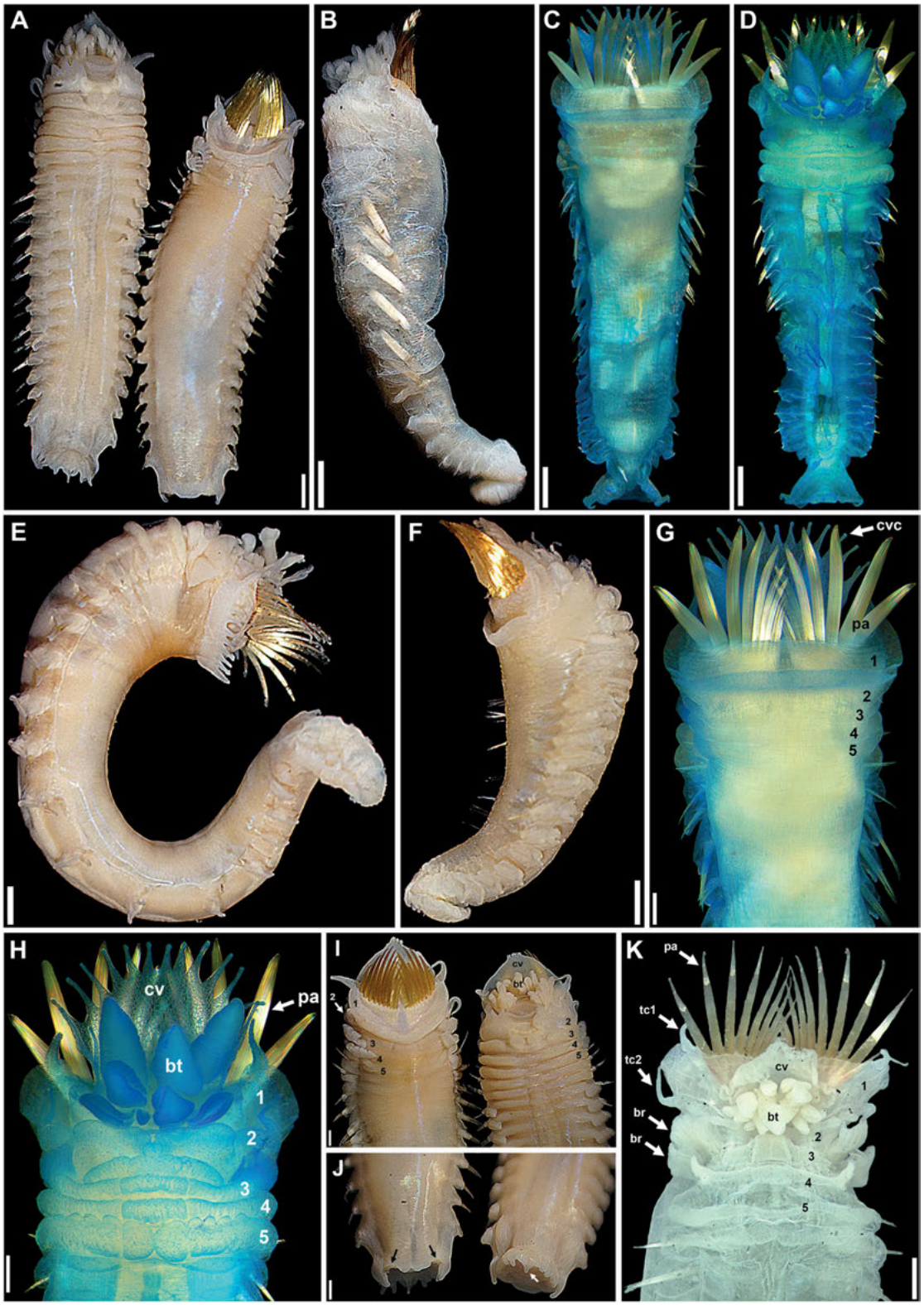


Fig. 7.7.1.2: *Petta pusilla*: A, entire worms, ventral (left) and dorsal (right) views; I, anterior end, dorsal (left) and ventral (right) views; J, posterior end, dorsal (right) and ventral (left) views. Black arrows point to scaphal hooks; white arrow points to anal flap. *Lagis koreni*: B, entire worm, left lateral view. *Pectinaria antipoda*, stained in methyl green: C, D, entire worm, dorsal and ventral views, respectively; G, H, anterior end, dorsal and ventral views, respectively. *Amphictene auricoma*: E, entire worm, left lateral view. *Cistenides granulata*: F, entire worm, right lateral view. *Pectinaria nonatoi*: K, anterior end, ventral view. Numbers refer to segments. br, branchiae; bt, buccal tentacles; cv, cephalic veil; cvc, cirri of cephalic veil; pa, paleae; tc1 and tc2, tentacular cirri of segments 1 and 2, respectively. Scale bars: A, E, F, K = 1 mm, B = 2 mm, C, D = 0.4 mm, G, H = 0.2 mm, I, J = 0.5 mm.

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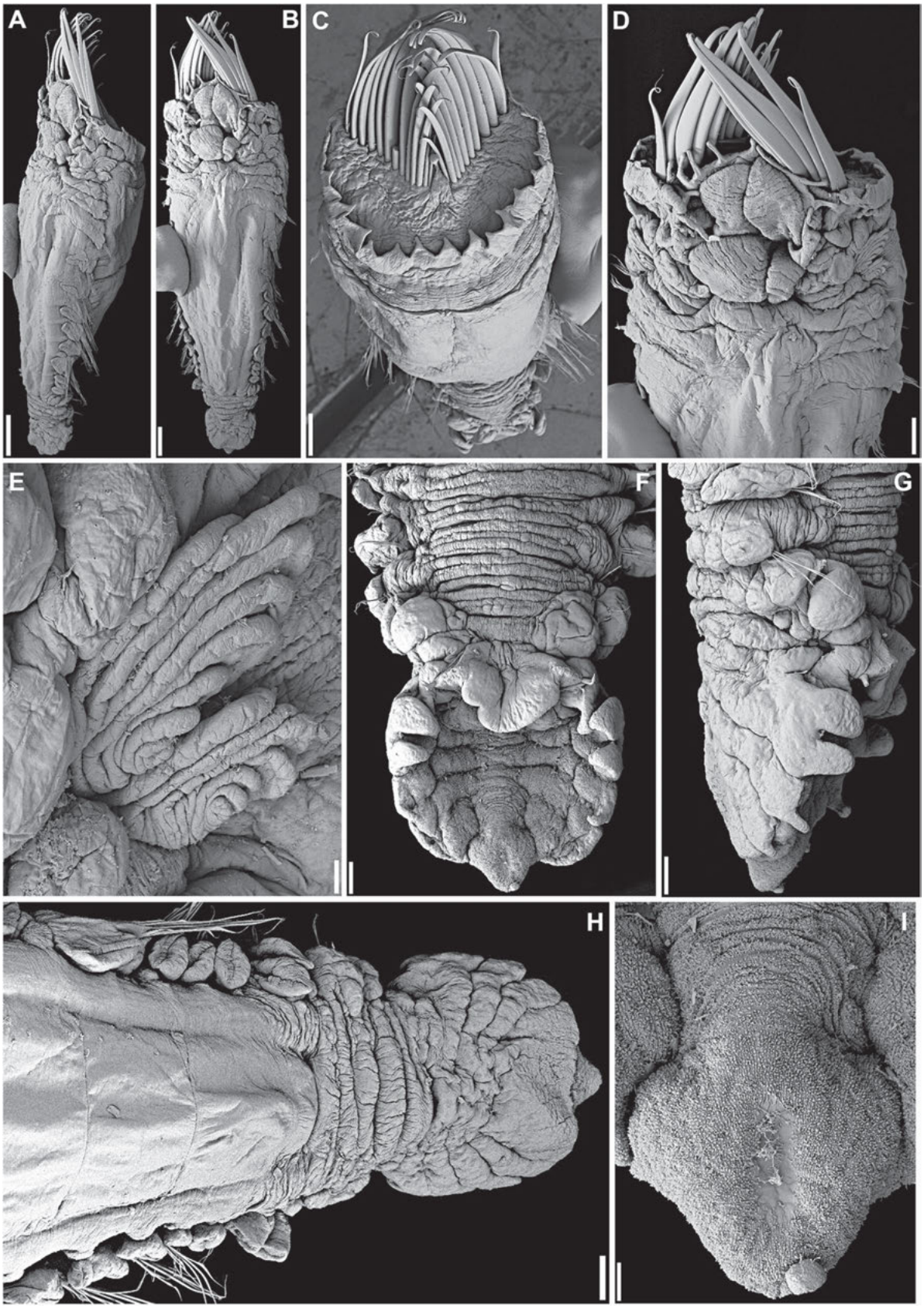


Fig. 7.7.1.3: *Amphictene lizardensis*: A, B, entire worm, left lateral and ventral views, respectively; C, D, anterior end, dorsal and ventral views, respectively; E, branchiae; F–H, posterior end, dorsal, left lateral and ventral views, respectively; I, close-up of ciliated foliaceous process of anal flaps. Scale bars: A = 400 µm, B = 300 µm, C = 200 µm, D = 150 µm, E, I = 20 µm, F, G = 70 µm, H = 100 µm.

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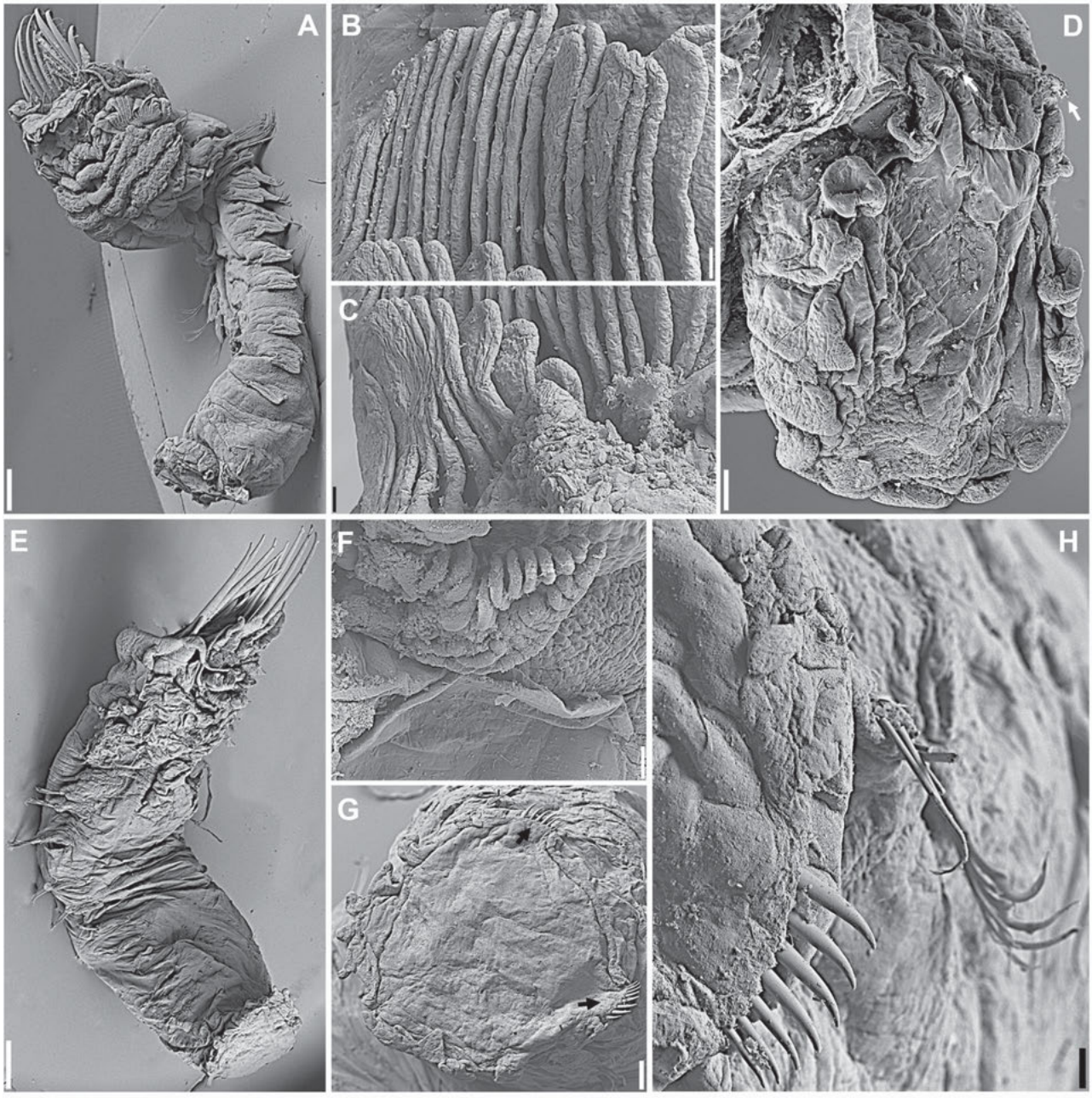


Fig. 7.7.1.4: *Pectinaria nonatoi*: A, entire worm, left ventrolateral view; B, C, branchiae; D, scaphe, dorsal view. *Petta alissoni*: E, entire worm, right ventrolateral view; F, branchiae; G, scaphe, dorsal view. Arrows point to scaphal hooks. H, last notopodium and scaphal hooks, left side of body. Scale bars: A = 500 µm, B, C = 30 µm, D = 80 µm, E = 400 µm, F = 40 µm, G = 100 µm, H = 25 µm.

F–H, 7.7.1.4A, D, E, G). Pectinariids are characterized by having a reduced prostomium that is completely fused to the peristomium (Holthe 1986a), forming a cephalic veil, which can bear distal cirri along the edge (Figs. 7.7.1.1H, 7.7.1.2C, D, G, H, K, 7.7.1.3B, D, 7.7.1.4A), a single medial projection, sometimes subdivided distally (Figs. 7.7.1.1D, 7.7.1.2A, I) or be smooth (Fig. 1B).

Antennae are absent. The prostomial palps (buccal tentacles) (Nogueira et al. 2013) are relatively short in comparison to those of other Terebelliformia, which are grooved and inserted ventrally to the cephalic veil, around the mouth, and cannot be retracted into the buccal cavity (Figs. 7.7.1.1B, D, F, H, I, 7.7.1.2A, B, D–F, H, I, K, 7.7.1.3A, B, D, 7.7.1.4A, E). Early larval stages initially have a pair of these palps, which are also clearly seen in sabellariids (Watson 1928). The cephalic veil is the result of the fusion between the prostomium and the peristomium, the buccal tentacles are inserted ventrally to it, and nuchal organs appear to be represented by dorsal ciliated crests (Nilsson 1912, Söderström 1930, Rullier 1951). However, the innervation of these structures should be examined to confirm this (Fauchald and Rouse 1997).

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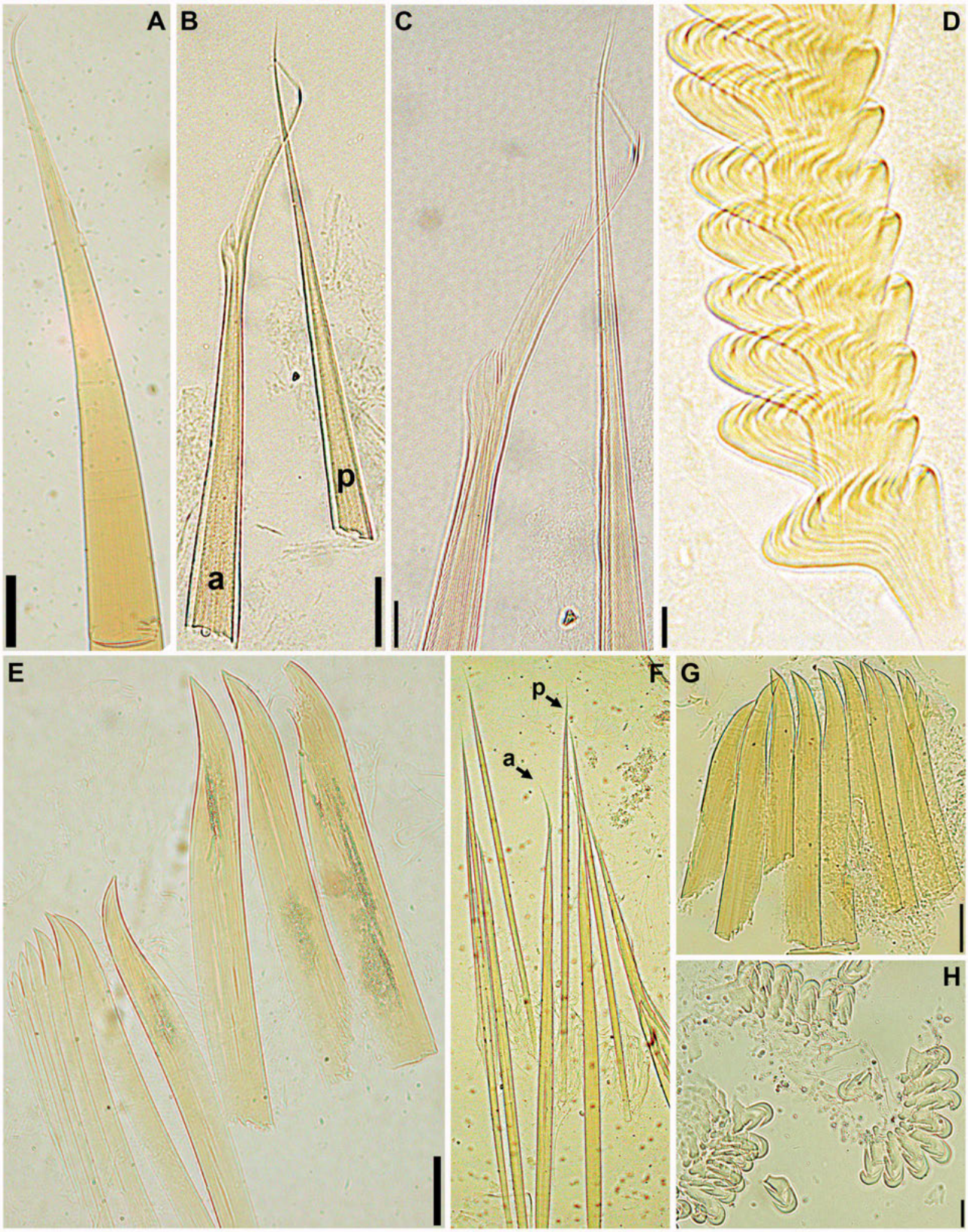


Fig. 7.7.1.5: *Amphictene catharinensis*: A, palea; B, C, notochaetae from anterior (a) and posterior (p) rows, in progressively higher magnifications; D, uncini; E, scaphal hooks. *Pectinaria nonatoi*: F, notochaetae from anterior (a) and posterior (p) rows; G, scaphal hooks. *Petta alissoni*: H, uncini. Scale bars: A = 100 µm, B = 5 µm, C = 2 µm, D = 0.5 µm, E, G = 50 µm, F = 200 µm, H = 15 µm.

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In juveniles of pectinariids, the cephalic veil can bear a pair of eyes; according to Thorson (1946), those eyes develop before metamorphosis and are present in front of the prostomial eyes in larval stages.

Segment 1 forms an operculum as a cushion-like rounded structure, which may be well or poorly developed; the margins of the operculum present a distal lobe, which may be smooth (Figs, 7.7.1.1C, D, G, I, 7.7.1.2A, C, F–H, 7.7.1.4E) or divided into triangular lappets or cirri (Figs. 7.7.1.2E, 7.7.1.3A, C, D). Segment 1 bears golden notopodial paleae arranged in a pair of arches at the proximal margin of the operculum (Figs. 7.7.1.1B–D, F–I, 7.7.1.2A–I, K, 7.7.1.3A–D, 7.7.1.4A, E). Longitudinal muscles are grouped in bundles, and the segmentation is distinct from the second segment, although less marked posteriorly and only visible on the scaphe through the paired lateral papillae (Figs. 7.7.1.1B–K, 7.7.1.2A–K, 7.7.1.3A–D, F, H, 7.7.1.4A, D, E, G). The ventral surface of anterior segments is highly glandular; the anterior margins of the segments are distinctly raised, forming transverse crests, frequently with midventral shields or lobes (Figs. 7.7.1.1B–D, F, H, I, 7.7.1.2A, B, D–F, H, I–K, 7.7.1.3A–B, D, 7.7.1.4A–E). Notopodia other than those bearing paleae are short, truncate cylinders with simple capillary chaetae originating from retractile core on top (Figs. 7.7.1.1B–D, F–K, 7.7.1.2A–K, 7.7.1.3A–D, F–H, 7.7.1.4A, E, H). Notochaetae are arranged in two rows of narrowly winged notochaetae or, more frequently, chaetae of the anterior row are basally winged and terminate in an alimbate, finely serrated blade, whereas those of the posterior row are narrowly winged throughout (Figs. 7.7.1.5B, C, F, 7.7.1.6B, C, F, G). The neuropodia bear tori with rows of uncini; the uncini are pectinate or avicular. In the first case, a main fang is usually absent, and the uncini have longitudinal rows of almost evenly sized teeth, a curved anterior peg, which looks solid under light microscopy but is composed of numerous minute teeth under scanning electron microscopy (SEM), and a posterior handle about as long as denticulate region (crest) (Figs. 7.7.1.5D, 7.7.1.6A, D, E). Avicular uncini, in contrast, have a conspicuous main fang and secondary teeth arranged in transverse rows of progressively smaller teeth (Figs. 7.7.1.5H, 7.7.1.6H). Anteriorly, two pairs of dorsal, lamellate branchiae are present on segments 3 and 4 (Figs. 7.7.1.1C, D, I, 7.7.1.2A, B, E, F, H, I, K, 7.7.1.3A, B, D, E, 7.7.1.4A–C, E, F). Lateral organs are present (Rullier 1951), as internally ciliated pits between the notopodia and neuropodia and occur on anterior segments and/or the scaphe on *Amphictene*, *Lagis*, and *Petta*. The last five segments are fused, forming a flattened plate or scaphe with dorsolateral rows of spine-like hooked chaetae at the base (scaphal hooks), lateral papillae along the edges, and paired anal flaps (Figs. 7.7.1.1B, C, E–G, J, K, 7.7.1.2A–F, J, 7.7.1.3A–B, F–H, 7.7.1.4A, D, G, H). A terminal cirrus may be present dorsally to the anal flaps, and sometimes the anal flaps are fused, forming triangular, highly ciliated foliaceous processes (Fig. 7.7.1.3F–I). The scaphe is typically separated from the posterior body segments by conspicuous constriction (Figs. 7.7.1.1F, G, J, K, 7.7.1.2B–F, 7.7.1.3A, B, F–H), except for members of *Petta*, where such a constriction does not occur and the transition between the scaphe and posterior body segments is poorly marked (Figs. 7.7.1.1B, C, E, 7.7.1.2A, J, 7.7.1.4A, G).

Bartolomaeus (1995) described the structure and formation of the neurochaetal uncini in detail for *Pectinaria* based on the development of trochophores and juvenile stages. He provided a series of images to illustrate this; see also Hausen (2005) for additional illustrations. The chaetoblast generates microvilli along an apicobasal axis, and a surrounding follicle cell secretes chaetal material around the tips of the microvilli. As this chaetal material is deposited, it forms the spines or secondary teeth of the uncinus and the microvilli form their core.

Anatomy

Pectinariids have a ventral buccal organ and a thin-walled looped gut twice the length of the body. The anatomy of the digestive system of pectinariids was given by Wirén (1885), and he also illustrated the blood system (Wirén 1885: plate 6, figs. 8, 9). The gut forms a distinctive loop. The ventral pharynx was described by Watson (1928), and Dales (1963) referred to it as the ventral buccal organ, in which the lips are used to sort food particles. The alimentary canal is much longer than the animal and forms one or two loops in the anterior part of the body (Michel 1988). As there are no internal septa other than the gular membrane, the gut basically lies free in the body cavity (Fauchald and Rouse 1997). The gut is delicate, distensible, and long, and the ciliated esophagus passes through a nonciliated secretory region followed by an absorptive region with a ciliated ventral groove, which passes through the rectum (Dales 1963). Ronan (1977) found that most nematodes, crustaceans, and foraminiferans pass through the gut unharmed, and about 30% of the smallest copepods and polychaetes are partially digested. Brasil (1904) reported that the intestine of *Lagis koreni* (as *Pectinaria koreni*) secretes amylase, trypsin, and probably lipase, but it is difficult to compare it to other species, as there have been very few studies of polychaetes at this level.

A gular membrane is present between segments 4 and 5. Nephridia are mixonephridia (Goodrich 1945) consisting of a few pairs of anterior nephridia and posterior gonoducts. Bartolomaeus (1999) investigated the development of nephridia in *Lagis koreni* (as *P. koreni*) and traced the development from a few cells to the mature nephridia and

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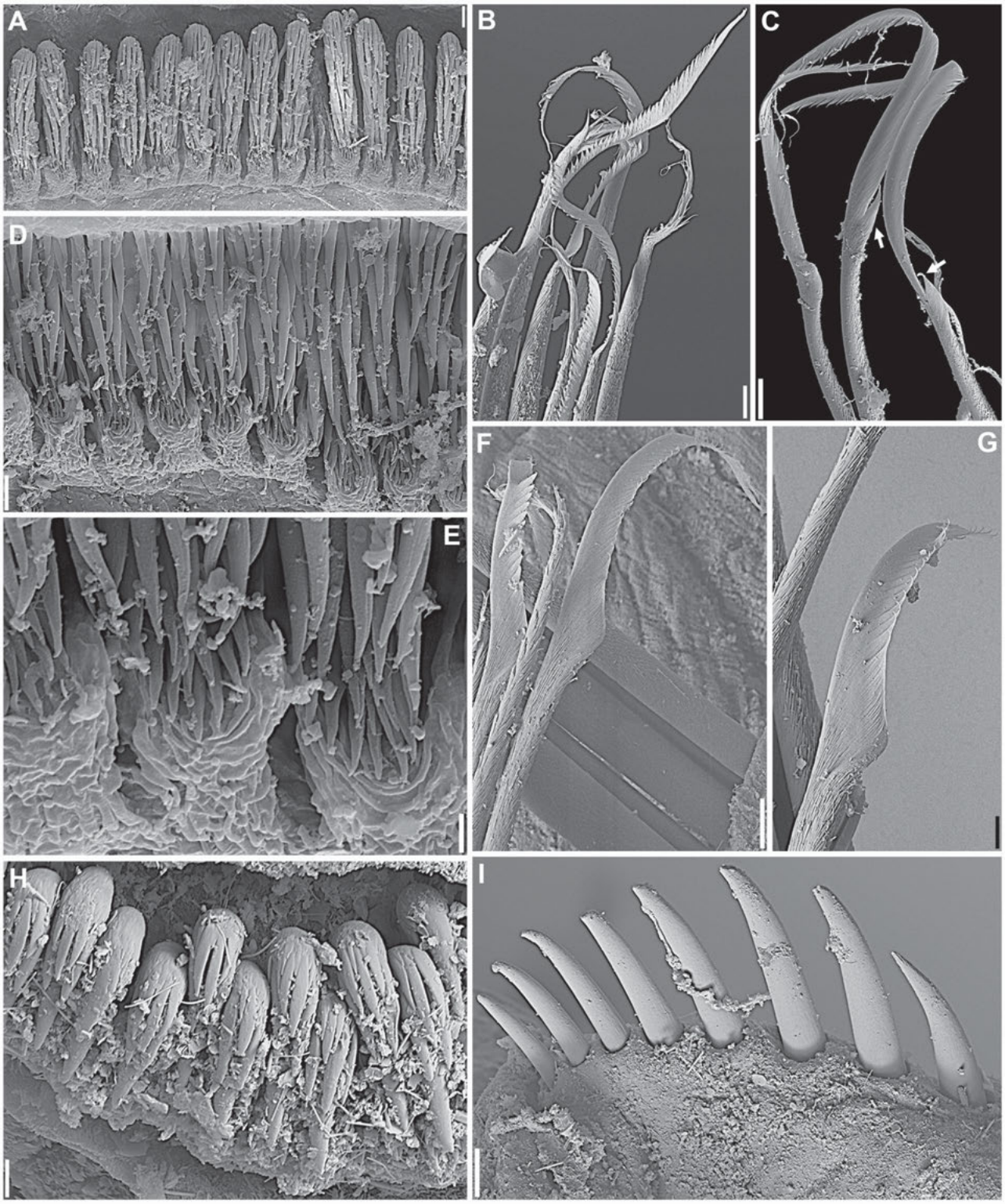


Fig. 7.7.1.6: *Pectinaria nonatoi*: A, uncini; C, notochaetae of anterior row. Arrows point to foliaceous process at the base of serrated blades. D, E, anterior peg of uncini in progressively higher magnifications. *Petta alissoni*: B, notochaetae; F, G, notochaetae in progressively higher magnifications; H, uncini; I, scaphal hooks. Scale bars: A, H = 2 µm, B, F = 8 µm, C = 10 µm, D = 1.5 µm, E = 0.5 µm, G = 4 µm, I = 15 µm.

how an extracellular matrix appears between the developing nephridia and the coelomic lining. The circulatory system is closed with a heart body.

Glandular cells in the integument are responsible for tube building. Truchet and Vovelle (1977) investigated in detail the inorganic composition of these cement secretory

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glands. These specialized cells produce granules that are spherical and vary in size and contain sulfhydryl proteins and phosphorous-rich polysaccharides, calcium, magnesium, and iron. Vovelle (1979a, 1979b) studied in detail these secretory granules in *Petta pusilla* and *Lagis koreni*, which form the cement that consolidates the tube to which the sand grains adhere as well as form a mucous lining of the tube, which presumably facilitates the animal moving up and down within the tube. The cuticle is mainly composed of layers of unbanded collagen fibers, which crisscross one another at about 55° to the longitudinal axis of the animal (Storch 1988).

The gular membrane, often called the diaphragm in the older literature (Meyer 1887), forms a complete or nearly complete muscularized septum between segments 3 and 4, according to Hessle (1917), but this is in disagreement with previous studies by Meyer (1887) and Fauvel (1897), who stated that it was present between segments 4 and 5. The presence of a gular membrane is often associated with anterior eversible structures such as the extensible grooved buccal tentacles (Fauchald and Rouse 1997), although in pectinariids the buccal tentacles are not retractile into the buccal cavity.

Although presumably the two branchiae in addition to the entire body surface are used in gas exchange, no detailed studies on physiology of respiration have been carried out. Storch and Alberti (1978) examined the structure of the parallel lamellae of *Lagis koreni* (as *P. koreni*) and found clusters of cilia present and cuboidal to flattened epithelial cells and subepidermal spaces. No coelomic epithelium is present within the branchiae. The cuticle covering the integument is thin and covered with microvilli. Storch and Alberti (1978) suggested that the subepithelial blood vessels release blood into a system of spaces immediately below the epidermis of the branchial lamellae and are important sites for gas exchange. Each pair of branchiae has blood vessels originating from different segments and a heart body associated with the dorsal blood vessel (Picton 1899). Kennedy and Dales (1958) suggested that heart bodies are responsible for the formation of blood cells. Watson (1928) provided some evidence based on field observations that the scaphe may also be involved in gas exchange.

No detailed studies on the segmental organs of pectinariids have been undertaken. Although Goodrich (1945) made general comments on the nephridia of terebelliforms, he did not specifically mention pectinariids. Rouse and Fauchald (1997), in their study on polychaete phylogeny, highlighted the need for detailed studies on these structures. It is suggested that the anteriormost pairs of mixonephridia function as nephridia and the posterior ones as coelomoducts (Meyer 1887, Hessle 1917, Nogueira et al. 2010, 2013). Rouse and Pleijel (2001) suggested that the first pair is excretory only with funnels in front of the gular membrane and exits from the body in segment 4. In *Petta*, there are also segmental organs in the following four segments, whereas in other taxa they are present on segments 4, 7, and 8 (Rouse and Pleijel 2001).

Eyes have been reported on the pygidium of one species of *Petta* (Nilsson 1912), although they are not present on the Brazilian species (Nogueira et al. 2019) and also have not been seen in any species during the revision of the genus (Zhang et al. 2019).

A generalized description of the nervous system was given by Nilsson (1912) and Orrhage (2001). Orrhage and Müller (2005) in their review of the morphology of the nervous system of polychaetes included a species of *Pectinaria*. Although four transverse commissures have been found in many sedentary polychaetes, they could not be found in the brains of ampharetids, pectinariids, and terebellids (see figs. 2E–G, 3C, F in Orrhage and Müller 2005) or traces of equivalents to the four commissures of the circumesophageal roots. In most polychaete families studied, the circumesophageal connective is proximally divided into a dorsal root and a ventral root, whereas in pectinariids and other terebelliform families it only has a ventral root. A schematic diagram of the cephalic nervous system of *Amphictene auricoma* is given by Orrhage (2001) and Orrhage and Müller (2005, fig. 3C). The nerves of the buccal tentacles of pectinariids are closely associated with those of the alimentary canal; whereas many emanate from the brain, others are rooted in the tract leading to the anterior stomatogastric nerves.

Reproduction and development

Pectinariids are typically monoecious, although Dehorne (1925) reported that *Lagis koreni* is a simultaneous hermaphrodite and that eggs and sperm appear to be produced on the same germinal epithelium (Schroeder and Hermans 1975). Gonads are associated with the segmental organs behind the gular membrane. Gametes develop freely in the coelomic cavity before being spawned through the posterior segmental organs. Of the two species studied (*Amphictene auricoma* and *Lagis koreni*), pectinariids undergo mass spawning and have planktotrophic larvae (Wilson 1991). The eggs have a small diameter (~65 µm), and fertilization is external, giving rise to planktotrophic trochophores, although how they feed is unknown (Rouse and Pleijel 2001). After a few weeks, the larvae undergo rapid metamorphosis, form the adult head, and secrete a larval tube while still in the plankton and have the adult number of segments (Lambert et al. 1996). Tweedel (1961, 1966, 1980) undertook detailed

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studies of vitellogenesis and found that RNA is synthesized by the developing eggs in *Pectinaria*, as in species of nereidids and syllids. He also observed that oocytes are shed into the water column, where the final maturation occurs before fertilization. Austin (1963) found that polyspermy is more common in eggs of *Pectinaria* with intact germinal vesicles than in eggs that have progressed past germinal vesicle breakdown, and he suggested that eggs are probably normally fertilized at metaphase 1. This was subsequently confirmed by Tweedel (1980). Anstrom and Summers (1981) suggested that Ca^{2+} may be important in reinitiating meiosis at metaphase 1 and allowing the continued development of the eggs. Dorresteijn (2005) studied the development of embryos in *Pectinaria* and found that they divide unequally by spindle asymmetry similar to species of Terebellidae.

Early stages of larval development were described by Wilson (1936) for *Lagis koreni* (as *P. koreni*), and Gravely (1909) described a later stage in the plankton off Port Erin, northwest England. Paleae are seen very early on, and recently, metamorphosed worms along with their tubes stay in the plankton for a little while before settling. The larvae actively select their settlement site and prefer habitats where other individuals are present (Desroy et al. 1997), and the larvae can move many centimeters over several days before choosing to settle.

Populations of *Pectinaria gouldii* off the coast of New York, USA, breed over a long time, with juveniles being collected from early July to October, with a life span of 1 year or more (Busch and Loveland 1975). This species prefers coarse sediments, and densities of 51,160 m^2 have been recorded in one sampling period. Estcourt (personal communication), working off the northeast coast of UK, found that entire populations would disappear after spawning, and in the following years, the population would return via larval recruitment, indicating that individuals die after spawning. Estcourt (1974) studied *Lagis australis* (as *Pectinaria*) in New Zealand and found, like in the studies of Irlinger et al. (1991) on *Lagis koreni*, that individuals live for less than 1 year and die after spawning.

Widespread larval dispersal facilitating population connectivity has been inferred for *Lagis koreni* (as *P. koreni*) along the northern coast of France (Jolly et al. 2004), with evidence of past divergence due to historical processes and of contemporary dispersal with ocean currents.

Biology and ecology

Pectinariids live in soft sediments and seagrass beds and have been reported from the intertidal down to depths of more than 2,000 m, although most have been recorded from shallow waters. They live head down in the sediment with the narrower end of the tube just protruding from the surface of sediment. They can move through the sediment using their paleae to move the sediment (Hessle 1925, Watson 1928). Also, these same structures can be used to close the tube and protect the animal from predation.

Pectinariids are selective subsurface deposit feeders (Dobbs and Scholly 1986). Two types of feeding have been observed in *Lagis koreni* (as *P. koreni*). In the first type, paleae and tentacles are used to excavate a cavity that extends from the broad end of the tube and through a narrow channel to the surface of the sediment, and this "U-shaped" space is irrigated by the respiratory movements of the worm (Hessle 1925). As the animal moves through the sediment, particles are collected by the tentacles, which then remove and swallow the fine algal/bacterial film covering the particles. In the second type, the same species has been reported as collecting subsurface sediments on their tentacles, which are then transported along the ciliated grooves, without any digging by the paleae (Dobbs and Scholly 1986).

Nicolaidou (1988) reported that the burrowing rates of *Lagis koreni* (as *P. koreni*) are affected by light and temperature. He suggested that there is a diurnal rhythm associated with feeding rates. The species is most active at higher temperatures and in the dark, confirming the observations of Watson (1928). The animals move up in the sediment around sunset and descend around sunrise, and there is some evidence that this is an endogenous rhythm. The amount of sediment reworking is significantly higher at 10°C than at 7°C, and there are no differences between 15°C and 10°C. It is suggested that being deeper in the sediment during daylight hours would provide some protection from predation by predominantly visual feeders, such as plaice (*Pleuronectes platessa*), the flounder (*Pleuronectes flesus*), and the dab (*Limanda limanda*), which are all more active on the bottom during daytime (Groot 1971).

Pectinariids eject unconsolidated feces from the tube onto adjacent sediment surfaces. They can also produce unconsolidated pseudofeces, which textually resemble feces. These are produced by the sediment being transported from the depth, moving up between the worm and its tube, and ejected (Watson 1928, Schäfer 1972). Rhoads (1974) used the term "conveyor-belt species" for this process, which transfers material from the depth to the sediment surface. As the worm is doing this, water is being pumped through the tube, creating an environment in which very fine particles in suspension are drawn into the feeding area, where the tentacles can collect them (Watson 1928).

Studies have shown that ingested particles take between 1 and 6.5 hours to move through the gut in

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Lagis koreni (as *P. koreni*), which has an anterior diameter of 2 to 5 mm (Dobbs and Scholly 1986). These rates increase as a function of increasing diameter of the tube. Also, larger worms preferentially ingest large-sized sediment grains. They only build U-shaped tubes in hypoxic, high nutrient, fine-grained sediments, as hypothesized by Fauchald and Jumars (1979), and individuals living in coarse sediments do not live in U-shaped burrows or develop a permanent burrow system. Dobbs and Scholly (1986) suggested that the ingestion of larger particles by *L. koreni* (as *P. koreni*) confounds the current perception of optimal foraging by deposit feeders, and they should select the smaller particles (Taghon et al. 1978). However, such behavior of selecting the larger ones may allow them to ingest fecal pellets of the co-occurring bivalve *Abra alba* (Wood, 1802), which gives the pectinariids organics and microbes from the pellet surface and/or soluble compounds within the pellets, suggesting an example of a trophic interaction, which has also been reported for other pectinariids (Whitlatch 1974, Ronan 1977).

Some studies have investigated rates of sediment reworking, with rates varying according temperature, organic content, and availability of interstitial water in the sediment. Gordon (1966) recorded rates of 6 g/day, whereas Dobbs and Scholly (1986) reported lower rates. Rhoads and Young (1970) suggested that this sediment reworking creates an unstable surface that is easily resuspended by tidal current and may limit the distribution of suspension feeders and sessile epifauna.

Phylogeny and taxonomy

The characters used to separate the genera are the degree of fusion of the cephalic veil to the operculum, the marginal ornamentation of the cephalic veil and the operculum, the degree of separation between the scaphe and abdomen, and the number of rows of vertical teeth on the uncini. To separate species, characters such as the presence or absence of scaphal papillae and their shape, the morphology of notochaetae and uncini, and the morphology of the cephalic veil and ventral lobes of anterior segments are important. Zhang and Hutchings (2019), in their revision of Australian pectinariids, have found some additional soft-tissue characters to separate species. These include a pair of ear-shaped lobes that are adjacent to both sides of the dorsal base of the cephalic veil in species of *Pectinaria* and *Amphictene*, whereas in *Lagis* they are present between the buccal cavity and lateral margin of segment 1 and a pair of ventral lappets that have not previously been described on the lateral margin of segment 1 in all Australian species of pectinariids.

Fauchald (1977) recorded 46 described species for this family, many of which are only known from the type locality. Subsequently, Hutchings and Peart (2002) recorded 2 genera and 6 species in Australian waters, of which 5 were described as new. Zhang and Hutchings (2019) have recorded 3 genera and 13 species from Australia, including 5 new species. Simultaneously, Nogueira et al. (2019) described 2 new species from Brazilian waters.

In Australia, at least, all species are endemic, except for one that occurs in Northern Australia and Papua New Guinea, although some species have a wider distribution than others (Zhang and Hutchings 2019).

The genus *Petta* is restricted to cold waters or the deep sea (Zhang et al. 2019), although a recently described species from Brazil occurs in depths of 101 to 258 m (Nogueira et al. 2019). In contrast, it seems as if the other genera appear to be restricted to the intertidal to shallow subtidal, but we should stress that, apart from the studies of Hutchings and Peart (2002), Nogueira et al. (2019), and Zhang and Hutchings (2019), no comprehensive biogeographic studies have been carried out in other parts of the world, except for the Holthe (1986a) study from Scandinavia and northern Europe, where he illustrated the distribution of the five species recorded from the region.

One fossilized pectinariid tube has been recorded from Japan (Katto 1976).

Phylogeny

Since the study of Rouse and Fauchald (1997), several authors have investigated the internal relationships in Annelida using morphological (Bartolomaeus et al. 2005) or molecular (Hall et al. 2004, Rousset et al. 2007, Struck et al. 2007, Struck 2011) data or both combined (Zrzavý et al. 2009). Although those papers have provided some interesting insights on the arrangements between the major clades of annelids, the results have been frequently conflicting, and as a consequence of the utilization of a very limited number of taxa of each group, the monophyly of the families and their arrangement within each of the major groups have not been properly tested.

Except for Rousset et al. (2007), who found Pectinariidae out of Terebelliformia and very distant phylogenetically from that group, all other studies agree that Pectinariidae is part of Terebelliformia, but their position within that group changes substantially from one paper to another. Hall et al. (2004), in their study on the phylogeny

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of polychaetes, used five taxa of Terebellidae s.s., one Pectinariidae and another Alvinellidae, and found a monophyletic Terebellidae, a sister clade to a group containing Pectinariidae and Alvinellidae. Struck et al. (2007), using one species of Pectinariidae, two of Terebellidae s.s., and another of each Alvinellidae, Ampharetidae, and Trichobranchidae, found Pectinariidae as the most basal family of Terebelliformia, a sister clade to a group containing (Terebellidae s.s. [Ampharetidae {Trichobranchidae-Alvinellidae}]), exactly the same result as that obtained by Zrzavý et al. (2009). In contrast, Struck (2011), using one species each of Pectinariidae, Terebellidae s.s., and Alvinellidae, found alvinellids basal and sister group to the clade containing Terebellidae s.s. and Pectinariidae.

Zhong et al. (2011), using a multigene phylogenetic analysis of terebelliform annelids, found a mixture of results as to the relationship of pectinariids with other members of this group, although they only sequenced two species, *Pectinaria gouldii* and *Lagis koreni* (as *Pectinaria koreni*), and only limited sequences have been obtained for *L. koreni* (only elongation factor-1α). Analyses using nuclear ML found that *P. gouldii* is a sister taxon to a sipunculan and not closely related to terebellids or alvinellids. In contrast, when the mitochondrial ML data have been analyzed, *P. gouldii* is sister to clades of terebellids, trichobranchids, and alvinellids. A similar pattern has been found with the combined ML tree. The authors commented on the problems of detecting symplesiomorphy traps, where molecular data from different cellular components, such as the mitochondrion and nucleus, may be inconsistent with each other (Zhong et al. 2011). However, that study focused more on the placement of trichobranchids. A later paper by Weigert et al. (2016), using mitochondrial gene order, in one analysis found *Pectinaria* as a sister clade to a group including maldanids, alvinellids, trichobranchids, and terebellids.

Finally, Nogueira et al. (2013) investigated the internal relationships of Terebelliformia based on morphological characters and used 2 species of Alvinellidae, 4 of Ampharetidae, 2 of Pectinariidae, 8 of Polycirridae, 7 of Telothelepodidae, 45 of Terebellidae s.s., 8 of Thelepodidae, and 5 of Trichobranchidae. This is by far the most comprehensive study ever made on the relationships within Terebelliformia, and the results show a highly derived Pectinariidae, which is monophyletic and nested within a paraphyletic Ampharetidae, and the group is sister clade to Alvinellidae. Obviously, more studies are required and combining molecular and morphological data, with a better representation of pectinariids, to really clarify their position.

Taxonomy

Pectinariidae consists of five genera. Its members are distinguished by the morphology of the opercular margin, cephalic veil, uncini, and degree of separation of the scaphe and the posterior body. All genera were considered as subgenera of *Pectinaria* in the past (Hartman 1941, Day 1967, Holthe 1986a, 1986b, except for *Petta*) until Fauchald (1977), following other authors (Long 1973), raised them all to generic level. The classification proposed by Fauchald (1977) was followed by subsequent authors (Wolf 1984, Hutchings and Peart 2002, Sun and Qiu 2012, García-Garza and León-González 2014, Zhang et al. 2015, Choi et al. 2017, Zhang and Qiu 2017) and adopted in this chapter.

Genera diagnoses

Pectinariidae Quatrefages, 1866

Type genus: *Pectinaria* Lamarck, 1818.

Definition: Typical ice-cream cone-shaped tubes, composed of sand grains and small stones cemented in mucus. Conical and short body, with 26 segments. Prostomium fused to peristomium, forming circular to ovate membranous cephalic veil, at which base buccal tentacles originate ventrally, distal margin of the cephalic veil smooth or cirrate; relatively few buccal tentacles, short, broad and tapering distally, almost triangular. Segment 1 distinctly short to inconspicuous ventrally, developed laterally and dorsally, forming cushion-like rounded operculum with low marginal lobe of even length, distal margin smooth or cirrate, and large golden and flattened notopodial paleae tapering to tips, arranged in two dorsolateral arched rows, near proximal margin of operculum; segment 1 with pair of digitiform tentacular cirri located ventrolaterally, one cirrus at each lateral margin of opercular lobe. Segments 2 to 6 forming distinctly raised crests ventrally, as ventral ridges, first crest more developed, sometimes with ventral lobe(s), cirrated or not; segment 2 also with pair of digitiform tentacular cirri, usually ventrally aligned to cirri of segment 1. Two pairs of lamellate branchiae, on segments 3 and 4, branchial filaments originating in pectinate arrangement from dorsal stalks; branchial lamellae relatively loosely packed, flat and smooth. Notopodia beginning on segment 5, extending until segments 20 and 21; neuropodia beginning on segment 8, extending until segments 20 and 21; one to two achaetous or only notopodia-bearing segments may be present at the base of scaphe. Narrowly winged notochaetae throughout in both rows or, more commonly, only on posterior row, and those of anterior row with narrow limbation from

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base, terminating with a finely serrated alimbate blade, sometimes with specializations at the base of blade, in the form of a foliaceous process, which has been recently described in a new species of *Pectinaria* (Nogueira et al. 2019). Neurochaetae as uncini, arranged in single, straight tori; uncini with anterior peg made of densely packed denticles; uncinial teeth long and thin, arranged in longitudinal rows, and main fang absent (pectinate) or main fang present and secondary teeth in transverse rows and progressively shorter distalward (avicular); uncini with base extending posteriorly as stout handle. Posterior 5 segments fused into sucker-like scaphe, with pair of transverse rows of stout hooks dorsally at base, paired lateral lamellae and longer anal flaps distally, but reduced in *Petta*, frequently with terminal cirrus in between.
Main references: Rouse and Pleijel 2001, Hutchings and Peart 2002, Zhang and Qiu 2017, Nogueira et al. 2019.

Amphictene Savigny, 1822

Type species: *Amphitrite auricoma* (Müller 1776) subsequent designation by Hartman (1959).
14 species (Read and Fauchald 2018a, Zhang and Hutchings 2019).
Diagnosis: Pectinariids with both cephalic veil and margin of opercular lobe cirrate, scaphe well separated from the abdomen and pectinate uncini, with crest with at least two longitudinal rows of thin, nearly evenly sized teeth and stout handle posteriorly.
Main references: Nilsson 1928, Hutchings and Peart 2002, Nogueira et al. 2019, Zhang and Hutchings 2019.

Cistenides Malmgren, 1866

Type species: *Sabella granulata* Linnaeus, 1767, by original designation.
7 species (Read and Fauchald 2018b).
Diagnosis: Pectinariids with cirrate cephalic veil and smooth margin of opercular lobe, straight, scaphe well separated from the abdomen and pectinate uncini, with crest with single longitudinal row of thin, nearly evenly sized teeth and stout handle posteriorly.
Main references: Hutchings and Peart 2002.

Lagis Malmgren, 1866

Type species: *Lagis koreni* Malmgren, 1866, by monotypy.
11 species (Read and Fauchald 2018c, Zhang and Hutchings 2019).
Diagnosis: Pectinariids with cirrate cephalic veil and smooth margin of opercular lobe, straight, cephalic veil fused laterally with opercular lobe, scaphe well separated from the abdomen and pectinate uncini, with crest with at least two longitudinal rows of thin, nearly evenly sized teeth and stout handle posteriorly.
Main references: Hutchings and Peart 2002, Sun and Qiu 2012, Choi et al. 2017, Zhang and Hutchings 2019.

Pectinaria Savigny, 1822

Type species: *Nereis cylindraria belgica* Pallas, 1766, designated by Hartman (1959).
28 species (Read and Fauchald 2018d, Nogueira et al. 2019, Zhang and Hutchings 2019).
Diagnosis: Pectinariids with cirrate cephalic veil and smooth margin of opercular lobe, straight, scaphe well separated from the abdomen and pectinate uncini, with crest with at least two longitudinal rows of thin, nearly evenly sized teeth and stout handle posteriorly.
Main references: Hutchings and Peart 2002, Zhang and Qiu 2017, Nogueira et al. 2019, Zhang and Hutchings 2019.

Petta Malmgren, 1866

Type species: *Petta pusilla* Malmgren, 1866, by monotypy.
5 species (Read and Fauchald 2018e, Nogueira et al. 2019).
Diagnosis: Pectinariids with both cephalic veil and margin of opercular lobe smooth, although cephalic veil has a medial extension, scaphe not as clearly separated from posterior body segments as in animals of other genera, and avicular uncini, with crest with transverse rows of progressively shorter teeth.
Main references: Nogueira et al. 2019, Zhang et al. 2019.

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References

Anstrom, J. & Summers, R.G. (1981): The role of extracellular Ca^{2+} in the activation of *Pectinaria* oocytes. *Development, Growth & Differentiation* 23: 415–420.

Austin, C.R. (1963): Fertilisation in *Pectinaria gouldii*. *Biological Bulletin* 124: 115–124.

Bartolomaeus, T. (1995): Structure and formation of the uncini in *Pectinaria koreni*, *Pectinaria auricoma* (Terebellida) and

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Spirorbis spirorbis (Sabellida): Implications for annelid phylogeny and the position of the Pogonophora. *Zoomorphology* 115: 161–177.

Bartolomaeus, T. (1999): Structure, function and development of segmental organs in Annelida. *Hydrobiologia* 402: 21–37.

Bartolomaeus, T., Purschke, G. & Hausen, H. (2005): Polychaete phylogeny based on morphological data — A comparison of current attempts. *Hydrobiologia* 535–536: 341–356.

Brasil, L. (1904): Contribution à connaissance de l'appareil digestif des Annélides polychètes. L'epithelium intestinal de la Pectinaire. *Archives de Zoologie Expérimentale et Générale, Paris*, Série 4 2: 91–255.

Busch, D.A. & Loveland, R.E. (1975): Tube-worm-sediment relationships in populations of *Pectinaria gouldii* (Polychaeta: Pectinariidae) from Barnegat Bay, New Jersey, USA. *Marine Biology Berlin* 33: 255–264.

Choi, H.K., Jung, T.W. & Yoon, S.M. (2017): A new species of *Lagis* (Annelida: Polychaeta: Pectinariidae) from Korean waters. *Zootaxa* 4227: 279–286.

Dales, R.P. (1963): *Annelids*. Hutchinson University Library, London: 200 pp.

Day, J.H. (1967): *A Monograph on the Polychaeta of South Africa. Part 2. Sedentaria*. British Museum (Natural History), London.

Dehorne, A. (1925): Observations sur *Lagis koreni*: Hermaphrodisme; formations paramyéliniques dans l'ovule; cellules néphridiennes avec capsules à corps central. *Compte Rendu Hebdomadaire des Séances de Académie des Sciences, Paris* 181: 432–434.

Desroy, N., Oliver, F. & Retière, C. (1997): Effects of individual behaviors, inter-individual interactions with adult *Pectinaria koreni* and *Owenia fusiformis* (Annelida, Polychaeta), and hydrodynamism on *Pectinaria koreni* recruitment. In: Reish, D.J. & Qian, P.Y. (eds). Fifth International Polychaete Conference held at Qingdao, Peoples' Republic of China, July 1–6, 1995. *Bulletin of Marine Science* 60: 547–558.

Dobbs, F.C. & Scholly, T.A. (1986): Sediment processing and selective feeding by *Pectinaria koreni* (Polychaeta: Pectinariidae). *Marine Ecology Progress Series* 29: 165–176.

Dorresteijn, A. (2005): Cell lineage and gene expression in the development of polychaetes. *Hydrobiologia* 535/536: 1–22.

Estcourt, I.N. (1974): Population study of *Pectinaria australis* (Polychaeta) in Tasman Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 8: 283–290.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County* 28: 1–188.

Fauchald, K. & Jumars, P. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology, Annual Review* 17: 193–284.

Fauchald, K. & Rouse, G. (1997): Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71–138.

Fauvel, P. (1897): Recherches sur les Ampharetiens, Annélides polychètes sédentaires. Morphologie, Anatomie, Histologie, Physiologie. *Bulletin Scientifique de la France et de la Belgique* 30: 277–489.

Fauvel, P. (1927): Polychètes sédentaires. Addenda aux errantes, Arachiannélides, Myzostomaires. *Faune de France* 16. Lechevalier, Paris: 494 pp.

García-Garza, M.E. & León-González, J.A. (2014): A new species of *Amphictene* (Annelida, Pectinariidae) from the Gulf of Mexico, with a redescription of *Amphictene guatemalensis* (Nilsson, 1928). *ZooKeys* 367: 1–9.

Goodrich, E.S. (1945): The study of nephridia and genital ducts since 1895. *Quarterly Journal of Microscopical Science, London* 86: 113–392.

Gordon, D.C. (1966): The effects of the deposit feeding polychaete *Pectinaria gouldii* on the intertidal sediments of Barnstable Harbor. *Limnology and Oceanography* 11: 327–332.

Gravely, F.H. (1909): Polychaete larvae of Port Erin. *Proceedings and Transactions of the Liverpool Biological Society* 23: 575–653.

Groot, S.J. de (1971): On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). *Netherlands Journal of Sea Research* 5: 121–196.

Grube, A.-E. (1850): Die Familien der Anneliden. *Archiv für Naturgeschichte Berlin* 16: 249–364.

Hall, K.A., Hutchings, P.A. & Colgan, D.J. (2004): Further phylogenetic studies of the Polychaeta using 18S rDNA sequence data. *Journal of the Marine Biological Association of the United Kingdom* 84: 949–960.

Hartman, O. (1941): Polychaetous annelids. Part IV. Pectinariidae. *Allan Hancock Pacific Expeditions* 7: 325–345.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Parts I & II. *Occasional Papers of the Allan Hancock Foundation* 23: 1– 628.

Hausen, H. (2005): Chaetae and chaetogenesis in polychaetes (Annelida). *Hydrobiologia* 535/536: 37–52.

Hessle, C. (1917): Zur Kenntnis der terebellomorphen Polychaeten. *Zoologiska Bidrag från Uppsala* 5: 39–258.

Hessle, C. (1925): Bidrag till kännedomen om de terebellomorphen polychaeternas biologi. *Arkiv för Zoologi, Stockholm* 17a: 1–29.

Holthe, T. (1986a): Polychaeta Terebellomorpha. *Marine Invertebrates of Scandinavia* No. 7. Norwegian University Press, Oslo: 194 pp.

Holthe, T. (1986b): Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. *Gunneria* 55: 1–236.

Hutchings, P. & Peart, R. (2002): A review of the genera of Pectinariidae (Polychaeta) together with a description of the Australian fauna. *Records of the Australian Museum* 54: 99–127.

ICZN (International Commission on Zoological Nomenclature) (1982): OPINION 1225: *Pectinaria* Lamarck, 1818, *Nereis cylindraria belgica* Pallas, 1766 and *Lagis koreni* Malmgren, 1866 (Polychaeta): conserved. *Bulletin of Zoological Nomenclature* 39: 186–191.

Irlinger, J.P., Gentil, F. & Quintino, V. (1991): Reproductive biology of the polychaete *Pectinaria koreni* (Malmgren) in the Bay of Seine (English Channel). *Ophelia Supplement* 5: 343–350.

Jolly, M.T., Jollivet, D., Gentil, F., Thiebaut, E. & Viard, F. (2004): Sharp genetic break between Atlantic and English Channel populations of the polychaete *Pectinaria koreni*, along the North coast of France. *Heredity* 94: 23–32.

Katto, J. (1976): Additional problematica from southwest Japan. *Research Reports, Kochi University, National Science* 25: 17–24.

Kennedy, G.Y. & Dales, R.P. (1958): The function of the heart-body in polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 37: 15–31.

Lamarck, J.B. de (1818): *Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs*

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familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédés d'une Introduction offrant la détermination des caractères essentiels de l'Animal, sa distinction du végétal et desautres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Deterville, Paris: 612 pp.

Lambert, R., Retière, C. & Lagadeuc, Y. (1996): Metamorphosis of *Pectinaria koreni* (Annelida: Polychaeta) and recruitment of an isolated population in the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 76: 23–36.

Levinsen, G.M.R. (1883): Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Første Halvdel. Videnskabelige Meddelelser fra Dansk naturhistorik Førening i Kjøbenhavn* 1882: 160–251.

Linnaeus, C.v. (1767): *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Copenhagen.

Long, C.D. (1973): Pectinariidae (Polychaeta) from Caribbean and associated waters. *Bulletin of Marine Science* 23: 857–874.

Lucas, J.A.W. & Holthuis, L.B. (1975): On the identity and nomenclature of *Pectinaria belgica* (Pallas, 1766) (Polychaeta, Amphictenidae). *Zoologische Mededelingen* 49: 85–90.

Malmgren, A. J. (1866): Nordiska Hafs-Annulater. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 22: 355–410.

Meyer, E. (1887): Studien über Körperbau der Anneliden. Teil 1–3. *Mitteilungen aus der Zoologischen Station zu Neapel* 7: 592–741.

Michel, C. (1988): Intestine and digestive glands. In: Westheide, W. & Hermans, C.O. (eds.). *The Ultrastructure of Polychaeta*. *Microfauna Marina* Vol. 4. Gustav Fischer Verlag, Stuttgart: 157–175.

Müller, O.F. (1776): *Zoologicae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium*. Typis Hallageriis, Copenhagen: 282 pp.

Nicolaidou, A. (1988): Notes on the behaviour of *Pectinaria koreni*. *Journal of the Marine Biological Association of the United Kingdom* 68: 55–59.

Nielsen, C. & Kirkegaard, J.B. (1978): Amended proposal for validating *Pectinaria* Lamarck, 1818 (Polychaeta), *P. belgica* (Pallas, 1766) and *P. koreni* (Malmgren, 1866) under the plenary powers. Z.N. (S.) 2202. *Bulletin of Zoological Nomenclature* 35: 25–29.

Nilsson, D. (1912): Beiträge zur Kenntnis der Nervensystems der Polychaeten. *Zoologiska Bidrag från Uppsala* 1: 85–161.

Nilsson, D. (1928): Neue und alte Amphicteniden. Göteborgs Kunge. *Vetenskaps - och Vitterhets Samhälles Handlingar*, Series 4, 33: 1–96.

Nogueira, J.M.M., Hutchings, P. & Fukuda, M.V. (2010): Morphology of terebelliform polychaetes (Annelida: Polychaeta: Terebelliformia), with a focus on Terebellidae. *Zootaxa* 2460: 1–185.

Nogueira, J.M.M., Fitzhugh, K. & Hutchings, P. (2013): The continuing challenge of phylogenetic relationships in (Annelida: Polychaeta). *Invertebrate Systematics* 27: 186–238.

Nogueira, J.M.M., Ribeiro, W.M.G., Carrerette, O. & Hutchings, P. (2019): Pectinariidae (Annelida, Terebelliformia) from off southeastern Brazil, southwestern Atlantic. *Zootaxa* 4571: 489–509.

Orrhage, L. (2001): On the anatomy of the central nervous system and the morphological value of the anterior end appendages of Ampharetidae, Pectinariidae and Terebellidae (Polychaeta). *Acta Zoologica* 82: 57–71.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.

Pallas, P.S. (1766): *Miscellanea zoologica. Quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur*. Petrum van Cleef, Hague: xii + 224.

Picton, L.J. (1899): On the heartbody and coelomic fluid of certain Polychaeta. *Quarterly Journal of Microscopical Science, New Series* 41: 263–302 [Issued in 1898].

Quatrefages, A. (1866): Histoire naturelle des Annelés marins et d'eau douce. *Annélides et Géphyriens*. Vol. 2. Librarie Encyclopédique de Roret, Paris: 1–794.

Read, G. & Fauchald, K. (eds.) (2018a): World Polychaeta database. *Amphictene* Savigny, 1822. Accessed through: *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=152447 (Accessed on 2019-11-04).

Read, G. & Fauchald, K. (eds.) (2018b): World Polychaeta database. *Cistenides* Malmgren, 1866. Accessed through: *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=157316 (Accessed on 2019-11-04).

Read, G. & Fauchald, K. (eds.) (2018c): World Polychaeta database. *Lagis* Malmgren, 1866. Accessed through: *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=152367 (Accessed on 2019-11-04).

Read, G. & Fauchald, K. (eds.) (2018d): World Polychaeta database. *Pectinaria* Lamarck, 1818. Accessed through: *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=129437 (Accessed on 2019-11-04).

Read, G. & Fauchald, K. (eds.) (2018e): World Polychaeta database. *Petta* Malmgren, 1866. Accessed through: *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=129438 (Accessed on 2019-11-04).

Ronan, T.E. (1977): Formation and paleontologic recognition of structures caused by marine annelids. *Paleobiology* 3: 389–403.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Rhoads, D.C. (1974): Organism-sediment relationships on the muddy sea floor. *Oceanography and Marine Biology, Annual Review* 12: 263–300.

Rhoads, D.C. & Young, D.K. (1970): The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28: 150–178.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford.

Rullier, F. (1951): Étude morphologique, histologique et physiologique de l'organe nucal chez les annélides polychètes sedentaires. *Annee Biologique* 27: 51–56.

Savigny, M.J.C. de (1822): Système des annélides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les caractères

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tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Espèces. *Description de l'Egypte Histoire Naturelle, Paris* 1: 1–128 [According to Opinion 1461, *Bulletin of Zoological Nomenclature* 44: 219–220, the date is 1822. The paper was published as 1: 235–472, 1809, but not issued then; also issued as a separate, paginated 1–128, 2nd ed. in 1826].

Schäfer, W. (Trans.) (1972): *Ecology and Palaeoecology of Marine Environments.* University of Chicago Press, Chicago: 568 pp. [First published in German 1962. Translation by Oertel.]

Schmarda, L.K. (1861): *Neue wirbellose Thiere beobachtet und gesammelt auf einer* Reise *um die Erde 1853 bis 1857. Erster Band (zweite Hälfte) Turbellarien, Rotatorien und Anneliden*. Wilhelm Engelmann, Leipzig: 164 pp.

Schroeder, P.C. & Hermans, C.O. (1975): Annelids: Polychaeta. In: Giese, A.C. & Pearse, J.S. (eds.). *Reproduction of Marine Invertebrates*. Vol. III. Annelids and Echiurans. Academic Press, New York: 1–213.

Söderström, A. (1930): Über segmental wiederholte 'Nuchalorgane' bei Polychäten. *Zoologiska Bidrag från Uppsala* 12: 1–18.

Storch, V. (1988): Integument. In: Westheide, W. & Hermans, C.O. (eds.). *The Ultrastructure of Polychaeta. Microfauna Marina*. Vol. 4. Gustav Fischer Verlag, Stuttgart: 13–36.

Storch, V. & Alberti, G. (1978): Ultrastructural observations on the gills of polychaetes. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 31: 169–179.

Struck, T.H. (2011): Direction of evolution within Annelida and the definition of Pleistoannelida. *Journal of Zoological Systematics and Evolutionary* 49(4): 340–345.

Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7: 57.

Sun, Y. & Qiu, J.W. (2012): A new species of *Lagis* (Polychaeta: Pectinariidae) from Hong Kong. *Zootaxa* 3264: 61–68.

Taghon, G.L., Self, R.F.L. & Jumars, P.A. (1978): Predicting particle selection by deposit feeders: A model and its implications. *Limnology and Oceanography* 23: 752–759.

Thorson, G. (1946): Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Komissionen for Danmarks Fiskeri-Og Havundersøgelser, Serie Plancton* 4: 1–523.

Truchet, M. & Vovelle, J. (1977): Etude de la glande cémentaire d'un polychète tubicole (*Pectinaria (=Lagis) koreni*) à l'aide de la microsonde électronique, du microanalyseur ionique et du microscope électronique à balayage. *Calcified Tissue Research* 24: 231–238.

Tweedel, K.S. (1961): Factors affecting germinal epithelium vesicle breakdown in *Pectinaria* (*Cistenides*) *gouldii*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 121: 412 (abstract).

Tweedel, K.S. (1966): Oocyte development and incorporation of H3 thymidine and H3 uridine in *Pectinaria* (*Cistenides*) *gouldii*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 131: 516–538.

Tweedel, K.S. (1980): The activation of gamete migration, maturation and spawning in *Pectinaria gouldii*. *International Journal of Invertebrate Reproduction* 2: 516–538 [pp. 131–151 in *Zoological Record*].

Vovelle, J. (1979a): Le ciment organo-minérale de *Petta pusilla* Malmgren, polychète tubicole. *Compte Rendu Hebdomadaire des Séances de Académie des Sciences, Paris* 288D: 1599–1602.

Vovelle, J. (1979b): Les glandes cémentaires de *Petta pusilla* Malmgren, polychète tubicole Amphictenidae, et leur sécrétion organo-minérale. *Archives de Zoologie Expérimentale et Générale* 120: 219–246.

Watson, A.T. (1928): Observations on the habits and life history of *Pectinaria* (*Lagis*) *koreni* Mgr. (Edited and with an introduction by P. Fauvel). *Proceedings and Transactions of the Liverpool Biological Society* 42: 25–60.

Weigert, A., Golombek, A., Gerth, M., Scharz, F. & Struck, T.H. (2016): Evolution of mitochondrial gene order in Annelida. *Molecular Phylogenetics and Evolution* 94: 196–206.

Whitlatch, R.B. (1974): Food-resource partitioning in the deposit feeding polychaete *Pectinaria gouldii*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 147: 227–235.

Wilson, D.P. (1936): Notes on the early stages of two polychaetes, *Nephthys hombergi* Lamarck and *Pectinaria koreni* Malmgren. *Journal of the Marine Biological Association of the United Kingdom* 21: 305–310.

Wilson, W.H. (1991): Sexual reproductive modes in polychaetes: Classification and diversity. In: Reish, D.J. (ed.) Third International Polychaete Conference held at California State University, Long Beach, California, August 6–11, 1989. *Bulletin of Marine Science* 48: 500–516.

Wirén, A. (1885): Om Cirkulation- och digestions-organen hos Annelider af familjerna Ampharetidae Terebellidae och Amphictenidae. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1–58.

Wolf, P.S. (1984): Family Pectinariidae Quatrefages, 1865. In: Uebelacker, J.M. & Johnson, P.G. (eds.). *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. Vol. VII, Chapter 50: 50-1–50-10.

Wong, E. & Hutchings, P. (2015): New records of Pectinariidae (Polychaeta) from Lizard Island, Great Barrier Reef, Australia and the description of two new species. *Zootaxa* 4019: 733–744.

Wood, W. (1802): Observations on the hinges of British bivalve shells. *Transactions of the Linnean Society of London* 6: 154–176.

Zhang, J. & Hutchings, P. (2019): A revision of Australian Pectinariidae (Polychaeta), with new species and new records. *Zootaxa* 4611: 1–70.

Zhang, J. & Qiu, J.-W. (2017): A new species of *Pectinaria* (Annelida, Pectinariidae), with a key to pectinariids from the South China Sea. *ZooKeys* 683: 139–150.

Zhang, J., Zhang, Y. & Qiu, J.-W. (2015): A new species of *Amphictene* (Annelida, Pectinariidae) from the northern South China Sea. *ZooKeys* 545: 27–36.

Zhang, J., Hutchings, P. & Kupriyanova, E. (2019): A revision of the genus *Petta* (Polychaeta Pectinariidae), with two new species from the abyss of south-eastern Australia, and comments on the phylogeny of the family. *Zootaxa* 4614: 303–330.

Zhong, M., Hansen, B., Nesnidal, M.P., Golombek, A., Halanych, K.M. & Struck, T.H. (2011): Detecting the symplesiomorphy trap: A multigene phylogenetic analysis for terebelliform annelids. *BMC Evolutionary Biology* 11: 369.

Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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Brigitte Ebbe and Günter Purschke

7.7.2 Ampharetidae Malmgren, 1866

Introduction

Ampharetids are tube-dwelling polychaetes occurring essentially everywhere in the marine realm (exceptionally in freshwater or brackish water) but usually in low abundances. Only species from "extreme" habitats are known to occur in high abundances and even are numerically dominant. *Grassleia hydrothermalis* Solis-Weiss, 1993 from the Gorda Ridge, Pacific Ocean, has been reported to contribute 37% to the total fauna (Solis-Weiss 1993), *Amphisamytha galapagensis* Zottoli, 1983 reach densities between about 2200 and nearly 3000 individuals/m^2 near hydrothermal vents in the Juan de Fuca area (Petrecca and Grassle 1990, McHugh and Tunnicliffe 1994), and *Paedampharete acutiseries* Russell, 1987 has been reported from the HEBBLE site off Georges Bank, Atlantic Ocean (Thistle et al. 1991), a site characterized by extremely instable sediments and exposure to benthic storms. *Melinna palmata* Grube, 1870 has been reported to occur in densities of more than 1500 individuals/m^2 in Galway Bay (Grehan et al. 1991), and *Melinna cristata* (Sars, 1851) has been reported to be "highly gregarious" in an area off the coast of Northumberland (Hutchings 1973a, b). Olafsson et al. (1990) investigated the impact of fecal casts of *M. palmata* on the meiofaunal community and reported densities of 240 individuals/m^2.

The large family Ampharetidae, consisting of approximately 300 species in 64 genera, is divided into two subfamilies based on morphological details of the anterior end. Melinninae shows a number of very fine capillary neurochaetae in up to four anteriormost segments, a membrane across the dorsum of the segment, and sometimes a pair of large dorsal hooks just anterior to the membrane. The second subfamily Ampharetinae includes all genera devoid of these characters.

Morphology and anatomy

External morphology

Body regions. Ampharetidae are usually recognized by a clear separation between an anterior thoracic region with chaetigerous notopodia and uncinigerous neuropodia and a posterior abdominal region with uncinigerous neuropdia only, without chaetigerous notopodia, and a small number of branchiae arranged across one to maximally three anterior segments behind the prostomium (Fig. 7.7.2.2A). As the taxonomy of Ampharetidae has traditionally been based on many meristic characters, such as the number of thoracic chaetigers and uncinigers or the number of branchiae, one of the most discussed characters in ampharetids is the interpretation of the segmentation of the anterior end. We follow here the method of Reuscher et al. (2009), interpreting the first visible "segment" behind the prostomium as peristomium and consequently chaetiger 1 as segment 2. The first thoracic unciniger then is always segment 6 (not segment 7 as traditionally stated). This view is consistent with Orrhage's (2001) observations on the nervous system.

Color. Pigment patterns are generally inconspicuous; in some cases, nuchal organs are surrounded by dark pigment, giving them the appearance of large eyes. Branchiae may also show pigmentation, usually as darkish rings. Live specimens are often nearly transparent so that inner organs are visible, but the integument may be speckled (Fig. 7.7.2.1). When preserved, the body wall is opaque and beige. *Melinna cristata* is reported to be reddish brown with golden hooks (Gunton personal observation).

Anterior segments. The prostomium is typically spatulate, roughly pentagonal, and often divided into a



Fig. 7.7.2.1: Live specimen of *Amphicteis* sp., lateral view, showing the coloration of the semitransparent integument, a relatively short abdomen, and paleae on segment 2. © F. Pleijel.

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midsuperior lobe and a posterior lobe surrounding the former on three sides, giving a trilobed appearance to the anterior prostomial margin. Glandular ridges may be present, but these ridges may prove to be nuchal organs (Hilbig 2000, see Orrhage 2001). Eyes, when present, are single or arranged in rows or patches of small eyespots, for example, on the ventral side of the upper lip (*Ampharete labrops* Hartman, 1961). Buccal tentacles are considered to be of peristomial origin. They arise from the roof of the buccal cavity and can be retracted into the mouth. Some authors regard these tentacles as homologous with palps (e.g., Rouse and Pleijel 2001). However, the innervation pattern of these appendages does not support this view and argues that buccal appendages belong to the alimentary canal (Orrhage 2001). They may be smooth, grooved, or pinnate (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A, B, 7.7.2.4). Jirkov (2001, 2009, 2011) presented a classification of prostomia into 11 main categories based on which he proposed a number of synonymizations of ampharetid genera. By doing so, he reduced the number of valid genera from more than 80 to 22; however, 14 genera did not fit into this scheme and were listed as "of uncertain taxonomical status" (Jirkov 2011). Day (1964), however, in his review of diagnostic characters within the Ampharetidae stated that "... the exact shape of the prostomium is of little systematic value", as it changes depending on the extension of the buccal tentacles. Moreover, the synonymies are only partly followed by other more recent authors, such as Reuscher et al. (2015a, b) (see also WoRMS Editorial Board 2018), and the list of valid genera in this chapter is composed accordingly.

Currently, the peristomium is interpreted as a single apodous and achaetous ring (Fig. 7.7.2.3A, B), a view that follows the opinion of several earlier authors (Annenkova 1930, Eliason 1955, Uschakov 1955) and summarized by Day (1964). It has been widely misinterpreted as first segment (e.g., Thorson 1946). The presence of two peristomial rings rather than one, which was argued by earlier authors such as Malmgren (1865) and Fauvel (1897), is no longer agreed on. As a consequence, the first thoracic chaetiger is segment 2 rather than segment 3 (Fig. 7.7.2.3A) (Reuscher et al. 2009, Imajima et al. 2013).

Thorax. Segments of the thorax are well defined, rigid, and ventrally equipped with glandular cells arranged in shields or scutes (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A). The anterior

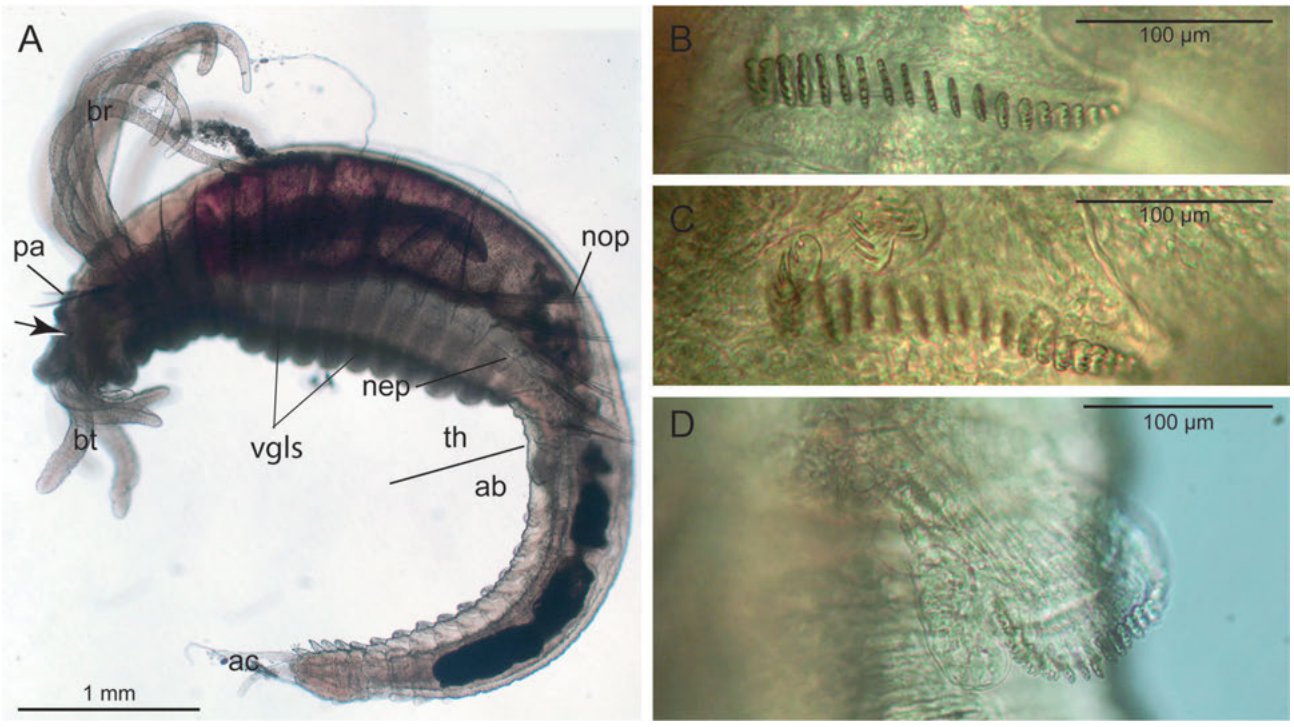


Fig. 7.7.2.2: *Amphicteis gunneri* (Sars, 1835), light microscopy images, live observations. A, Entire immature animal, lateral view, arrow points to minute eyes; B, C, Thoracic uncini from thorax segment 16 at different focus planes; C, Somewhat deeper focus, showing replacement chaetae in lateral view; D, Abdominal uncini from second abdominal segment with reduced notopodial cirrus on the left. ab, abdomen; ac, anal cirri; br, branchiae; bt, buccal tentacles; nep, neuropodium; nop, notopodium; pa, paleae; th, thorax; vgls, ventral glandular shield. Original.

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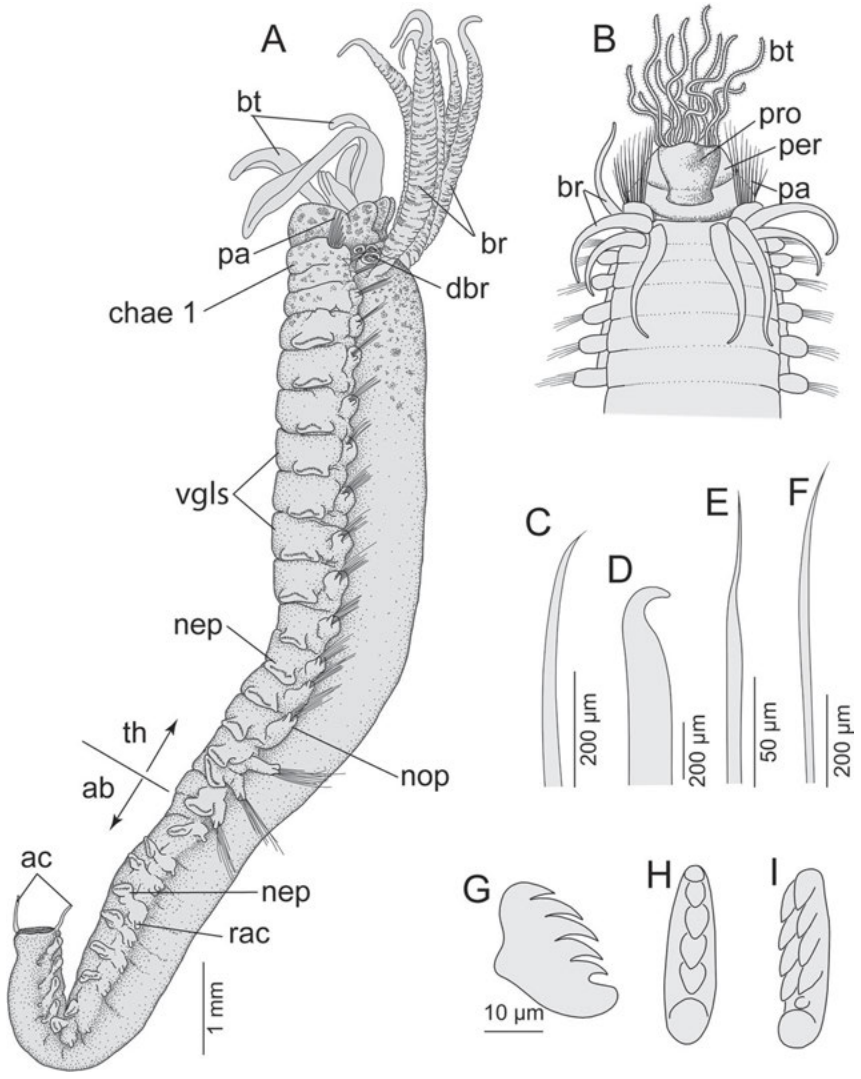


Fig. 7.7.2.3: Morphology of Ampharetidae. A, *Amphicteis dalmatica* Hutchings & Rainer, 1979, entire animal, lateral view; B, *Ampharete acutifrons* (Grube, 1860), anterior end, dorsal view, arrangement of prostomium (pro), peristomium (per) buccal tentacles (bt), and branchiae (br); C–I, chaetae; C, *A. dalmatica*, paleae; D, *Isolda pulchella* Müller in Grube, 1858, hook from chaetiger 4; E, *I. pulchella*, acicular chaeta from chaetiger 1; F, *A. dalmatica,* capillary notochaeta; G, H, *A. dalmatica,* neurochaetal uncinus from chaetiger 15; I, *Auchenoplax* sp. neurochaetal uncinus; G–I, Same scale. ab, abdomen; ac, anal cirri; br, branchiae; bt, buccal tentacles; chae 1, chaetiger 1 (=segment 2); dbr, dissected brnaichiae; nep, neuropodium; nop, notopodium; pa, paleae; per, peristomium; pro, prostomium; rac, reduced abdominal cirrus; th, thorax; vgls, ventral glandular shield. A, C–I, Modified from Hutchings (2000); B, Modified from Malmgren (1865).

segments of the thorax are subject to great morphological variability. Segments 1 and 2 are usually reduced, fused, or telescoped and ventrally form the lower lip, which may be smooth or crenulated. Segments 2 to 5 bear the branchiae and may also carry typically enlarged, forward-directed notochaetae referred to as paleae (segment 2 or chaetiger 1) (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A–C), modified hook-like and/or very slender, short capillary chaetae (Figs. 7.7.2.3D–F, 7.7.2.5), as well as a varying number of reduced notopodia with few and short regular notochaetae.

Intermediate segments. As part of a generic review of all Ampharetidae, Jirkov (2011) introduced a new character that he found useful for generic discrimination, the so-called intermediate uncinigers. This character was first recognized by Mackie (1994) in his description of *Adercodon pleijeli* Mackie, 1994. The author recognized their taxonomic importance but considered adding these segments to the thorax. These segments do not bear notopodia, but contrary to true abdominal segments the neuropodia are formed as tori-like in the thorax and not as pinnules like in the abdomen. Furthermore, the uncini are of the same type as the ones in the thorax and not like those in the abdomen. Subsequently, Imajima et al. (2012) included this character in their review of genus *Ampharete* from Japan.

Abdomen. The abdomen usually is distinctly narrower than the thorax, and the segments are soft-walled and more elongated than the thoracic ones (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A). Their number is often fixed, particularly in the subfamily Ampharetinae, but as they are added during individual development this character contains information only if several demonstrably adult specimens are examined (Reuscher et al. 2009). Many ampharetids have rather short abdominal regions, which may reflect a trend toward loss of abdominal segments during evolution (Holthe 1986a), but this hypothesis has not been proven through phylogenetic studies.

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Parapodia and chaetae. By definition, the first pair of complete, biramous parapodia is located on segment 6. Notopodia are conical, sometimes with small presetal and postsetal lobes and ventral cirri, and bear slender, limbate capillary chaetae (Fig. 7.7.2.3A, D–F). Notochaetae on segment 2 may be modified to long, broad paleae (Figs. 7.7.2.1, 7.7.2.3A–C), sometimes arranged in conspicuous whirls (genus *Anobothrus*), or are thinner and shorter than those on subsequent segments or entirely absent. Supposedly, the paleae are used for digging or as an operculum to close the worm's tube. In some genera, such as *Sosane* (Fig. 7.7.2.4), one or more pairs of thoracic notopodia may be elevated and bear specialized notochaetae most likely to enhance irrigation in the tube (Holthe 1986a).



Fig. 7.7.2.4: Live specimen of *Sosane sulcata* Malmgren, 1866 in lateral view, showing elevated notopodia in the third-to-last thoracic segment. © F. Pleijel.



Fig. 7.7.2.5: Live specimen of *Melinna albicincta* Mackie & Pleijel, 1995 in lateral view. © F. Pleijel.

Thoracic neuropodia are tori bearing single rows of small uncini (Figs. 7.7.2.2B, C, 7.7.2.3G). In the subfamily Melinninae, uncini in the first three to four segments are shaped as fine, short capillary chaetae (Fig. 7.7.2.5). In the abdomen, achaetigerous notopodial rudiments may be present on all or some segments (Figs. 7.7.2.2D, 7.7.2.3A). Abdominal neuropodia are formed as pinnules that may bear cirri (e.g., *Paiwa* Chamberlin, 1919 and *Weddellia* Hartman, 1967). Neurochaetae are small, short uncini, usually differing in shape from the thoracic ones, especially in the number of rows of teeth (Fig. 7.7.2.3H, I). Holthe (1986a) has named the different parts of uncini, and his terminology is still in use (Fig. 7.7.2.6).

Branchiae. Branchiae are simple and unbranched and typically seem to originate from one or two segments, although they are appendages of segments 2 to 5 (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A, B, 7.7.2.4). Usually, there are two to four pairs of branchiae, with four pairs as the most common number. In a few cases, branchiae are pinnate (papillated) or bear ciliary rings (*Pseudampharete* Hilbig, 2000). Their number is one of the most conspicuous taxonomic characters used for genus discrimination, but in recent years a different view has developed (Reuscher et al. 2009, 2015a, b, Reuscher and Fiege 2016).

For most species, a pair of nephridial papillae located dorsally on segment 4 is reported (e.g., Imajima et al. 2012). In some cases, these papillae are fused into a median one (Hessle 1917).

Pygidium. Typically, the pygidium is a simple ring, the central anus sometimes surrounded by a few rounded papillae and/or slender cirri (Figs. 7.7.2.1, 7.7.2.2A, 7.7.2.3A). Fauchald (1972) proposed to use the shape and number of pygidial appendages for species discrimination in *Samythella*. In a recently described species, *Ampharete oculicirrata* Parapar, Moreira & Barnich, 2019, a pair of

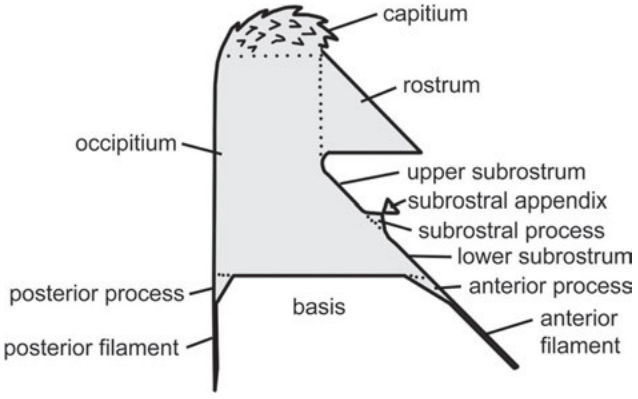


Fig. 7.7.2.6: Morphological features of ampharetid uncini. Redrawn from Holthe (1986a).

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eyes has been described to occur on the pygidial cirri (Parapar et al. 2019).

Tube morphology. Tubes are typically straight, made of a mucous inner lining and an outer layer of sediment grains. As they are constantly being rebuilt, the tubes do not outlast the animals and disintegrate once the animal dies. *Ampharete falcata* Eliason, 1955 from the Dogger Bank, North Sea, has been observed to build tubes with coarse sand grains on the posterior end and very fine grains in the middle and anterior ends (Fig. 7.7.2.7A) (personal observation). The vent species *Amphisamytha galapagensis* has been shown to build tubes composed of mucus and sulfur particles, apparently covering only the posterior end of the animals. Moreover, the species has been reported to frequently leave its tube and supposedly live freely when tube building material is scarce (McHugh and Tunnicliffe 1994).

Only one species, *Andamanella bellis* Holthe, 2002, has been suspected to be nontubiculous because of the complete absence of uncini.

Anatomy

Excretory system and nephridia. Hessle (1917) was the first who tried to use the number and shapes of nephridia for systematic purposes. He divided the nephridia into anterior ones (usually represented by just one pair) with an aperture on segment 4 (i.e., in front of the diaphragm) and posterior ones with apertures on segments behind the diaphragm. In a key to the then-known genera of ampharetids, he used anatomical details of the nephridia as part of generic diagnoses. Unfortunately, his very meticulous studies have not been carried any further.

Ampharetids, as all terebellomorph families, possess a special septum in the anterior thorax, which is referred to as gular membrane or diaphragm (Hessle 1917, Zhadan and Tzetlin 2003). The gular membrane essentially separates the anterior thoracic body cavity with the openings of the excretory nephridia from the posterior thoracic cavity with funnels of the gonoducts. All other septa in the thorax are lacking. Zhadan and Tzetlin (2003) investigated the anatomical details of the gular membrane using light and electron microscopy, revealing a funnel-shaped diaphragm attached

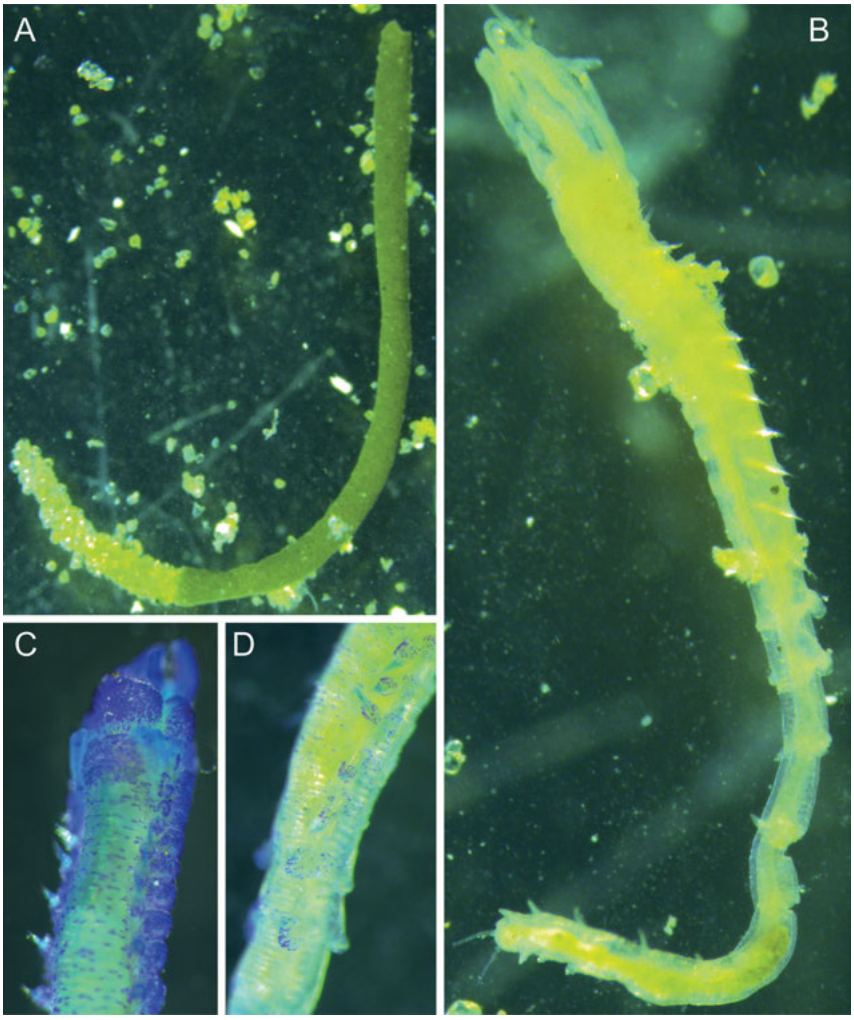


Fig. 7.7.2.7: *Amphisamytha falcata*. A, Tube with coarse sediment grains near the base and mud particles in the middle and anterior regions; B, Habitus; C, Anterior end, showing a broad gap between the two groups of branchial scars; D, Rudimentary notopodia on the first two abdominal segments.

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to the body wall between segments 3 and 4 and reaching back several segments. A portion of the diaphragm with particularly strong muscle cells may be formed into one or two contractile terminal sacs. The contraction of the diaphragm results in the extension of the buccal tentacles. The funnel shape was already reported by Fauvel (1897), who, however, did not discover any muscle cells. Another septum defines the border between the thorax and the abdomen.

Body cavities and coelom. Parapar et al. (2018) described the anatomy of a new species of *Ampharete* using both classical histology and micro-computed tomography. The buccal tentacles can be retracted into the muscular pharynx, which is characterized by a ventral buccal organ. An esophagus leads to a large stomach that, at least in *Ampharete santillani* Parapar et al., *2017*, has two anterior lobes pointing forward (Parapar et al. 2018). The intestine is simple, coiled in the thorax, and straight in the abdomen. Day (1964) gave a short but comprehensive review of the studies of the internal anatomy of 18 ampharetid genera. Like other Terebelliforma, ampharetids have a muscular ventral pharynx with a ciliated buccal cavity (Zhadan and Tzetlin 2002). In *Ampharete*, it is partly eversible (Rouse and Pleijel 2001). Aside from buccal tentacles, the pharynx may exceptionally bear jaws (genus *Gnathampharete*). The gut is supplied with a ventral ciliated gutter that is thought to accelerate the departure of particles that enter it, providing a means to increase the input rate of more nutritious particles without increasing gut volume (Jumars et al. 2015a). This is seen as a common trait in deposit feeders.

Blood vascular system. The blood vascular system is closed and has been described in detail by Wirén (1885), Meyer (1887), and Fauvel (1897). A dorsal blood vessel can often be observed through the body wall, especially in segments of the anterior thorax. In the anterior part of this vessel, the heart, a heart-body is present (Kennedy and Dales 1958). Due to its contents in porphyrin pigments, it is regarded to represent a hematopoietic organ. Parapar et al. (2018) reported a large sinus surrounding the stomach.

Nervous system and sensory organs. The most recent investigation of the nervous system has been carried out by Orrhage (2001), with special emphasis on the structure of the brain and innervation of the anterior appendages. Three species have been studied: *Amphicteis* cf. *gunneri*, *Anobothrus gracilis*, and *Melinna* cf. *cristata*, all of which exhibit a rather similar architecture of the central nervous system. As in other terebellifrom polychaetes, the brain is comparatively simple and consists of a ribbon-shaped band above the pharynx covered by the somata. The circumesophageal connectives are not distinctly set off from the brain and not split into dorsal and ventral roots as is typical of most polychaetes (Purschke 2016). The buccal tentacles and the foregut are innervated by a paired nerve emanating from the circumesophageal connectives. Thus, the innervation of these appendages and the alimentary canal have the same origin and are intensively connected to one another. This innervation pattern is untypical for palps and is the reason why they are regarded as nonhomologous with palps by Orrhage (2001).

The buccal segment is innervated from the circumesophageal connectives, whereas the following segments, starting with that bearing the paleae, are innervated from the ventral cord. All these segments are supplied with lateral organs. Other important sense organs are the nuchal organs that are directly innervated from the brain (Orrhage 2001). Eyes are not present in every species; if present, they are generally small, inconspicuous, and located posteriorly on the prostomium; only in *Ampharete oculicirrata*, a pair of additional eyes have been found basally on the pygidial cirri (Parapar et al. 2019). Ultrastructural studies on the nervous system and sense organs are lacking so far.

Reproduction and development

The sperm morphology of an ampharetid was first described by McHugh and Tunnicliffe (1994) for the vent species *Amphisamytha galapagensis*. Reproduction has been found to be continuous rather than seasonal, fertilization is external, and demersal larvae are nonfeeding. The reproduction of *Melinna cristata* was investigated by Nyholm (1951). Some two decades later, Hutchings (1973a, b) investigated the reproduction of a population of what she considered to be *M. cristata* from Northumberland, which was later revised by Mackie and Pleijel (1995), who reported the population to belong to *Melinna elisabethae* McIntosh, 1914. The reproductive period has been found to be restricted to a few days once per year.

Grehan et al. (1991) studied the larval development of *Melinna palmata*. The planktonic stage lasts for about 6 days, at the end of which a 3-chaetiger nectochaeta (Fig. 7.7.2.8A) settles on the seabed and builds a tube. As 5-chaetiger juveniles, the worms start actively feeding, protruding a first buccal tentacle. Branchiae develop gradually, the first pair occurring at the 7-chaetiger stage (Fig. 7.7.2.8B) and the fourth pair at the 24-chaetiger stage. Thoracic chaetigers are formed in two ways, the first four occurring initially with spatulate and capillary chaetae and the subsequent ones are added by the transformation of the anteriormost abdominal chaetigers, i.e., growth of notochaetae until 14 thoracic uncinigers are present at the 24-chaetiger stage. The characteristic fine capillary neurochaetae on segments 2 to 4 and the postbranchial hooks also arise at that time.

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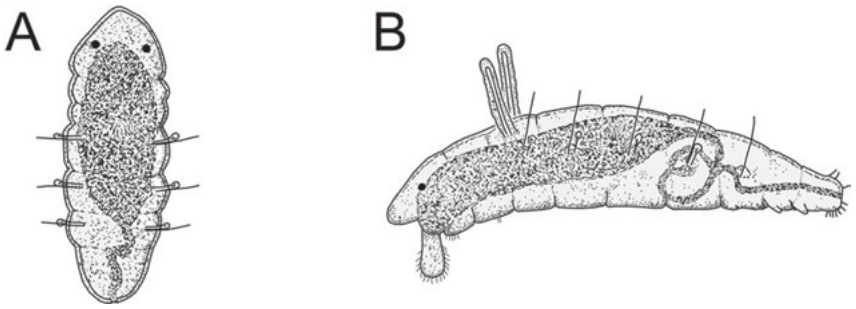


Fig. 7.7.2.8: Developmental stages of *Ampharete acutifrons*. A, 3-Chaetiger larva, dorsal view; B, 7-Chaetiger larva with the first pair of branchiae and the first buccal tentacle, lateral view. Modified and redrawn from Clavier (1984).

Okuda (1947) described the early development during the planktonic phase of *Schistocomus sovjeticus* Annenkova, 1937. Settlement occurred after about 5 days, but the author did not succeed in raising the benthic juveniles any further. Larval development within the maternal tube was observed by Zottoli (1974) for *Hobsonia florida* (Hartman, 1951) (as *Amphicteis floridus*). The 2-chaetiger stages leave the tube to settle on the bottom. Buccal tentacles are first visible on 6-chaetiger stages, whereas branchiae start to occur in 11-chaetiger stages. The eclectic species *Paedampharete acutiseries* appears to exhibit highly variable larval characters throughout its lifespan.

Biology and ecology

Burrowing and feeding. All Ampharetidae are tubicolous and infaunal species in sands and muds. The anterior part of the tube is usually parallel with the sediment surface and may be flushed with the sediment-water interface in certain species (Jumars et al. 2015b). In some species, the tubes are elevated as much as several diameters above this interface. The normal feeding posture holds the body axis parallel to the sediment-water interface, ventral side down in the horizontal, anterior portion of the tube. The tube is 2 to 10, but typically about 3, times as long as the worm, with the posterior portion curving downward into the sediment. Ampharetid species move by either tube extension or leaving the tube. The members of this family are regarded as discretely mobile by Jumars et al. (2015b).

Feeding has been described by Zottoli (1983). They feed by extending their buccal tentacles over the sediment and collecting detritus. Food particles are trapped in the ciliated grooves of the tentacles by mucus and transported into the mouth by ciliary beating aided by tentacle contraction into the buccal cavity. Thus, Ampharetidae may be classified as deposit feeders (according to Jumars et al. 2015a, they are individuals that ingest dilute food whose principal content by weight is mineral material). As the majority of surface deposit feeders that use tentacles, Ampharetidae ingest particles smaller than the median grain size and that are biased toward particles low in specific gravity (Jumars et al. 2015b). Particle selectivity has been examined in detail in *Hobsonia florida* (Jumars et al. 1982, Self and Jumars 1988). They show a preference of ingesting particles of lower specific gravity, but postingestion selectivity occurs as well by eliminating preferably denser particles.

Phylogeny and taxonomy

Phylogeny

Rouse and Fauchald (1997) placed Ampharetidae in Terebellida (Canalipalpata). Because of the different origin of the buccal tentacles, which have been regarded as palps (peristomial in ampharetids and prostomial in terebellids), Ampharetidae are closer to Alvinellidae than to Terebellidae (Rouse and Glasby 2000).

Holthe (1986a) tried to define evolutionary pathways for certain characters, such as the details in the neuropodial uncini, elevation of thoracic notopodia, and numbers of chaetigers in the thorax and abdomen. The definition of plesiomorphous versus apomorphous characters has, however, proven to be very difficult. Consequently, attempts to synonymize genera based on evolutionary events leading to, e.g., the occurrence of elevated notopodia in several genera, have remained controversial (see Jirkov 2001, 2011).

Rousset et al. (2007) used a set of genes to investigate relationships of annelid families, and Terebellida has been proven to be monophyletic if Pectinariidae were excluded. Molecular evidence has also been generated to shed light on the phylogeny of ampharetids, for example, for the genus *Amphisamytha* (see Stiller et al. 2013). The authors provided a molecular clock, indicating that the genus originated in shallow waters and expanded into chemosynthetic environments in the deep sea. Distributional patterns could in part be resolved. Eilertsen et al. (2017) found that adaptations to chemosynthesis-based ecosystems such as hydrothermal vents most likely occurred several times within Ampharetinae. Parapar et al. (2018) used COI sequences to elicit relationships among North Atlantic species of *Ampharete*. They found

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that the species discrimination based on molecular data matched the morphological definitions quite well. Nonetheless, several questions concerning the systematics of Ampharetidae still remain unanswered. The existence of numerous monotypic genera as well as the validity of the subfamilies has not been sufficiently investigated. In particular, Ampharetinae are defined merely on the absence of special morphological features joining Melinninae. In a recently published phylogenomic study using members of all families of Terebelliformia, Ampharetidae are rendered paraphyletic with Ampharetinae as sister to Alvinellidae and Melinninae as sister to Terebellidae. As a consequence, both subfamilies should be treated as separate families in the future (Stiller et al. 2020).

Taxonomy

The great number of easily countable characters still represents a problem for generic definitions. Day (1964) was the first to present a review of the family after a long temporal gap of nearly 50 years, the last publication on the issue was the one by Hessle (1917). Holthe (1986a) pointed out that generic definitions mainly based on meristic characters result in polyphyletic taxa. He was one of the first authors who attempted to establish a natural system of the family Ampharetidae. Reuscher et al. (2009) presented a table of all then-valid genera of both subfamilies together with diagnostic characters they considered informative for genus discrimination. Salazar-Vallejo and Hutchings (2012) provided a review of taxonomic characters used for the family Ampharetidae and commented on their usefulness. The diagnoses below are mainly based on the publications by Reuscher et al. (2009), Holthe (1986a), and Jirkov (2011). The character "number of thoracic chaetigers" includes segment 2 (i.e., "paleae" are counted with the segments bearing regular notochaetae).

The large family Ampharetidae is traditionally divided into two subfamilies: Melinninae characterized by needlelike neurochaetae in anterior segments and Ampharetinae lacking such neurochaetae. The subfamily Uschakovinae, established by Holthe (1986a) for the eclectic genus *Uschakovius* Laubier, 1973, has not been adopted by other taxonomists and is not listed in WoRMS. Despite attempts to reduce the number of monotypic genera, several are still present, and some of these are known only through the original description of the type species that has only been reported once.

Ampharetidae Malmgren, 1866

Diagnosis: Body comparatively short, comprising a limited number of segments, divided into thorax and abdomen. Tubiculous animals. Thorax with dorsal chaetae and with or without ventral chaetae in anterior segments and neuropodial uncini. Abdomen with reduced or lacking notopodia, always without chaetae, neuropodia with uncini. Pygidium with or without anal cirri or papillae. First segment without chaetae and uncini, second segment with capillary chaetae or paleae. Parapodia starting on the following segment. Uncini arranged in a single or double row. Prostomium distinct, triangular; eyes present or absent, nuchal organs present. Numerous buccal tentacles of different structure present retractable into buccal cavity. Two to four pairs of branchiae may be present on anterior segments starting on first chaetiger. Branchiae smooth, lamellate or papillose.

Melinninae Chamberlin, 1919

Diagnosis: Neurochaetae present before segment 6, in anteriormost parapodia needlelike; three or four pairs of branchiae, emerging close together, smooth or pinnate; often dorsal nuchal hooks and membrane across segment 6 present.

Genus *Isolda* Müller, 1858 (Fig. 7.7.2.3D, E)

Synonyms: *Irana* Wesenberg-Lund, 1949 (subjective synonym), *Oeorpata* Kinberg, 1867 (subjective synonym)
Type species: *Isolda pulchella* Müller in Grube, 1858
6 species.
Diagnosis: One pair of dorsal nuchal hooks and membrane across segment 6 present; two to four pairs of branchiae, two smooth and two pinnate; first three (exceptionally four) thoracic chaetigers with needlelike neurochaetae, first notochaetae on chaetiger 5, subsequent 12 or 13 chaetigers uncinigerous; abdomen with up to 90 segments; oral tentacles smooth.

Genus *Melinantipoda* Hartman, 1967

Type species: *Melinantipoda antarctica* Hartman, 1967
Monotypic.
Diagnosis: Dorsal nuchal hooks absent, dorsal membrane across segment 6 present, crenulated; four pairs of smooth branchiae; needlelike neurochaetae on first four thoracic chaetigers, small notochaetae on chaetigers 3 and 4; subsequent 12 or 13 thoracic chaetigers with regular notochaetae, 11 or 12 uncinigerous; abdomen with at least 15 segments; oral tentacles smooth, emerging from large membrane.

Genus *Melinna* Malmgren, 1866 (Fig. 7.7.2.5)

Type species: *Sabellides cristata* M. Sars, 1851
6 species.
Diagnosis: Dorsal nuchal hooks and dorsal membrane across segment 6 present, crenulated; first two to four thoracic chaetigers with rows of minute, fine, short capillary neurochaetae, first notochaetae on segment 5 or 6.

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Subsequent 13 to 14 thoracic chaetigers with larger fascicles of notochaetae and neuropodial uncini; four pairs of usually smooth branchiae; abdomen long, with 50 to 70 segments; oral tentacles smooth.

Genus *Melinnopsides* Day, 1964
Type species: *Melinnopsis capensis* Day, 1955
Monotypic.
Diagnosis: Dorsal nuchal hooks and dorsal membrane absent; three pairs of smooth branchiae; first three chaetigers with needlelike spines, first notochaetae on segment 5. Subsequent chaetigers with notochaetae, 10 uncinigerous; abdomen with 28 segments; oral tentacles not mentioned.

Genus *Melinnopsis* McIntosh, 1885
Synonyms: *Amelinna* Hartman, 1969, *Melinnexis* Annenkova, 1931, *Melinnides* Wesenberg-Lund, 1950
Type species: *Melinnopsis atlantica* McIntosh, 1885
18 species.
Diagnosis: Dorsal nuchal hooks absent, dorsal membrane present; four pairs of smooth branchiae; first three (exceptionally four) chaetigers with needlelike spines, first notochaetae on segment 5. Subsequent chaetigers with notochaetae, 10 to 14 uncinigerous; abdomen with 20 to 50 segments; oral tentacles of two kinds, smooth and papillated.

Genus *Moyanus* Chamberlin, 1919
Type species: *Moyanus explorans* Chamberlin, 1919
Monotypic.
Diagnosis: Prostomium probosciform (Reuscher et al. 2009); two pairs of dorsal nuchal hooks ("stout spines" fide Chamberlin) and dorsal membrane present; first three chaetigers with needlelike hooks; 15 thoracic chaetigers with notochaetae, 12 uncinigerous; abdomen with approximately 65 segments; buccal tentacles smooth, partly flattened, extending from a membrane.

Ampharetinae Malmgren, 1866
Diagnosis: All neurochaetae formed as uncini, present from segment 6. Two to four pairs of branchiae, smooth, annulated or pinnate, cirriform to foliose.

Genus *Abderos* Schüller & Jirkov, 2013
Type species: *Abderos minotaurus* Schüller & Jirkov, 2013
Monotypic.
Diagnosis: Prostomium without glandular ridges; two pairs of branchiae; first segment with pair of lateral papillae, giving specimens a somewhat horned appearance; 14 thoracic chaetigers, 12 uncinigerous; last 3 thoracic chaetigers with somewhat elevated notopodia; paleae absent; two intermediate uncinigers; buccal tentacles pinnate.

Genus *Adercodon* Mackie, 1994
Synonyms: Jirkov (2011) considered *Adercodon* as a synonym of *Gnathampharete* Desbruyères, 1978. This view is not shared by other authors, and the synonymy is not listed in WoRMS Editorial Board (2018). The genus is therefore considered valid.
Type species: *Adercodon pleijeli* Mackie, 1994
Monotypic.
Diagnosis: Three pairs of smooth branchiae; 13 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 absent; abdominal notopodial rudiments present; buccal tentacles papillose; ventral row of buccal teeth.

Genus *Alkmaria* Horst, 1919
Synonyms: *Microsamytha* Augener, 1928 (subjective synonym)
Jirkov (2011) proposed *Alkmaria* to be a junior synonym of *Hypania* Ostoumow, 1897. This synonymy was not accepted by other authors and is not listed in WoRMS Editorial Board (2018). The genus is therefore considered valid.
Type species: *Alkmaria romijni* Horst, 1919
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae; 16 thoracic chaetigers, 13 uncinigerous; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Amage* Malmgren, 1866
Synonyms: *Egamella* Fauchald, 1972 (subjective synonym), *Mexamage* Fauchald, 1972 (subjective synonym), *Paramage* Caullery, 1944 (subjective synonym)
Type species: *Amage auricula* Malmgren, 1866
24 species.
Diagnosis: Prostomium with or without glandular ridges; two or four pairs of branchiae; 12 to 17 thoracic chaetigers, 9 to 14 uncinigerous; no intermediate uncinigers; notochaetae on segment 2 absent; abdominal notopodial rudiments present; buccal tentacles smooth.
24 valid species.

Genus *Amagopsis* Pergament & Khlebovich, 1964
Synonyms: Jirkov (2001) synonymized *Amagopsis* with *Grubianella* McIntosh, 1885. This view is followed by WoRMS Editorial Board (2018) but not by Reuscher et al. (2009). For the time being, the genus therefore is considered valid.
Type species: *Amagopsis klugei* Pergament & Khlebovich, 1964
2 species.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae; 15 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 present; abdominal notopodial rudiments present; buccal tentacles smooth.

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Genus *Ampharana* Hartman, 1967
Type species: *Ampharana antarctica* Hartman, 1967
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of branchiae; 14 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 absent; buccal tentacles few, emerging from folded membrane.

Genus *Ampharete* Malmgren, 1866 (Figs. 7.7.2.7A–D, 7.7.2.8A, B)
Synonyms: *Asabellides* Annenkova, 1929 (subjective synonym), *Branchiosabella* Claparède, 1863 (subjective synonym), *Heterobranchus* Wagner, 1885 (subjective synonym), *Parampharete* Hartman, 1978 (subjective synonym), *Pseudosabellides* Berkeley & Berkeley, 1943 (subjective synonym), *Pterampharete* Augener, 1918, *Sabellides* Milne Edwards in Lamarck, 1838 (subjective synonym)
Type species: *Amphicteis acutifrons* Grube, 1860
48 species, including 1 homonym.
Diagnosis: Prostomium without glandular ridges; four, or exceptionally three, pairs of cirriform, or exceptionally pinnate, branchiae; 15 thoracic chaetigers, 11 or 12 uncinigerous; two intermediate uncinigers; notochaetae in fused segments 2 + 3 absent or present in varying size from enlarged (paleae) to regular notochaetae size; buccal tentacles pinnate.

Genus *Amphicteis* Grube, 1850 (Figs. 7.7.2.1, 7.7.2.2, 7.7.2.3A, C, F–H)
Synonyms: *Crossostoma* Gosse, 1855 (subjective synonym)
Type species: *Amphitrite gunneri* M. Sars, 1835
33 species.
Diagnosis: Prostomium with glandular ridges; four pairs of branchiae; 18 thoracic chaetigers, 14 uncinigerous; no intermediate uncinigers; notochaetae on segment 2 present; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Amphisamytha* Hessle, 1917
Synonyms: *Amathys* Desbruyères & Laubier, 1996 (subjective synonym)
Type species: *Amphisamytha japonica* Hessle, 1917
12 species.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae; notochaetae on segment 2 absent; 17 thoracic chaetigers, 14 uncinigerous; no intermediate uncinigers; abdominal notopodial rudiments present (sometimes referred to as papillae or glandular pads); buccal tentacles smooth.
Remarks: A 13th species has been incompletely described by Zhou et al. (2019) due to the collection of only incomplete specimens as *Amphisamytha* sp. *longqi*. Molecular data indicate that it is a separate species. Moreover, phylogenetic analyses of four genes did not recover monophyletic *Amphisamytha*, prompting to the necessity of a revision of the group (Zhou et al. 2019).

Genus *Amythas* Benham, 1921
Type species: *Amythas membranifera* Benham, 1921
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of branchiae; notochaetae on segment 2 absent; 17 thoracic chaetigers, 14 uncinigerous; buccal tentacles rudimentary, broad tentacular membrane present.

Genus *Amythasides* Eliason, 1955
Synonyms: *Amythasides* was proposed as a possible synonym of *Ampharete* Malmgren, 1866. This possible synonymy is not listed in WoRMS Editorial Board (2018) or by any other authors, and genus *Amythasides* is considered valid.
Type species: *Amythasides macroglossus* Eliason, 1955
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of branchiae, groups connected by high membrane; 15 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 present, few and thin; buccal tentacles few, smooth, very thick.

Genus *Andamanella* Holthe, 2002
Type species: *Andamanella bellis* Holthe, 2002
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of branchiae; 15 thoracic chaetigers, none uncinigerous; abdomen without uncini; one single large smooth buccal tentacle.

Genus *Anobothrus* Levinsen, 1884
Synonyms: *Anobothrella* Hartman, 1967 (subjective synonym), *Melythasides* Desbruyères, 1978 (subjective synonym), *Sosanides* Hartmann-Schröder, 1965 (subjective synonym)
Type species: *Ampharete gracilis* Malmgren, 1866
21 species, including 1 *nomen nudum*.
Diagnosis: Prostomium without glandular ridges; three or four pairs of branchiae; 14 to 16 thoracic chaetigers, 11 or 12 uncinigerous; two intermediate uncinigers; one pair of notopodia in posterior thorax slightly elevated, connected by a low, usually ciliated glandular band; modified chaetae in elevated notopodia, more or less distinctly differing from regular notochaetae; circular ciliary band in anterior thorax; notochaetae on segment

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2 present (except for *Anobothrus apaleatus* Reuscher, Fiege & Wehe, 2009 and *Anobothrus fimbriatus* Imajima, Reuscher & Fiege, 2013); buccal tentacles smooth or papillose.

Genus *Auchenoplax* Ehlers, 1887 (Fig. 7.7.2.3I)
Type species: *Auchenoplax crinita* Ehlers, 1887
5 species.
Diagnosis: Prostomium without glandular ridges; two pairs of branchiae; 14 thoracic chaetigers, 12 uncinigerous; first or first two tori on thorax prolonged; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Decemunciger* Zottoli, 1982
Type species: *Decemunciger apalea* Zottoli, 1982
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 13 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Ecamphicteis* Fauchald, 1972
Type species: *Ecamphicteis elongata* Fauchald, 1972
Monotypic.
Diagnosis: Prostomium without glandular ridges; two pairs of branchiae; crenulated lower lip; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present; buccal tentacles smooth.

Genus *Eclysippe* Eliason, 1955
Type species: *Lysippe vanelli* Fauvel, 1936
4 species.
Diagnosis: Prostomium without glandular ridges; three or four pairs of branchiae; 16 thoracic chaetigers, posterior ones distinctly elongate, 12 uncinigerous; two intermediate uncinigers; notochaetae on segment 2 present; buccal tentacles smooth.

Genus *Emaga* Hartman, 1978
Type species: *Emaga laevis* Hartman, 1978
Monotypic.
Diagnosis: Prostomium without glandular ridges; branchiae absent; 15 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 present; buccal tentacles few, smooth.

Genus *Endecamera* Zottoli, 1982
Type species: *Endecamera palea* Zottoli, 1982
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 15 thoracic chaetigers, 11 uncinigerous: notochaetae on segment 2 present; buccal tentacles grooved, smooth.

Genus *Eusamythella* Hartman, 1971
Synonyms: *Eusamytha* McIntosh, 1885, *Eusamytha* Hartman, 1971 (junior homonym)
Jirkov (2011) considered *Eusamythella* as a junior synonym of *Melinnampharete* Annenkova, 1937), apparently not putting much weight on the presence or absence of intermediate uncinigers (*Eusamythella* none, *Melinnampharete* two). The synonymy is not listed in WoRMS Editorial Board (2018) and has not been accepted by other authors. *Eusamythella* is therefore considered valid.
Type species: *Eusamytha sexdentata* Hartman, 1967
2 species.
Diagnosis: Prostomium without glandular ridges; three pairs of branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Glyphanostomum* Levinsen, 1884
Type species: *Samytha pallescens* Théel, 1879
6 species.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 14 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Gnathampharete* Desbruyères, 1978
Type species: *Gnathampharete paradoxa* Desbruyères, 1978
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of pinnate branchiae; 15 thoracic chaetigers, 12 uncinigerous; two intermediate uncinigers; notochaetae on segment 2 present; buccal tentacles absent, buccal membrane and two rows of jaw elements present.

Genus *Grassleia* Solis-Weiss, 1993
Type species: *Grassleia hydrothermalis* Solis-Weiss, 1993
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 15 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 present, small; buccal tentacles smooth; abdomen short, with seven uncinigers.

Genus *Grubianella* McIntosh, 1885
Synonyms: Jirkov (2001) considered *Amagopsis* a junior synonym of *Grubianella* apparently based on the morphology of the prostomium. This view is not shared by other authors.

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Type species: *Grubianella antarctica* McIntosh, 1885
2 species.
Diagnosis: Prostomium with glandular ridges; four pairs of smooth branchiae; 14 thoracic chaetigers, 11 uncinigerous; one intermediate unciniger; notochaetae on segment 2 absent; buccal tentacles smooth.

Genus *Hobsonia* Banse, 1979

Type species: *Amphicteis floridus* Hartman, 1951
Monotypic.
Diagnosis: Prostomium with glandular ridges; four pairs of smooth branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present, thin; buccal tentacles smooth. In fresh and brackish water.

Genus *Hypania* Ostroumov, 1897

Synonyms: *Parhypania* Annenkova, 1928 (subjective synonym)
Jirkov (2011) considered all other freshwater and brackish water genera to be junior synonyms of *Hypania* apparently based on the presence of two types of uncini in abdominal neuropodia. This view was not accepted by WoRMS Editorial Board (2018) — with the exception of *Parhypania* — and is not followed here.
Type species: *Amphicteis invalida* Grube, 1860
3 species.
Diagnosis: Prostomium with glandular ridges; four pairs of smooth branchiae; 16 thoracic chaetigers, 13 uncinigerous; notochaetae on segment 2 present, long and thin; abdominal notopodial rudiments present; buccal tentacles smooth. In freshwater and brackish water.

Genus *Hypaniola* Annenkova, 1927

Synonyms: Jirkov (2011) listed *Hypaniola* as junior synonym of *Hypania* Ostroumov, 1897. This synonymy was not accepted by other authors and is not listed in WoRMS Editorial Board (2018). The genus is therefore considered valid.
Type species: *Amphicteis kowalewskii* Grimm in Annenkova, 1927
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present, short and thin; abdominal notopodial rudiments present; buccal tentacles smooth. In freshwater and brackish water.

Genus *Jugamphicteis* Fauchald & Hancock, 1981

Type species: *Jugamphicteis paleata* Fauchald & Hancock, 1981
3 species.
Diagnosis: Prostomium with crescentic to folded glandular ridges; four pairs of smooth branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present, well developed; notopodia of first abdominal segment dorsally fused, forming valve-like structure; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Lysippe* Malmgren, 1866

Synonyms: *Lysippides* Hessle, 1917 (subjective synonym), *Paralysippe* Williams, 1987 (subjective synonym), *Pterolysippe* Augener, 1918 (subjective synonym)
Jirkov (2011) proposed two additional genera, *Pseudampharete* Hilbig, 2000 and *Samytha* Malmgren, 1866 as junior synonyms of *Lysippe*. This view has not been followed by other authors, and the synonymies are not listed in WoRMS Editorial Board (2018).
Type species: *Lysippe labiata* Malmgren, 1866
7 species.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 17 to 18 thoracic chaetigers, 13 to 14 uncinigerous; two intermediate uncinigers; notochaetae on segment 2 present, very short and thin; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Melinnampharete* Annenkova, 1937

Type species: *Melinnampharete eoa* Annenkova, 1937
3 species.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 15 thoracic chaetigers, 12 uncinigerous; two intermediate uncinigers; notochaetae on segment 2 present, well developed; anteriormost few notopodia shifted dorsally, smooth dorsal ridge across first thoracic unciniger (chaetiger 4); buccal tentacles pinnate or papillose.

Genus *Melinnata* Hartman, 1965

Type species: *Melinnata americana* Hartman, 1965
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 13 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 present, well developed; dorsal ridge between chaetigers 3 and 4; buccal tentacles smooth.

Genus *Melinnoides* Benham, 1927

Type species: *Melinnoides nelsoni* Benham, 1927
Monotypic.
Diagnosis: Prostomium without glandular ridges; two pairs of smooth branchiae; 14 thoracic chaetigers,

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12 uncinigerous; notochaetae on segment 2 present, very small; buccal tentacles grooved, smooth.

Genus *Neopaiwa* Hartman & Fauchald, 1971
Synonymies: According to Jirkov (2011), *Neopaiwa* could be a junior synonym of *Samythopsis* McIntosh, 1885 (see remarks there). The synonymy is not accepted here.
Type species: *Neopaiwa cirrata* Hartman & Fauchald, 1971
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 not mentioned but very likely to be present, short; abdominal notopodial rudiments present; abdominal neuropodia with long cirri; buccal tentacles smooth.

Genus *Neosabellides* Hessle, 1917
Type species: *Sabellides elongatus* Ehlers, 1913
4 species.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 14 thoracic chaetigers, 12 uncinigerous; two intermediate uncinigers; notochaetae on segment 2 not mentioned; buccal tentacles pinnate.

Genus *Neosamytha* Hartman, 1967
Type species: *Neosamytha gracilis* Hartman, 1967
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 present, well developed; dorsal ridge across segment 4 (not illustrated); buccal tentacles smooth.

Genus *Noanelia* Desbruyères & Laubier, 1977
Type species: *Noanelia hartmanae* Desbruyères & Laubier, 1977
2 species.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae, two pairs much thinner and shorter than the others; 16 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 not mentioned; buccal tentacles smooth, originating from roof of buccal cavity, not retracted in preserved animals.

Genus *Orochi* Reuscher, Fiege & Imajima, 2015
Type species: *Orochi palacephalus* Reuscher, Fiege & Imajima, 2015
Monotypic.
Diagnosis: Prostomium without(?) glandular ridges; four pairs of flattened, slender branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 absent; 1 intermediate unciniger; buccal tentacles smooth.

Genus *Pabits* Chamberlin, 1919
Type species: *Pabits deroderus* Chamberlin, 1919
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 absent; abdominal notopodial rudiments present; buccal tentacles emerging from prolonged membrane, smooth.

Genus *Paedampharete* Russell, 1987
Type species: *Paedampharete acutiseries* Russell, 1987
Monotypic.
Diagnosis: Progenetic; two or three pairs of smooth or slightly papillated branchiae; 5 to 15 thoracic chaetigers, 2 to 12 uncinigerous; paleae present or absent; larval spatulate chaetae present or absent; buccal tentacles smooth, relatively large.

Genus *Paiwa* Chamberlin, 1919
Synonymies: According to Jirkov (2011), *Paiwa* could be a junior synonym of *Samythopsis* McIntosh, 1885 (see remarks there).
Type species: *Paiwa abyssi* Chamberlin, 1919
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of smooth branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 not mentioned but likely to be present; abdominal neuropodia with long cirri; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Parampharete* Hartman, 1978
Synonymies: According to Imajima et al. 2012, *Parampharete* is a synonym of *Ampharete*. This view is not followed by WoRMS Editorial Board (2018) and therefore not accepted here.
Type species: *Parampharete weddellia* Hartman, 1978
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 present; abdominal neuropodia with long cirri; buccal tentacles papillated.

Genus *Paramphicteis* Caullery, 1944
Synonyms: *Pseudoamphicteis* Hutchings, 1977 (subjective synonym). Jirkov (2011) synonymized *Paramphicteis* and *Pseudamphicteis*, together with *Phyllamphicteis*, with

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Amphicteis Grube, 1850 based mainly on the prostomial shape. Other authors and WoRMS Editorial Board (2018) do not follow that opinion. *Paramphicteis* is therefore considered valid.
Type species: *Sabellides angustifolia* Grube, 1878
4 species.
Diagnosis: Prostomium with glandular ridges; two to four pairs of branchiae, at least one pair foliose; 17 to 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present or absent; abdominal notopodial rudiments present or absent; buccal tentacles papillose.

Genus *Paramytha* Kongsrud, Eilertsen, Alvestad, Kongshavn & Rapp, 2017

Type species: *Paramytha schanderi* Kongsrud, Eilertsen, Alvestad, Kongshavn & Rapp, 2017
2 species.
Diagnosis: Prostomium glandular ridges; four pairs of cirriform branchiae; 15 to 20 thoracic chaetigers, 12 to 17 uncinigerous; notochaetae on segment 2 absent; abdominal notopodial rudiments absent; buccal tentacles smooth.

Genus *Pavelius* Kuznetsov & Levenstein, 1988

Synonyms: Jirkov (2011) considered *Pavelius* to be a junior synonym of *Phyllocomus* Grube, 1877 based on prostomial morphology but also morphologically similar uncini in thoracic and abdominal neuropodia. The latter character has not been mentioned in other publications, and *Pavelius* is thus considered valid for the time being. However, further discussion on this character is warranted. The synonymy was also rejected by Reuscher and Fiege (2016).
Type species: *Pavelius uschakovi* Kuznetsov & Levenstein, 1988
3 species.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae; 16 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 present; buccal tentacles smooth.

Genus *Phyllampharete* Hartman & Fauchald, 1971

Synonyms: *Phyllampharete* was proposed as a synonym of *Amage* Malmgren, 1866 by Jirkov (2011). This synonymy was not accepted by other authors and is not accepted by WoRMS Editorial Board (2018), and *Phyllampharete* is therefore considered valid.
Type species: *Phyllampharete longicirra* Hartman & Fauchald, 1971
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of foliose branchiae; 14 thoracic chaetigers, 11 uncinigerous; notochaetae on segment 2 absent; abdominal neuropodia with long cirri; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Phyllamphicteis* Augener, 1918

Synonyms: Jirkov (2011) stated *Phyllamphicteis* to be a synonym of *Amphicteis*. This view is not followed by other authors and is not listed in WoRMS. The genus is therefore considered valid.
Type species: *Phyllamphicteis collaribranchis* Augener, 1918
2 species.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae, two pairs lamellate; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present, well developed; buccal tentacles smooth.

Genus *Phyllocomus* Grube, 1877

Synonyms: *Schistocomus* Chamberlin, 1919 (subjective synonym)
Suggested synonymy by Jirkov (2011); see *Pavelius*.
Type species: *Phyllocomus crocea* Grube, 1877
6 species.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae, at least two foliose; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 absent; abdominal notopodial rudiments present; buccal tentacles smooth; abdomen unusually long, with approximately 30 to 50 uncinigers.

Genus *Pseudampharete* Hilbig, 2000

Synonymies: Jirkov (2011) considered *Pseudampharete* to be a junior synonym of *Lysippe*. Reuscher et al. (2015b) agreed with Jirkov; however, according to WoRMS Editorial Board (2018), *Pseudampharete* is valid.
Type species: *Lysippe mexicana* Fauchald, 1972
Monotypic.
Diagnosis: Prostomium without glandular ridges; four pairs of branchiae, two pairs smooth, two pairs ridged; 16 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 present; buccal tentacles smooth.

Genus *Samytha* Malmgren, 1866

Type species: *Sabellides sexcirrata* Sars, 1856
9 species.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 17 thoracic chaetigers, 14 uncinigerous; Notochaetae on segment 2 absent; abdominal notopodial rudiments present; buccal tentacles smooth.

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Genus *Samythella* Verrill, 1873
Synonyms: *Eusamytha* McIntosh, 1885 (subjective synonym)
Type species: *Samythella elongata* Verrill, 1873
7 species.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 15 thoracic chaetigers, 12 uncinigerous; notochaetae on segment 2 absent; buccal tentacles very long and slender, smooth.

Genus *Samythopsis* McIntosh, 1855
Synonyms: Jirkov (2011) synonymized all deep-sea genera with long abdominal dorsal cirri (i.e., *Neopaiwa* Hartman & Fauchald, 1971, *Paiwa* Chamberlin, 1919, and *Weddellia* Hartman, 1967) with *Samythopsis*. Although he did not list this character among presumed apomorphies, one could very well argue for a single evolutionary event resulting in this distinct feature. As the synonymies are not followed by WoRMS Editorial Board (2018), the genera are for the time being considered valid.
Type species: *Samythopsis grubei* McIntosh, 1885
Monotypic.
Diagnosis: Prostomium with glandular ridges; three pairs of smooth branchiae; 17 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 not mentioned; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Sosane* Malmgren, 1866 (Fig. 7.7.2.4)
Synonyms: *Mugga* Eliason, 1955 (subjective synonym), *Muggoides* Hartman, 1965 (subjective synonym), *Sosanella* Hartman, 1965 (subjective synonym), *Sosanopsis* Hessle, 1917 (subjective synonym), (?)*Melinnata* Hartman, 1965 (doubtful)
Type species: *Sosane sulcata* Malmgren, 1866
16 species.
Diagnosis: Prostomium without glandular ridges; three to four pairs of cirriform branchiae; 13 to 16 thoracic chaetigers, 9 to 13 uncinigerous; notochaetae on segment 2 present, very small, or absent; last, second-, third-, or fourth-to-last thoracic unciniger with elevated, enlarged notopodia, sometimes connected by middorsal ridge; notochaetae of modified notopodia with hirsute tips; one or two intermediate uncinigers; buccal tentacles usually smooth.

Genus *Tanseimaruana* Imajima, Reuscher & Fiege, 2013
Type species: *Amphicteis vestis* Hartman, 1965
2 species.
Diagnosis: Prostomium without glandular ridges; four pairs of cirriform branchiae; 18 thoracic chaetigers, 14 uncinigerous; notochaetae on segment 2 present; first abdominal unciniger with 4 dorsal foliose lobes with smooth margin, emerging from transverse dermal fold; intermediate uncinigers absent; buccal tentacles smooth.

Genus *Watatsumi* Reuscher, Fiege & Imajima, 2015
Type species: *Watatsumi grubei* Reuscher, Fiege & Imajima, 2015
Monotypic.
Diagnosis: Prostomium without incisions or glandular ridges but with transverse nuchal ridges; four pairs of branchiae; 18 thoracic chaetigers, 14 uncinigerous; intermediate uncinigers absent; notochaetae on segment 2 present; buccal tentacles mostly pinnate.

Genus *Weddellia* Hartman, 1967
Synonymies: According to Jirkov (2011), *Weddellia* could be a junior synonym of *Samythopsis* McIntosh, 1885 (see remarks there).
Type species: *Weddellia profunda* Hartman, 1967
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 18 thoracic chaetigers, 15 uncinigerous; notochaetae on segment 2 absent; abdominal parapodia with long dorsal cirri; abdominal notopodial rudiments present; buccal tentacles smooth.

Genus *Ymerana* Holthe, 1986
Type species: *Ymerana pteropoda* Holthe, 1986
Monotypic.
Diagnosis: Prostomium without glandular ridges; three pairs of smooth branchiae; 13 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 absent; last notopodium achaetous, transformed into flattened fan; buccal tentacles smooth (Holthe 1986b).

Genus *Zatsepinia* Jirkov, 1986
Type species: *Zatsepinia rittichae* Jirkov, 1986
3 species.
Diagnosis: Prostomium without glandular ridges; two or three pairs of cirriform branchiae; 12 thoracic chaetigers, 10 uncinigerous; notochaetae on segment 2 absent; second-to-last thoracic unciniger with elevated notopodia, connected by middorsal ridge; four intermediate uncinigers; buccal tentacles smooth.

Genera of doubtful affiliation

Genus *Aryandes* Kinberg, 1866
Type species: *Aryandes gracilis* Kinberg, 1866
Hartman (1948) examined the specimens of the two species that Kinberg assigned to this genus. According

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to her, the type species *Aryandes gracilis* is indeterminable, as of the specimens deposited in the Swedish State Museum only a small fragment still existed. The second species *Aryandes forficata* was referred to *Amphicteis* by Hessle (1917). The genus is therefore doubtful.

Genus *Rytocephalus* Quatrefages, 1866
Type species: *Rytocephalus ebranchiatus* Quatrefages, 1866
Monotypic; species doubtful.

Genus *Uschakovius* Laubier, 1973
Type species: *Uschakovius enigmaticus* Laubier & Ramos, 1973
Incertae sedis fide Reuscher et al. 2009
Monotypic.

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References

Annenkova, N. (1927): Über die pontokaspischen Polychaeten I. Die Gattungen *Hypania* Ostroumov und *Hypaniola* n.gen. *Annuaire du Musée Zoologique de l'Académie des Sciences de l'URSS*: 48–63.

Annenkova, N. (1930): Zur Polychaetenfauna von Franz-Joseph-Land. *Zoologischer Anzeiger* 95: 269–272.

Annenkova, N.P. (1937): Polychaete fauna of the northern part of the Japan Sea [in Russian, with English translation of new species text only]. *Issledovaniya fauny morei, Zoologicheskii Institut Akademii Nauk USSR Explorations des Mers de l'URSS* 23: 139–216.

Augener, H. (1918): Polychaeta. *Beitrage zur Kenntnis der Meeresfauna Westafrikas* 2: 67–625.

Banse, K. (1979): Ampharetidae (Polychaeta) from British Columbia and Washington. *Canadian Journal of Zoology* 57: 1543–1552.

Benham, W.B. (1927): Polychaeta. *British Antarctic 'Terra Nova' Expedition Natural History Reports, Zoology* 7: 47–182.

Caullery, M. (1944): Polychètes Sédentaires de l'Expédition du Siboga: Ariciidae, Spionidae, Chaetopteridae, Chlorhaemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. *Siboga-Expeditie Uitkomsten op Zoologisch, Bonatisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900* XXIV 2 bis: 1–204.

Chamberlin, R.V. (1919): The Annelida Polychaeta [Albatross Expeditions]. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48: 1–514.

Clavier, J. (1984): Description du cycle biologique d'*Ampharete acutifrons* (Grube, 1860) (Annélide, Polychète). *Comptes Rendus Hebdomadaire des Séances de l'Académie des Sciences III. Sciences de la Vie* 299: 59–62.

Day, J.H. (1964): A review of the family Ampharetidae (Polychaeta). *Annals of the South African Museum* 48: 97–120.

Desbruyères, D. (1978): Un Ampharetidae (Annélides Polychètes sédentaires) à structure buccale aberrante: *Gnathampharete paradoxa* gen. sp.n. *Comptes rendus hebdomaidaire des séances de l'Académie des sciences, Ser. D Sciences Naturelles* 286: 281–284.

Desbruyères, D. & Laubier, L. (1977): *Noanelia hartmanae* gen. sp. n., Ampharetidae (Annélides Polychètes Sédentaires) abyssal du Golfe de Gascogne. In: Reish, D.J. & Fauchald, K. (eds.), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman. The Allan Hancock Foundation*. University of Southern California, Los Angeles: 279–287.

Ehlers, E. (1887): Reports on the results of dredging, under the direction of L. F. Pourtalès, during the years 1868-1870, and of Alexander Agassiz, in the Gulf of Mexico (1877-78), and in the Caribbean Sea (1878-79), in the U.S. Coast Survey steamer "Blake", Lieut-Com. C. D. Sigsbee, U.S.N. and Commander J. R. Bartlett, U.S.N., commanding. XXXI. Report on the Annelids. *Memoirs of the Museum of Comparative Zoology at Harvard College* 15: vi and 335 pp.

Eilertsen, M.H., Kongsrud, J.A., Alvestad, T., Stiller, J., Rouse, G.W. & Rapp, H.T. (2017): Do ampharetids take sedimented steps between vents and seeps? Phylogeny and habitat-use of Ampharetidae (Annelida, Terebelliformia) in chemosynthesis-based ecosystems. *BMC Evolutionary Biology* 17:222: 1–15.

Eliason, A. (1955): Neue oder wenig bekannte Schwedische Ampharetiden (Polychaeta). *Göteborgs Kungliga vetenskaps- och vitterhets-samhälles handlingar. Sjätte Följden.* Series B 6: 1–17.

Fauvel, P. (1897): Recherches sur les ampharétiens, annélides polychètes sédentaires, morphologie, anatomie, histologie, physiologie. *Bulletin scientifique de la France et de la Belgique* 30: 277–488.

Fauchald, K. (1972): Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology* 7: 1–575.

Fauchald, K. & Hancock, D.R. (1981): Deep-water polychaetes from a transect off central Oregon. *Allan Hancock Foundation Monographs* 11: 1–73.

Grube, A.E. (1877): Anneliden - Ausbeute S.M.S. Gazelle. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1877: 509–554.

Grehan, A., Retière, C. & Keegan, B. (1991): Larval development in the ampharetid *Melinna palmata* Grube (Polychaeta). *Ophelia Supplement* 5: 321–332.

Hartman, O. (1948): The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Arkiv för Zoologi* 42A: 1–137, 18 plates.

Hartman, O. (1965): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation* 28: 1–378.

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Hartman, O. (1967): Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. *Allan Hancock Monographs in Marine Biology* 2: 1–387.

Hartman, O. (1971): Abyssal polychaetous annelids from the Mozambique Basin off southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. *Journal of the Fisheries Research Board of Canada* 28: 1407–1428.

Hartman, O. (1978): Polychaeta from the Weddell Sea quadrant, Antarctica. *Antarctic Research Series* 26: 125–223.

Hartman, O. & Fauchald, K. (1971): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. *Allan Hancock Monographs in Marine Biology* 6: 1–327.

Hessle, C. (1917): Zur Kenntnis der terebellomorphen Polychaeten. *Zoologiska Bidrag fran Uppsala* 5: 39–258.

Hilbig, B. (2000): Family Ampharetidae Malmgren, 1867. In: Blake, J. A., Hilbig, B. & Scott, P.V. *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. 7 — The Annelida Part 4. Polychaeta: Fabelligeridae to Sternaspidae.* Santa Barbara Museum of Natural History, Santa Barbara: 169–230.

Holthe, T. (1986a): Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. *Gunneria* 55: 1–236.

Holthe, T. (1986b): Polychaeta Terebellomorpha from the northern Norwegian Sea and the Polar Sea, with descriptions of *Mugga bathyalis* sp.n. and *Ymerana pteropoda* gen. and sp.n. *Sarsia* 71: 227–234.

Holthe, T. (2002): One new genus and three new species of the Ampharetidae (Polychaeta: Terebellida) from the Bioshelf project. *Phuket Marine Biological Center Special Publication* 24: 345–352.

Horst, R. (1919): Twee sedentaire Polychaeten uit he brakke water var Nederland. *Zoologische Mededeelingen* (*Leiden*) 5: 100–102.

Hutchings, P. (1973a): Gametogenesis in a Northumberland population of the polychaete *Melinna cristata*. *Marine Biology* 18: 199–211.

Hutchings, P. (1973b): Age structure and spawning of a Northumberland population of *Melinna cristata* (Polychaeta: Ampharetidae). *Marine Biology* 18: 218–227.

Hutchings, P.A. (2000): Family Ampharetidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing: Melbourne: 204–208.

Imajima, M., Reuscher, M.G. & Fiege, D. (2012): Ampharetidae (Annelida: Polychaeta) from Japan. Part I: The genus *Ampharete* Malmgren, 1866, along with a discussion of several taxonomic characters of the family and the introduction of a new identification tool. *Zootaxa* 3490: 75–88.

Imajima, M., Reuscher, M.G. & Fiege, D. (2013): Ampharetidae (Annelida: Polychaeta) from Japan. Part II: Genera with elevated and modified notopodia. *Zootaxa* 3647: 137–166.

Jirkov, I.A. (2001): Polychaeta of the Arctic Ocean. Moskva: Yanus-K. 632 pp. [in Russian]

Jirkov, I.A. (2009): Revision of Ampharetidae (Polychaeta) with modified thoracic parapodia. *Invertebrate Zoology* 5: 111–132.

Jirkov, I.A. (2011): Discussion of taxonomic characters and classification of Ampharetidae (Polychaeta). *Italian Journal of Zoology* 78: 78–94.

Jumars, P.A., Self, R.F.L. & Nowell, A.R.M. (1982): Mechanics of particle selection by tentaculate deposit feeders. *Journal of Experimental Marine Biology and Ecology* 64: 47–70.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.L. (2015a): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.L. (2015b): Diet of worms emended: An update of polychaete feeding guilds. Appendix A Family-by-Family Updates. *Supplemental Material: Annual Review of Marine Science* 7: 497–520.

Kennedy, G.Y. & Dales, R.P. (1958): The function of the heart-body in polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 37: 15–31.

Kongsrud, J.A., Eilertsen, M.H., Alvestad, T., Kongshavn, K. & Rapp, H.T. (2017): New species of Ampharetidae (Annelida: Polychaeta) from the Arctic Loki Castle vent field. *Deep-Sea Research II* 137: 232–245.

Kuznetsov, A.P. & Levenstein, R.Y. (1988): *Pavelius uschakovi* gen. et sp. n. (Polychaeta, Ampharetidae) from Paramushir Gas Hydrate Spring in the Okhotsk Sea. *Zoologicheskii Zhurnal* 67: 819–825. [in Russian]

Levinsen, G.M.R. (1884): Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Köbenhavn* 1883: 92–350.

Mackie, A.S.Y. (1994): *Adercodon pleijeli* gen. et sp. nov. (Polychaeta, Ampharetidae) from the Mediterranean Sea. *Mémoires du Muséum national D'histoire naturelle* 162: 243–250.

Mackie, A.S.Y. & Pleijel, F. (1995): A review of *Melinna cristata*-species group (Polychaeta: Ampharetidae) in the northeastern Atlantic. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92: 103–124.

Malmgren, A.J. (1865): Nordiska Hafs-Annulata. *Öfversigt af Königlich Vetenskaps-akademiens förhandlingar, Stockholm* 22: 51–110.

Malmgren, A.J. (1866): Nordiska Hafs-Annulater. *Öfversigt af Königlich Vetenskaps-akademiens förhandlingar, Stockholm* 22: 355–410.

McHugh, D. & Tunnicliffe, V. (1994): Ecology and reproductive biology of the hydrothermal vent polychaete *Amphisamytha galapagensis* (Ampharetidae). *Marine Ecology Progress Series* 106: 111–120.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-1876. *Reports on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1872-76, Ser. Zoology* 12: 1–554.

Meyer, E. (1887): Studien über den Körperbau der Anneliden. I-III. *Mitteilungen aus der Zoologischen Station zu Neapel* 7: 592–741.

Nyholm, K.G. (1951): Contributions to the life history of the ampharetid *Melinna cristata*. *Zoologiska Bidrag fran Uppsala* 29: 79–91.

Okuda, S. (1947): On an ampharetid worm, *Schistocomus sovjeticus* Annenkova, with notes on its larval development. *Journal of the Faculty of Science Hokkaido Imperial University* 9: 321–329.

Olafsson, E., Moore, C.G. & Bett, B.J. (1990): The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. *Estuarine, Coastal and Shelf Science* 31: 883–893.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Orrhage, L. (2001): On the anatomy of the central nervous system and the morphological value of the anterior end appendages of Ampharetidae, Pectinariidae and Terebellidae (Polychaeta). *Acta Zoologica* 82: 57–71.

Parapar, J., Kongsrud, J.A., Kongshavn, K., Alvestad, T., Aneiros, F. & Moreira, J. (2018): A new species of *Ampharete* (Annelida: Ampharetidae) from the NW Iberian Peninsula, with a synoptic table comparing NE Atlantic species of the genus. *Zoological Journal of the Linnean Society* 183: 526–555.

Petrecca, R.F. & Grassle, J.F. (1990): Notes on fauna from several deep-sea hydrothermal vent and cold seep soft-sediment communities. In: Gregory R. (ed.)., *Gorda Ridge*. McMurray: 279–283.

Purschke, G. (2016): Annelida: Basal groups and Pleistoannelida. In: Schmidt-Rhaesa, A., Harzsch, S. & Puschke, G. (eds.), *Structure and Evolution of Invertebrate Nervous Systems*. Oxford University Press, Oxford: 254–312.

Reuscher, M.G. & Fiege, D. (2016): Ampharetidae (Annelida: Polychaeta) from cold seeps off Pakistan and hydrothermal vents off Taiwan, with the description of three new species. *Zootaxa* 4139: 197–208.

Reuscher, M., Fiege, D. & Wehe, T. (2009): Four new species of Ampharetidae (Annelida: Polychaeta) from Pacific hot vents and cold seeps, with a key and synoptic table of characters for all genera. *Zootaxa* 2191: 1–40.

Reuscher, M., Fiege, D. & Imajima, M. (2015a): Ampharetidae (Annelida: Polychaeta) from Japanese waters. Part III: The genus *Amphicteis* Grube, 1850 and closely related genera. *Journal of the Marine Biological Association of the United Kingdom* 95: 929–940.

Reuscher, M., Fiege, D., Imajima, M. (2015b): Ampharetidae (Annelida: Polychaeta) from Japanese waters. Part IV. Miscellaneous genera. *Journal of the Marine Biological Association of the United Kingdom* 95: 1105–1125.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Glasby, C.J. (2000): Phylogeny. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing: Melbourne: 46–51; xii, 465 pp.

Rouse, G.W. & Pleijel, F. (2001): Polychaetes. Oxford University Press, Oxford: 354 pp.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Russell, D.E. (1987): *Paedampharete acutiseries*, a new genus and species of Ampharetidae (Polychaeta) from the North Atlantic Hebble area, exhibiting progenesis and broad intraspecific variation. *Bulletin of the Biological Society of Washington* 7: 140–151.

Salazar-Vallejo, S.I. & Hutchings, P. (2012): A review of characters useful in delineating ampharetid genera (Polychaeta). *Zootaxa* 3402: 45–53.

Sars, M. (1856): Nye Annelider. Fauna littoralis Norvegiae 2. Fredrik D. Beyer, Bergen. 24 pp.

Schüller, M. & Jirkov, I.A. (2013): New Ampharetidae (Polychaeta) from the deep Southern Ocean and shallow Patagonian waters. *Zootaxa* 3692: 204–237.

Self, R.F.L. & Jumars, P.A. (1988): Cross-phyletic patterns of particle selection by deposit feeders. *Journal of Marine Research* 46: 119–143.

Solis-Weiss, V. (1993): *Grassleia hydrothermalis*, a new genus and species of Ampharetidae (Annelida: Polychaeta) from the hydrothermal vents off the Oregon coast (U.S.A.) at Gorda Ridge. *Proceedings of the Biological Society of Washington* 106: 661–665.

Stiller, J., Rousset, V., Pleijel, F., Chevaldonné, P., Vrijenhoek, R.C. & Rouse, G.W. (2013): Phylogeny, biogeography and systematics of hydrothermal vent and methane seep *Amphisamytha* (Ampharetidae, Annelida), with descriptions of three new species. *Systematics and Biodiversity* 11: 35–65.

Stiller, J., Tilic, E., Rousset, V., Pleijel, F. & Rouse, G.W. (2020): Spaghetti to a tree: A robust phylogeny for Terebelliformia (Annelida) based on transcriptomes, molecular and morphological data. *Biology* 9:73: 1–29.

Thistle, D., Ertman, S.C. & Fauchald, K. (1991): The fauna of the HEBBLE site: patterns in standing stock and sediment-dynamic effects. In: Nowell, A.R.M. (ed.), Deep Ocean Sediment Transport. *Marine Geology* 99: 413–422.

Thorson, G. (1946): Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen for Danmarks Fiskeri- Og Havundersögelser, Serie: Plankton* 4, 1–523.

Uschakov, P.V. (1955): The polychaete worms of the far eastern seas of the U.S.S.R. [in Russian]. *Academy of Sciences of the USSR Zoological Institute Academy of Sciences of the USSR Zoological Institute* 56: 1–419.

Verrill, A.E. (1873): Results of recent dredging expeditions on the coast of New England. *American Journal of Science and Arts, Series 3* 5: 98–106.

Wirén, A. (1885): Om Cirkulations- och digestions-organen hos Annelider af familjerna Ampharetidae, Terebellidae och Amphipectinidae. *Kunglia Svenska vetenskapsakademiens Handlingar* 21: 1–58.

WoRMS Editorial Board (2018): *World Register of Marine Species*. Accessed through http://www.marinespecies.org at VLIZ. (Accessed on 2018-08-06 and 2020-08-19).

Zhadan, A.E. & Tzetlin, A.B. (2002): Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta). *Cahiers de Biologie Marine* 43: 149–164.

Zhadan, A.E. & Tzetlin, A.B. (2003): Comparative study of the diaphragm (gular membrane) in Terebelliformia (Polychaeta, Annelida). *Hydrobiologia* 496: 269–278.

Zhou, Y., Chen, C., Sun, Y., Watanabe, H.K., Zhang, R. & Wang, C. (2019): *Amphisamytha* (Annelida: Ampharetidae) from Indian Ocean hydrothermal vents: Biogeographic implications. *Deep-Sea Research Part I* 154: 103148.

Zottoli, R.A. (1974): Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus*. *Transactions of the American Microscopical Society* 93: 78–89.

Zottoli, R.A. (1982): Two new genera of deep-sea polychaete worms of the family Ampharetidae and the role of one species in deep-sea ecosystems. *Proceedings of the Biological Society of Washington* 95: 48–57.

Zottoli, R. A. (1983): *Amphisamytha galapagensis*, a new species of ampharetid polychaete from the vicinity of abyssal hydrothermal vents in the Galapagos Rift, and the role of this species in rift ecosystems. *Proceedings of the Biological Society of Washington* 96: 379–391.

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7.7.3 Terebellidae s.l.: Polycirridae Malmgren, 1866, Terebellidae Johnston, 1846, Thelepodidae Hessle, 1917, Trichobranchidae Malmgren, 1866, and Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013

Introduction

This chapter considers Terebellidae *sensu lato*, referring to the original taxa previously considered as subfamilies of the family Terebellidae Johnston, 1846, namely Polycirrinae Malmgren, 1866, Terebellinae Johnston, 1846 (previously referred to as Amphitritinae), and Thelepodidae Hessle, 1917, together with the closely related family Trichobranchidae Malmgren, 1866 and the recently described family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013.

Terebellidae *sensu lato* is a large group of polychaetes characterized by the presence of multiple grooved buccal tentacles of prostomial origin used for selective deposit feeding. These tentacles are typically smooth, but some polycirrids have papillose tentacles, and are not retractable into the mouth, as in members of the families Ampharetidae Malmgren, 1866 and Alvinellidae Desbruyères & Laubier, 1986.

Several different names have been used to refer to these animals; often, these included various combinations of families and subfamilies. Hessle (1917) used the name Terebellomorpha Hatschek, 1893 to refer to the families Ampharetidae, Pectinariidae Quatrefages, 1866 and Terebellidae. Later, Fauchald (1977) used the term Terebellida Dales, 1962 to include the families Ampharetidae, Bogueidae Hartman & Fauchald, 1971, Pectinariidae, Sabellariidae Johnston, 1865, Terebellidae (with the three subfamilies), and Trichobranchidae. Bogueidae was subsequently shown by Wolf (1983) to belong to Maldanidae.

Holthe (1986a) also used the name Terebellomorpha with the rank of order and included Alvinellidae. Rouse and Fauchald (1997) and Rouse and Pleijel (2001) used Terebellida to refer to Cirratuliformia and Terebelliformia together; this latter group included Alvinellidae, Ampharetidae, Pectinariidae, Terebellidae, and Trichobranchidae. Rouse and Pleijel (2001) went further on the subject, stating that Terebellomorpha and Terebelliformia were traditionally used to group the same families of polychaetes. It is not clear why Rouse and Pleijel (2001) preferred the name Terebelliformia to Terebellomorpha, which had been used by most specialists on this group for a long time (Hessle 1917, Holthe 1986a, b, among several other authors), but they were followed by several subsequent authors (Glasby et al. 2004, Nogueira et al. 2010, 2013, Fitzhugh et al. 2015).

Recently, species belonging to the three subfamilies of Terebellidae, together with some species of Trichobranchidae, which has historically often been considered as another subfamily of Terebellidae (Day 1967, Rouse and Pleijel 2001, Garraffoni and Lana 2004, 2008), Alvinellidae, Ampharetidae, and Pectinariidae were subjected to an intensive morphologically based phylogenetic analysis by Nogueira et al. (2013). The outgroup included species of Cirratulidae Ryckholt, 1851, Sabellariidae Johnston, 1865 and Spionidae Grube, 1850. Using 85 taxa and 118 subjects (characters), Nogueira et al. (2013) showed that, although these groups were closely related, each of the subfamilies previously included in Terebellidae *sensu lato* evolved independently within Terebelliformia and should be raised to family level, together with Trichobranchidae, which is nested among those families.

In this chapter, we use the name Terebelliformia to refer to the eight families with multiple grooved buccal tentacles of prostomial origin (e.g., Ampharetidae, Alvinellidae, Pectinariidae, Polycirridae, Telothelepodidae, Terebellidae, Thelepodidae, and Trichobranchidae), and we use the name Terebellidae *sensu lato* to include all the families previously considered as subfamilies of Terebellidae plus Trichobranchidae. The name Terebellidae *sensu stricto* refers herein to those species previously considered as belonging to the subfamily Terebellinae.

Artacaminae Malmgren, 1866 has previously been considered as a subfamily of Terebellidae, containing two genera, *Artacama* Malmgren, 1866 and *Artacamella* Hartman, 1955. The latter genus was transferred to Trichobranchidae by Holthe (1977) and Hutchings (1977) independently. The remaining genus *Artacama* was shown by McHugh (1995) to belong to Terebellidae *sensu stricto*, as it has uncini in double rows in some biramous parapodia. McHugh also showed that the previous name for the subfamily Amphitritinae should be replaced with Terebellinae, according to the rules of the International Code of Zoological Nomenclature (1985), and this group was elevated to Terebellidae *sensu stricto* by Nogueira et al. (2013).

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As all these newly erected families previously included within Terebellidae share many characters and habits in common, in the following discussion, we refer to them as belonging to Terebellidae *sensu lato*. In cases where there is specific information on a particular family, we provide this. We then give a list of the currently recognized genera in each of these newly created families and indicate the number of species currently known in each genus.

Terebellidae *sensu lato* consists of 73 genera and about 675 or more species among the five families. These animals are found throughout the world, from the intertidal to the deep ocean, as well as in the lower reaches of estuaries, where salinities are higher and more stable (Hutchings 2000). Most are tube dwellers and live attached on the undersurface of rocks or shells, or to seagrasses or brown algae, but some species are infaunal; instead of building a tube, animals of some species secrete a mucous sheath or live freely in the sediment. Tubes, when present, are made of sand, mud, shell fragments, small rocks, or sponge spicules stuck together, sometimes with some particle size selection; the tubes of *Lanice* Malmgren, 1866 typically have an ornamented entrance; one species of *Terebella* Linnaeus, 1767 constructs tubes of peloids formed by bacterial sulfate reduction within marine cave stalactites formed by serpulids (Guido et al. 2014).

Basically, all members of Terebellidae *sensu lato* are sedentary species, although *Biremis blandi* Polloni, Rowe & Teal, 1973, which normally lives in sediments at 411 to 597 m in the Florida Strait and Bahamas (Londoño-Mesa 2009), is able to swim in response to an apparent slumping event (Poloni et al. 1973). Other species can swim rapidly for a few seconds if removed from their tubes (Hutchings personal observations). Observations of a swimming *Loimia medusa* Savigny in Lamarck, 1818 off Madagascar were recorded by Westheide (2003), although unlikely to be that species (see Hutchings and Glasby 1995), which normally inhabits a U-shaped mud tube as an adult (Llansó and Diaz 1994, Seitz and Schaffner 1995). Levin and Greenblatt (1981) also recorded *L.* cf. *medusa* from two plankton collections separated by more than a year, at 90 m in a 2000 m water column, off the coast of San Diego, CA, USA, but that species identification also seems unlikely, given the type locality of *L. medusa*, in shallow water in the Red Sea (Hutchings and Glasby 1995). Others have recorded juvenile pelagic stages in plankton (Bhaud 1988, Hutchings personal observations).

Adult specimens of Terebellidae *sensu lato* range in length from a few mm to nearly 40 cm (McHugh 1993). They can be robust, with maximal diameters exceeding 2 cm. All Terebelliformia lack septa, except for a single one referred to as the gular membrane, transversing the body cavity between segments 4 and 5 (Hessle 1917, Sutton 1957, Zhadan and Tzetlin 2003) and consisting of a muscularized septum. Although traditionally the body of these animals has been divided into two regions, an anterior region (thorax) and a posterior one (abdomen), Nogueira et al. (2010, 2013) suggested that the terms thorax and abdomen should not be used, as these regions are not always well defined.

The group was first described by Johnston, 1846, who named as Terebellacea a species group consisting of *Terebella*, *Polycirrus* Grube, 1850, and *Terebellides* Sars, 1835. Malmgren (1866) reviewed this classification, described several additional genera, and divided the family into five subfamilies, Amphitritea Malmgren, 1866, Artacamacea Malmgren, 1866, Canephoridea Malmgren, 1866, Polycirridea Malmgren, 1866, and Trichobranchidea Malmgren, 1866, with Canephoridea containing only the genus *Terebellides* and Trichobranchidea containing only *Trichobranchus* Malmgren, 1866.

Later, Hessle (1917) changed the name of the group to Terebellidae, described several new genera, synonymized others, changed the subfamilies to an '-inae' ending, described the subfamily Thelepodinae (as Thelepinae), synonymized Artacaminae with Amphitritinae (=Terebellinae), and raised trichobranchids to family level. According to Hessle (1917), Terebellidae contained the subfamilies Amphitritinae, Polycirrinae, and Thelepinae.

Subsequently, Fauvel (1927) rejected these changes and resurrected the subfamilies Canephorinae, Trichobranchidea, and Artacaminae but maintained Amphitritinae, Polycirrinae, and Thelepodinae. Day (1967) synonymized Canephorinae with Trichobranchidae and regarded it as a subfamily of Terebellidae, Trichobranchinae. Day (1967) also synonymized Artacamacea with Amphitritinae and changed this name to Terebellinae. He also followed Fauvel (1927) in including all abranchiate genera within Polycirrinae regardless of the presence or absence of neuropodia and their uncinial arrangement. Hartmann-Schröder (1971) resurrected Artacaminae and considered Trichobranchinae as a separate family, Trichobranchidae, whereas Rouse and Pleijel (2001) and Garraffoni and Lana (2004, 2008) followed Day (1967) in viewing the group as a subfamily of Terebellidae. Thus, over the decades, trichobranchids have been regarded either as a separate family or a subfamily of Terebellidae by various workers, but they have always been considered as closely related to the latter group.

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Since Johnston (1846) erected the name Terebellacea, which was also used by Malmgren 1866, many additional genera and species have been described. Whereas Saint-Joseph (1894) stressed the value of the neurochaetae, Hessle (1917) discussed the relationship among Terebellidae, Trichobranchidae, Amphictenidae (=Pectinariidae), and Ampharetidae largely based on the structure of the nephridia, which he described in detail for these groups. However, although not disputing the value of the nephridia, in reality, it is often difficult to see them without dissection and the nephridial papillae on which the nephridiopores open. In some species, differences in the papillae occur between males and females in terms of size and shape, and mature individuals may also differ in color due to the presence of ripe oocytes or sperm in the coelom.

Holthe (1986a) reviewed Terebellomorpha (consisting of the families Pectinariidae, Ampharetidae, Terebellidae, and Trichobranchidae), with comments on the phylogeny and systematics, based largely on the Scandinavian fauna, but he clearly stated that it was not his intention to provide a new and complete classification of the group but rather to provide some principles, which should be incorporated into any such revisions. Although Holthe discussed various character sets, he made no attempt to undertake any phylogenetic analyses; instead, he provided some possible evolutionary trajectories of branchiae and uncini, which he illustrated, but without a detailed explanation of how he derived these trajectories. Because of this, it is difficult to use these ideas and Holthe's comments have not been incorporated into recent studies on the phylogeny of the group. Therefore, before the recent phylogenetic study based on morphological characters undertaken by Nogueira et al. (2013), the family Terebellidae has included either three or four subfamilies, Polycirrinae, Thelepodinae, Terebellinae, and sometimes Trichobranchidae, as discussed above. Polycirrinae is characterized by a lack of branchiae and notopodia, and neuropodia are either present or absent, but if present the neurochaetae (usually avicular uncini) are always arranged in single rows. Thelepodinae is characterized by simple unbranched branchiae and neuropodia with neurochaetae (avicular uncini) always arranged in single rows. Terebellinae is characterized by the presence or absence of branchiae, which if present have common basal stalks and usually branched filaments, and at least some neuropodia with neurochaetae (avicular uncini) arranged in double rows. Trichobranchidae is characterized by an expanded upper lip and filamentous and unbranched branchiae, sometimes foliaceous, or united into a single branchial trunk with four lamellate lobes, and thoracic neurochaetae as long acicular hooks (acicular uncini) with dentate crests, whereas abdominal neurochaetae are avicular uncini.

Morphology

External morphology

Body shape. Considerable confusion exists within the literature with regard to the external morphology of Terebellidae *sensu lato*, especially the anterior end (Nogueira et al. 2010, 2013). In part, this is due to the different names being given for the same structure; also, several authors have not been consistent over time, which makes it difficult to make comparisons and assess homologies (see Tab. 1 in Zhadan and Tetzlin 2002, Nogueira et al. 2010). Nogueira et al. (2010) performed a comprehensive study of the external morphology of the group after the examination of a large amount of type material or material from the type locality of the type species of nearly all genera of Terebellidae *sensu lato* and also some species of Alvinellidae, Ampharetidae, and Pectinariidae. We follow herein the terminology used by Nogueira et al. (2010) and subsequently by Nogueira et al. (2013) and Fitzhugh et al. (2015), with a few amendments.

The body is usually divided into thoracic and abdominal regions, the former typically with notochaetae and neurochaetae and the latter with neurochaetae only (Fig. 7.7.3.1A–C, H, J–L). Such demarcation is based purely on external features and not reflected internally. However, some polycirrids lack notopodia, neuropodia, or both (Fig. 7.7.3.1E–G), and there are several taxa in Terebellidae *sensu lato*, with notopodia and notochaetae continuing onto the posterior body (Fig. 7.7.3.1I).

In the genera of Polycirridae lacking notopodia and/or neuropodia, this demarcation between the thorax and the abdomen may not exist. However, the thoracic and abdominal regions are usually distinguished by the body width and papillae distribution. Typically, thoracic segments are distinctly swollen and papillate, especially ventrally, abruptly tapering to an almost uniformly cylindrical abdomen, with a smooth body wall (Fig. 7.7.3.1A, F), although sometimes the abdomen may also be markedly swollen, especially anteriorly (Fig. 7.7.3.1E). In *Hauchiella* Levinsen, 1893, parapodia are completely absent (Fig. 7.7.3.1E), *Enoplobranchus sanguineus* Verrill, 1873 possesses only notopodia, and these are branched (Fig. 7.7.3.1G). Species of *Polycirrus* have notopodia extending for a variable number of segments, with neuropodia beginning after the notopodia finish, just before that region, or from anterior segments (Fig. 7.7.3.1A). Species

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of *Lysilla* Malmgren, 1866 lack any abdominal parapodia. Among members of *Amaeana* Hartman, 1959, notopodia are present on the thorax, and spine-bearing neuropodia are found only on the abdomen. Finally, *Biremis blandi* has only neuropodia, beginning on the posterior thoracic region (Fig. 7.7.3.1F).

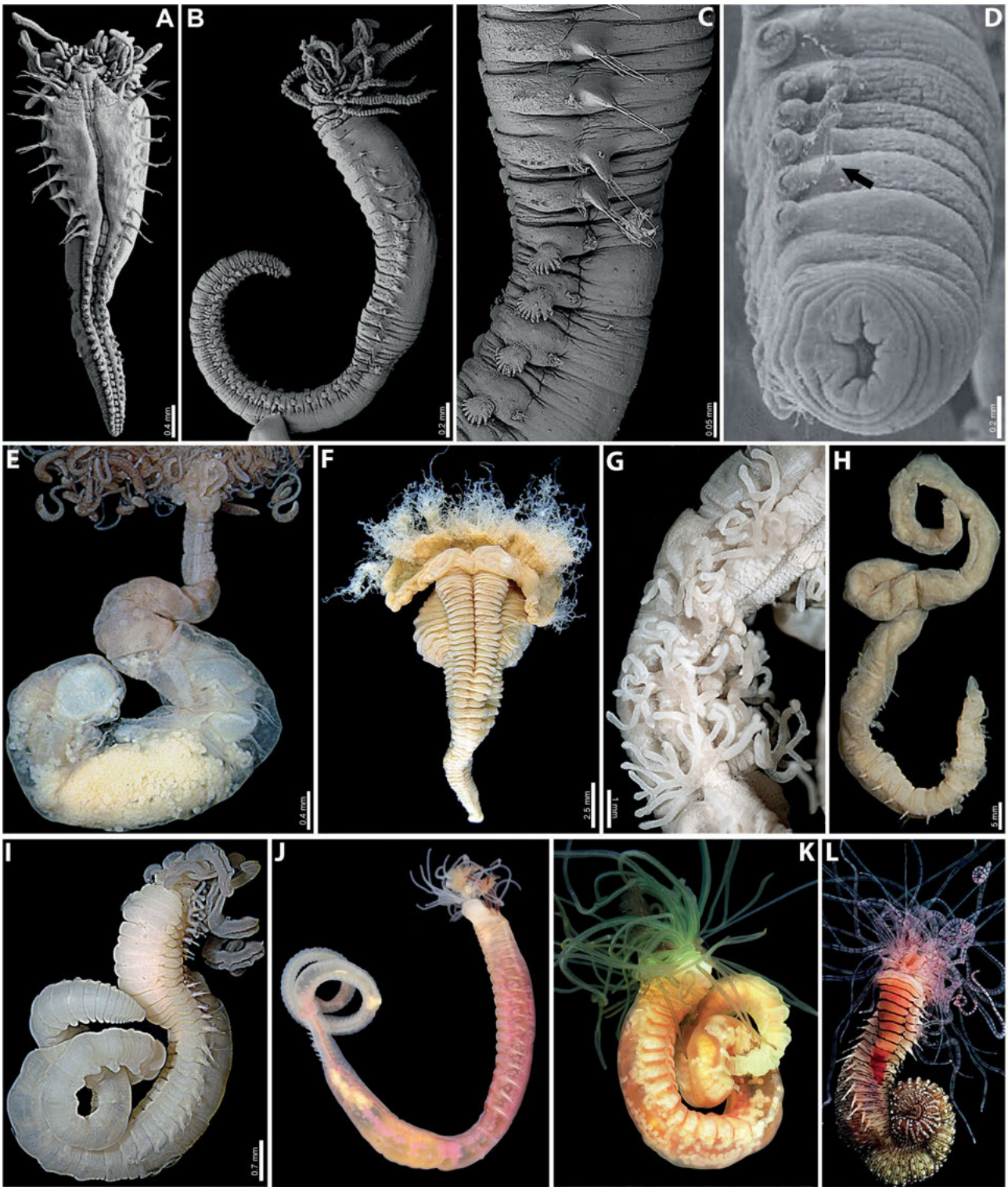


Fig. 7.7.3.1: Entire worms: A, *Polycirrus papillatus*; B, *Trichobranchus hirsutus*; C, *T. hirsutus*, transition between the thorax and the abdomen; D, *Streblosoma porchatensis*, posterior end, arrow points to last notopodium; E, *Hauchiella tentaculata*; F, *Biremis blandi*; G, *Enoplobranchus sanguineus*, midbody parapodia; H, *Parathelepus macer*; I, *Thelepus paiderotos*; J, *Pista kristiani*, alive; K, *Pista chloroplokamia*, alive; L, *Loimia tuberculata*, alive. The specimens photographed for each figure of this chapter and their taxonomic status are listed in Tab. 7.7.3.1.

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Tab. 7.7.3.1: List of specimens photographed for the figures, with corresponding collection number and taxonomic status. AM, Australian Museum, Sydney Australia; ASIZ, Academia Sinica, Taiwan; BCPM, Royal British Columbia Provincial Museum, Ontario, Canada; BMNH (new abbreviation: NHMUK), The Natural History Museum, London, UK; LACM-AHF, LA County Museum (Allan Hancock Foundation), Los Angeles, CA, USA; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; USNM, National Museum of Natural History, Washington, DC, USA; YPM, Yale Peabody Museum, New Haven, CT, USA; ZMUC, Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark.

Fig.	Taxonomic status and collection number
7.7.3.1	A, *Polycirrus papillatus* (paratype AM W.44622); B, C, *Trichobranchus hirsutus* (paratype AM W.47510); D, L, not preserved; E, *Hauchiella tentaculata* (holotype NTM W.023154); F, *Biremis blandi* (holotype USNM 47976); G, *Enoplobranchus sanguineus* (syntype YPM 181); H, *Parathelepus macer* (holotype AM W.6783); I, *Thelepus paiderotos* (holotype AM W.44968); J, *Pista kristiani* (holotype AM W.45451); K, *Pista chloroplokamia* (holotype AM W.44613).
7.7.3.2	A, *Nicolea vaili* (holotype AM W.47703); B, *Polycirrus minutus* (paratype AM W.47638); C, *Eupolymnia corae* (paratype MZUSP 2723); D, *Terebellides akares* (NTM W.025894); E, F, *Trichobranchus bunnabus* (AM W.24230); G, H, *Terebellides anguicomus* (AM W.34183); I, *Amaeana apheles* (holotype AM W.5239); J, *Polycirrus brutus* (holotype NTM W.023152); K, *E. sanguineus* (syntype YPM 40569); L, *Polycirrus papillosus* (holotype MZUSP 1216); M, N, *P. papillatus* (paratype AM W.47661).
7.7.3.3	A, D, H, *Amaeana brasiliensis* (holotype MZUSP 2349); B, *Lysilla pacifica* (AM W.47520); C, *P. brutus* (holotype NTM W.023152); E, *B. blandi* (holotype USNM 47976); F, *E. sanguineus* (syntype YPM 40568); G, *Polycirrus oculeus* (paratype AM W.44612); I, *Polycirrus cruciformis* (paratype AM W.47664); J, *Amaeana occidentalis* (LACM-AHF Poly 6518); K, *Hauchiella tentaculata* (holotype NTM W.023154); L, *P. minutus* (AM W.47638).
7.7.3.4	A, *P. cruciformis* (paratype AM W.47664); B, C, *A. occidentalis* (LACM-AHF Poly 6518); D, *P. minutus* (paratype AM W.47638); E, *T. hirsutus* (paratype AM W.47510); F, *P. macer* (holotype AM W.6783) *P. macer* (holotype AM W.6783); G, *Parathelepus oculeus* (holotype AM W.47507); H, I, *Rhinothelepus mexicanus* (holotype LACM-AHF Poly 1449); J, *Rhinothelepus lobatus* (holotype AM W.5234); K, *Rhinothelepus occabus* (paratype AM W.201904).
7.7.3.5	A–C, *Telothelepus capensis* (holotype BMNH 1961.16.87); D, *P. macer* (holotype AM W.6783); E, F, *R. mexicanus* (holotype LACM-AHF Poly 1449); G, *R. occabus* (holotype AM W.201903); H, I, *Parathelepus scutatum* (MZUSP 3028); J, *R. lobatus* (holotype AM W.5234).
7.7.3.6	A–C, *Euthelepus aserrula* (holotype AM W.47509); D–H, *Streblosoma patriciae* (D, H, paratype MZUSP 01040; E–G, holotype MZUSP 01039); I–K, *Streblosoma curvus* (holotype AM W.47508).
7.7.3.7	A–C, *E. corae* (paratype MZUSP 2723); D, *Artacama proboscidea* (D, AM W.34752); E–G, A. *benedeni* (unregistered); H, I, *Scionella japonica* (holotype USNM 15723); J, *Reteterebella lirrf* (paratype AM W.44545); K, *Lanice viridis* (paratype AM W.44611); L, *L. tuberculata* (holotype AM W.44280); M, *P. chloroplokamia* (holotype AM W.44613).
7.7.3.8	A, *Euthelepus serratus* (holotype AM W.199007); B, *Loimia pseudotriloba* (holotype AM W.47810); C–E, *P. chloroplokamia* (C, E, paratype AM W.44599; D, holotype AM W.44613); F, *P. kristiani* (holotype AM W.45451); G, K, L, *L. tuberculata* (paratype AM W.44285); H, I, *L. pseudotriloba* (paratype AM W.44594); J, *Loimia brasiliensis* (holotype MZUSP 02372).
7.7.3.9	A, *Amphitrite cirrata* (ZMUC Pol-2024); B, *S. japonica* (holotype USNM 15723); C, D, *Lanicola hutchingsae* (paratype MZUSP 2720); E, F, *Polycirrus* sp. (unregistered); G, H, *A. occidentalis* (LACM-AHF Poly 6518); I, *A. brasiliensis* (paratype MZUSP 2735); J, K, *Amaeana hsiehae* (paratype AM W.47362).
7.7.3.10	A, *Polycirrus bicrinalis* (paratype AM W.199638); B, *Parathelepus collaris* (BMNH 1983.1696); C, D, *R. lobatus* (holotype AM W.5234); E, *Pseudostreblosoma brevitentaculatum* (unregistered); F–H, *Streblsoma porchatensis* (F, G, unregistered; H, paratype AM W.24240); I, *T. anguicomus* (AM W.34183); J, K, *Streblosoma oligobranchiatum* (unregistered).
7.7.3.11	A, B, *P. brevitentaculatum* (unregistered); C, *E. serratus* (paratype AM W.5443); D–F, *Spinosphaera barega* (holotype AM W.30726); G, H, *Articulatia aberrans* (unregistered); I, J, *Eupolymnia koorangia* (AM W.34753); K, *Laphania boecki* (SMNH 72089); L, M, *A. proboscidea* (AM W.34752); N, *Leaena ebranchiata* (ZMUC Pol-2046).
7.7.3.12	A, *Streblosoma acymatum* (AM W.22478); B, *L. boecki*, (SMNH 72089); C–F, *Proclea malmgreni* (ZMUC Pol-2057); G, H, *Baffinia biseriata* (AM W.200437); I, *Hutchingsiella cowarrie* (paratype AM W.22542); J, *Hadrachaeta aspeta* (paratype AM W.6853).
7.7.3.13	A–D, *Terebella lapidaria* (BMNH 1928.4.26.330-32); E, *Longicarpus modestus* (AM W.34755); F, *Terebella pappus* (AM W.34757); G, H, *Phisidia rubra* (unregistered).
7.7.3.14	A, C, D, *T. hirsutus* (paratype AM W.47510); B, E, *T. akares* (paratype NTM W.025894); F–H, *Rhinothelepus buku* (holotype NTM W.9549); I, *E. aserrula* (holotype AM W.47509); J–L, *Thelepus paiderotus* (paratype AM W.47526).
7.7.3.15	A, *Artacama benedeni* (AM W.34749); B, *A. proboscidea* (AM W.34752); C, *Loimia ingens* (NTM W.6764); D, E, *Amphitrite lobocephala* (paratype AM W.20888); F, *Terebella* cf. *verrilli* (YPM 40571); G, *Amaeana breviachaeta* (holotype AM W.46526); H, *Amaeana crassispinulata* (holotype AM W.47365); I, *A. apheles* (holotype AM W.29203); J, *A. hsiehae* (holotype ASIZ W0000935).
7.7.3.16	A, *P. minutus* (paratype AM W.47638); B, *Polycirrus rubrointestinalis* (paratype AM W.47651); C, E, *P. bicrinalis* (C, holotype AM W.199637; E, paratype, AM W.199638); D, *Polycirrus disjunctus* (paratype AM W.199633); F–I, *P. papillatus* (F, G, I, paratype AM W.47661; H, holotype AM W.45149); J, *Polycirrus glossochelius* (holotype AM W.47642); K, *P. collaris* (BMNH 1983.1696); L, M, *Mesopothelepus macrothoracicus* (paratype BMNH 1971.77).
7.7.3.17	A, *Pseudostreblosoma serratum* (holotype AM W.18949); B, C, *S. porchatensis* (paratype AM W.29240); D, *Thelepus cincinnatus* (ZMUC Pol-2016); E, *A. lobocephala* (paratype AM W.20888); F, *A. cirrata* (ZMUC Pol-2023); G, *P. malmgreni* (ZMUC Pol-2057); H, I, *Pista cristata* (ZMUC Pol-707); J, *T.* cf. *lapidaria* (BMNH 1928.4.26.330-32); K, *Reteterebella queenslandia* (holotype AM W.3755); L, M, *H. aspeta* (paratype AM W.6856); N, *Betapista dekkerae* (holotype BCPM 978-00174-001); O, P, *L. modestus* (NMV F94344).

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Tab. 7.7.3.1 (continued)

Fig.	Taxonomic status and collection number
7.7.3.18	A, *A. proboscidea* (AM W.34752); B, *Loimia keablei* (paratype AM W.47787); C, D, *H. aspeta* (paratype AM W.6853); E, *L. pseudotriloba* (paratype AM W.44594); F, *Pista* sp. (AM W.34750); G, *Nicolea amnis* (AM W.34756); H, *Terebella tantabiddycreekensis* (AM W.34758); I, *Lanicides lacuna* (AM W.200878); J, K, *Thelepus paiderotus* (paratype AM W.47526).
7.7.3.19	A–D, *T. bunnabus* (A, B, AM W.35294; C, D, AM W.24230); E, F, *Trichobranchus dibranchiatus* (AM W.24136); G–L, *T. anguicomus* (G, J, L, AM W.34183; H, I, K, MCEM-BPO 327).
7.7.3.20	A–C, *T. hirsutus* (A, B, paratype AM W.47510; C, paratype AM W.44608); D–K, *T. akares* (D–F, holotype NTM W.023143; G–K, paratype NTM W.025894).
7.7.3.21	A, *R. lirrf* (paratype AM W.44545); B, *L. viridis* (paratype AM W.44611); C, D, *N. vaili* (paratype AM W.44522); E–H, *Pista anneae* (paratype AM W.44958); I–L, *P. chloroplokamia* (paratype AM W.44599).
7.7.3.22	A–F, *Pistella franciscana* (A, B, holotype AM W.45445; C–F, paratype AM W.44593); G, H, *L. tuberculata* (paratype AM W.44285).
7.7.3.23	A, *T. akares* (paratype NTM W.025894); B, C, *T. hirsutus* (paratype AM W.47510); D, E, *L. pseudotriloba* (paratype AM W.44594); F, G, *Parathelepus oculeus* (holotype AM W.47507); H, *L. keablei* (paratype AM W.47787); I, *P. chloroplokamia* (holotype AM W.44613); J, K, *Nicolea murrayae* (paratype AM W.44607); L–N, *P. franciscana* (L, M, holotype AM W.45445; N, paratype AM W.44593).

In Telothelepodidae, thoracic and abdominal regions are usually well marked, the thorax consisting of one to two achaetous segments, followed by some segments with notopodia only and then some biramous parapodia (except in *Telothelepus* Day, 1955, see below), and an abdominal region with neuropodia only, as very low pinnules (Fig. 7.7.3.1H). Most genera have 15 pairs of notopodia, but others have more. In the case of *Telothelepus*, there are no biramous parapodia, as the neuropodia only begin after the termination of notopodia.

In Thelepodidae, the anterior region is also broader and more glandular than the posterior region, but the transition between the thorax and the abdomen is usually more gradual, not occurring abruptly from one segment to the next (Fig. 7.7.3.1I), as in Polycirridae. All taxa have one to two achaetous segments anteriorly followed by two to three segments with notopodia only and then biramous parapodia for a variable number of segments, with several taxa having biramous parapodia throughout much of the body (Fig. 7.7.3.1D); others have them restricted to anterior segments, whereas subsequent segments have only neuropodia, with uncini on raised pinnules (Fig. 7.7.3.1I).

In Terebellidae *sensu stricto*, the majority of taxa have an abdominal region without notopodia (Fig. 7.7.3.1J–L), but some species of *Terebella* and several other genera have notopodia continuing almost to pygidium, and in these, there is no clear distinction between the thorax and the abdomen. Many genera of Terebellidae are defined by the number of pairs of notopodia, with 17 the most common number but can be 15, 21, 23, less than 15, or more. The segments on which notopodia and neuropodia begin are also important characters in defining Terebellidae genera.

In Trichobranchidae, the thoracic and abdominal regions are well marked, with the thorax consisting of some achaetous segments, followed by some with notopodia only, although in some species notopodia and neuropodia begin on the same segment (Fig. 7.7.3.1B) and in a few others the neuropodia may begin one segment before the notopodia, and then biramous segments, followed by an abdominal region with only neuropodia (Fig. 7.7.3.1B, C).

In summary, the division into thorax and abdomen is not always easy to define in Terebellidae *sensu lato*, as it is based entirely on the absence of notopodia and associated notochaetae on abdominal segments. If it were to be based on internal structures, we could refer to an anterior region anterior to the gular membrane, from the prostomium to segment 4, and a posterior region, from segment 5 to the pygidium (Zhadan and Tzetlin 2003).

Prostomium and peristomium. The anterior end of Terebellidae *sensu lato* is difficult to interpret. This is because of the difficulties of analyzing and comparing the structures that form the 'head' of these animals, as they are highly modified from the typical prostomium and peristomium head pattern found in many other polychaete families (Nogueira et al. 2010). Few studies on the larval development of Terebellidae *sensu lato* have been carried out, where the origins of particular structures have been determined (Garraffoni and Lana 2009).

The prostomium and peristomium are distinct in all Terebellidae *sensu lato*. The prostomium is much shorter, present only on the dorsal surface of the peristomial upper lip, and, except for some Polycirridae (Fig. 7.7.3.2B), does not form a complete ring around the body. The prostomium consists of a basal part often bearing eye spots, or ocelli (Fig. 7.7.3.5J), and a distal part from which the buccal tentacles originate. In trichobranchids and many terebellids, distinguishing between the basal and distal parts of the prostomium is difficult; eye spots, if present, occur on

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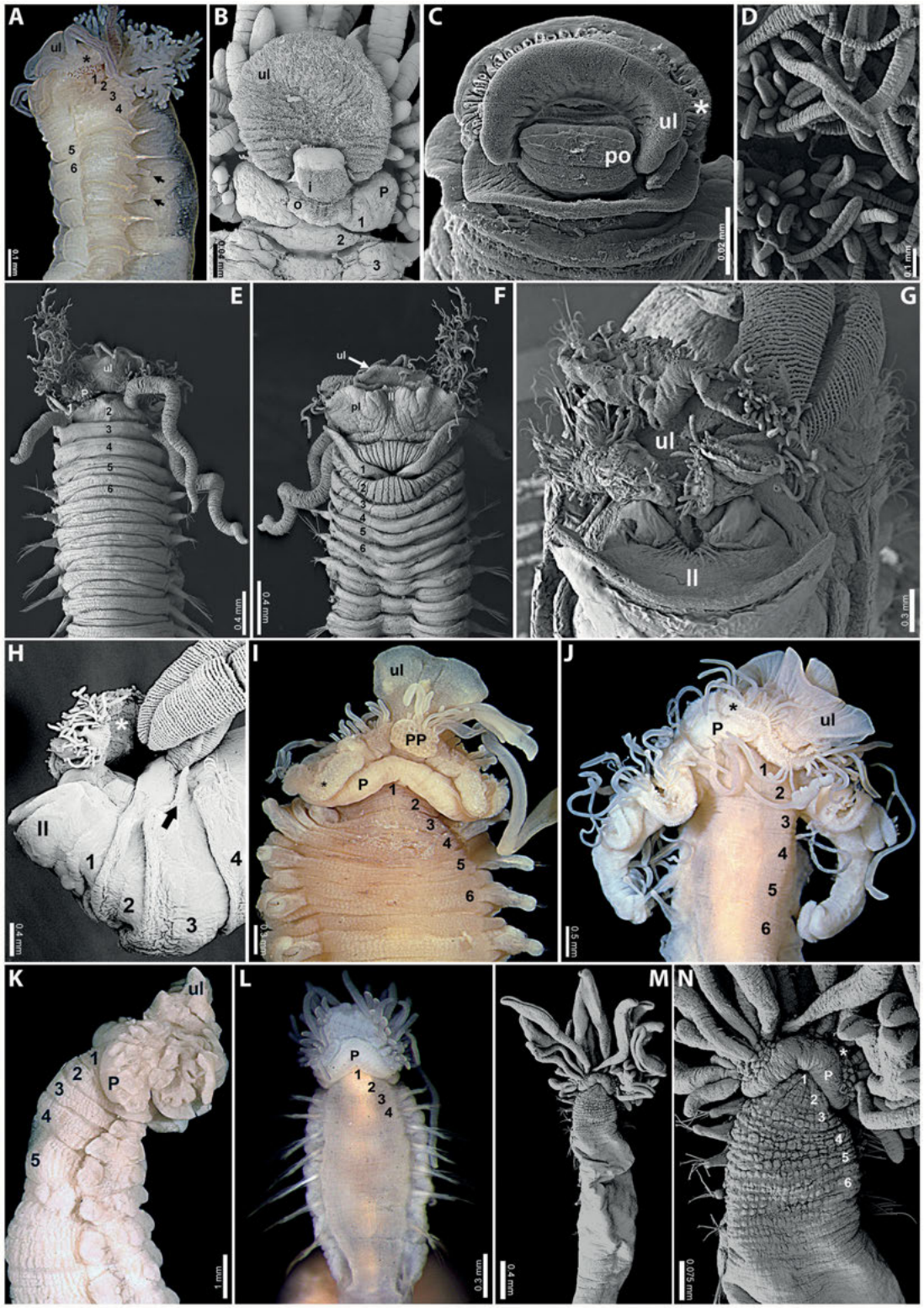


Fig. 7.7.3.2: Anterior ends: A, *Nicolea vaili*, lateral view; B, *Polycirrus minutus*, ventral view; C, *Eupolymnia corae*, frontal view; E, F, *Trichobranchus bunnabus*, dorsal and ventral views, respectively; G, H, *Terebellides anguicomus*, frontal and lateral views, respectively; I, *Amaeana apheles*, dorsal view; J, *Polycirrus brutus*, dorsal view; K, *Enoplobranchus sanguineus*, lateral view; L, *Polycirrus papillosus*, dorsal view; M, N, *Polycirrus papillatus*, dorsal views. Buccal tentacles: D, *Terebellides akares*. Arrows point to papillae. Numbers refer to segments; *, distal part of prostomium; i, inner region of lower lip; ll, lower lip; o, outer region of lower lip; P, basal part of prostomium; ul, upper lip.

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the basal part, and the buccal tentacles always arise from the distal part and are, therefore, prostomial in origin and cannot be retracted into the mouth (Figs. 7.7.3.1A, B, E, F, I–L, 7.7.3.2A–N). In Alvinellidae and Ampharetidae, the tentacles originate from inside the mouth and it is still being debated if they are of peristomial or prostomial origin (Orrhage 2001, Orrhage and Müller 2005, Nogueira et al. 2013). Therefore, although buccal tentacles are characteristic of all Terebelliformia, they may not be homologous structures between the families included in this group. The tentacles may be ciliated along their entire length, forming a longitudinal groove along which the food particles are carried to the mouth (see illustrations in Hutchings 2000, based on Dales 1955), whereas, in several species of Polycirridae, only the tips are expanded and ciliated, and they are probably brushed against the lips, or inserted inside the mouth, to transfer the food particles (Figs. 7.7.3.1A, E, 7.7.3.2D, I, J, L–N, 7.7.3.3A–C, E, G–L) (Nogueira et al. 2015a).

The eye spots at the base of the prostomium easily fade and may not be visible in preserved type material, although they were described as present originally. In contrast, in some species, eye spots are conspicuous even after more than 30 years of storage in alcohol. These may occur as a pair of dorsolateral clusters, in single or numerous rows across the entire base of the prostomium, except sometimes for a narrow middorsal gap, or may be completely lacking in fresh material; when present, juveniles frequently have more eye spots than adults of the same species. No studies have been undertaken to determine if these eye spots have any light sensitivity. Some deep-sea species have well-developed eyes and they may be sensitive to bioluminescence.

The peristomium forms the upper and lower lips and may also continue laterally and/or posteriorly from the mouth. The lips are often ciliated (Figs. 7.7.3.2B, C, F, 7.7.3.3D, 7.7.3.7B, C) and used for the selection of particles for either food or tube building (Dales 1962). There is also a partially eversible pharyngeal organ originating from the anterior part of the gut, which, when everted, lies just at the level of the mouth and has sometimes been referred to as the lower lip (Zhadan and Tzetlin 2002).

In trichobranchids, the prostomium is present as a low crest on the dorsal surface of the upper lip, and both the upper lip and buccal tentacles originate outside of the mouth and are not retractable (Figs. 7.7.3.1B, 7.7.3.2E–H). There are two types of tentacles, the longer ones have distally expanded tips and the shorter ones are almost uniformly cylindrical, tapering to the tip (Figs. 7.7.3.1B, 7.7.3.2E–H, 7.7.3.4E). The prostomium is situated either on the base of the upper lip (Figs. 7.7.3.1B, 7.7.3.2E, F) or extends along the lip until its anterior margin (Fig. 7.7.3.2G, H). The peristomium of members of this family is well developed, consisting of a large hood-like upper lip, an almost circular structure above the mouth and usually folded into three lobes (Fig. 7.7.3.2E–H), and a lower lip. This lower lip extends posteriorly or laterally from the mouth as an extension, and in *Terebellides*, it usually forms a large scoop-shaped structure that projects anteriorly (Fig. 7.7.3.2G, H) and has been regarded as segment 1 by some authors (Garraffoni and Lana 2004, Parapar and Moreira 2008a, b). In contrast, in most species of *Trichobranchus*, the peristomium does not extend posteriorly but continues laterally from the mouth as a pair of large lateral lobes, which are orientated dorsolaterally (Fig. 7.7.3.2F).

There is considerable morphological variation in the peristomium and prostomium in the remaining Terebellidae *sensu lato*. Among polycirrids, the prostomium forms thick crests on the dorsal part of the upper lip and usually extends posteriorly to cover segment 1 dorsolaterally; the distal margin is at the base of the upper lip (Figs. 7.7.3.1E, 7.7.3.2I, J, M, N, 7.7.3.4A), or the prostomium extends along the upper lip and terminates near the anterior margin (Figs. 7.7.3.2K, L, 7.7.3.3C–F). Several polycirrids have a middorsal oval to rectangular structure developed on the distal part of the prostomium (Figs. 7.7.3.2I, 7.7.3.3A, B), which may be sensory (Nogueira et al. 2015a, b). Polycirrids have at least two types of buccal tentacles, the long ones with distally or subdistally expanded tips and the short ones uniformly cylindrical or tapering to fine tips; more specialized buccal tentacles, such as subdistally expanded with blunt tips, are found among species of some genera (Figs. 7.7.3.2I, J, L–N, 7.7.3.3A–C, E, G–L, 7.7.3.4A–D). The buccal tentacles of several species of *Polycirrus* are luminescent; this is produced by mucus secreted by groups of glandular cells, which are present along the entire length of the tentacles (Harant and Grassé 1959). Although the details of the chemical processes have not been studied, the luminescence is activated when the animal is disturbed. In contrast, the buccal tentacles of *Polycirrus oculeus* Nogueira, Carrerette, & Hutchings, 2015a have paired subdistal red spots (Fig. 7.7.3.3G), which readily fade out after preservation; those red spots look like eye spots, but their nature has not been studied. The upper lip of the polycirrids is well developed, expanded, almost circular, and folded to form three lobes, whereas the lower lip is small, button-like (Figs. 7.7.3.1A, E, 7.7.3.3D, H, J), or divided into an inner region, usually button-like, and an expanded outer region, frequently covering at least segment 1 ventrally (Figs. 7.7.3.1F, 7.7.3.3F) (Glasby and Hutchings 2014,

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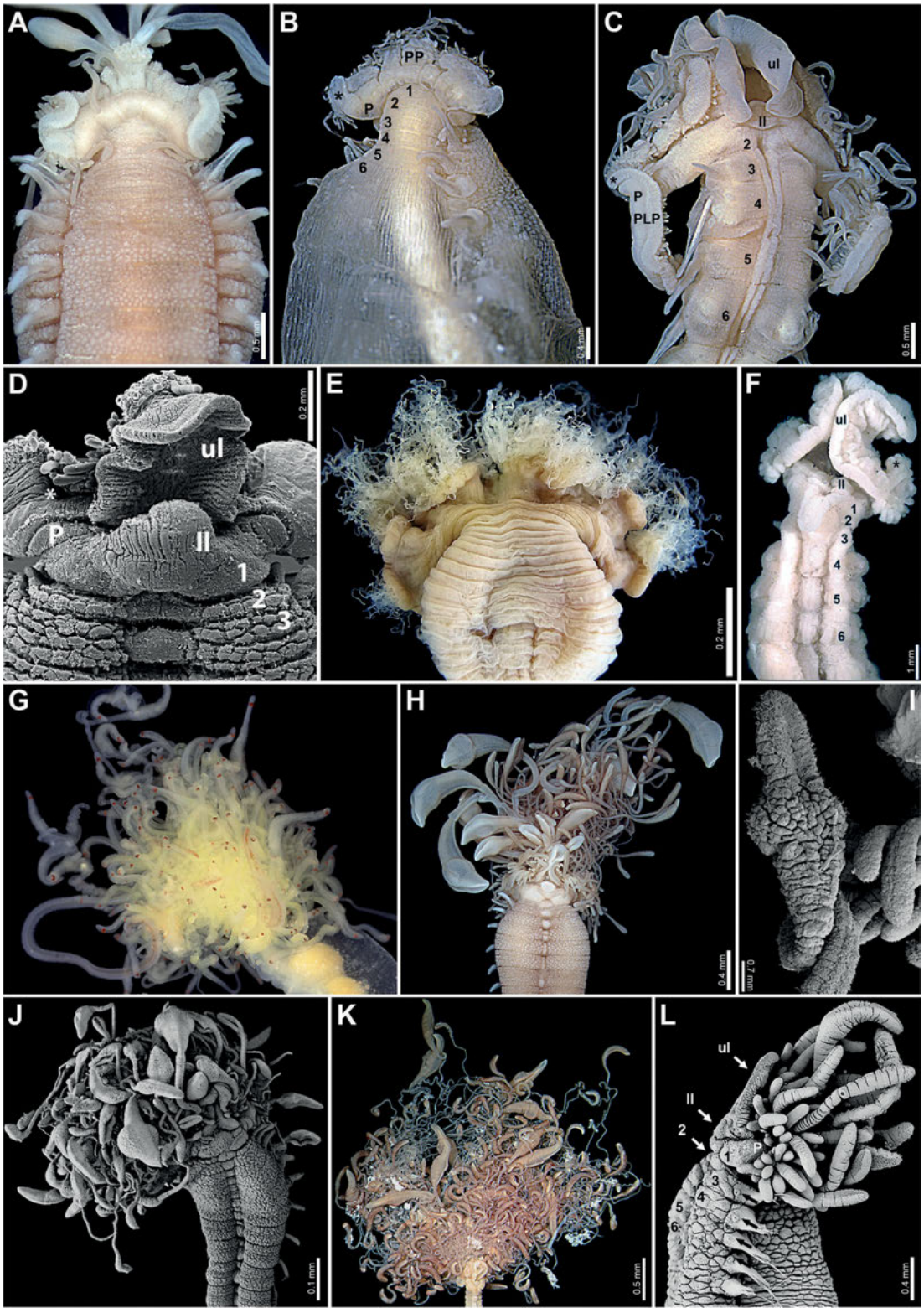


Fig. 7.7.3.3: Anterior ends: A, D, H, *Amaeana brasiliensis*, dorsal and two ventral views, respectively; B, *Lysilla pacifica*, dorsal view; C, *Polycirrus brutus*, ventral view; E, *Biremis blandi*, dorsal view; F, *Enoplobranchus sanguineus*, ventral view; G, *Polycirrus oculeus*, alive; J, *Amaeana occidentalis*, ventral view; K, *Hauchiella tentaculata*, ventral view; L, *Polycirrus minutus*, lateral view. Modified buccal tentacle: I, *Polycirrus cruciformis*. Numbers refer to segments; *, distal part of prostomium; II, lower lip; P, basal part of prostomium; PLP, prostomial lateral process; PP, prostomial process; ul, upper lip.

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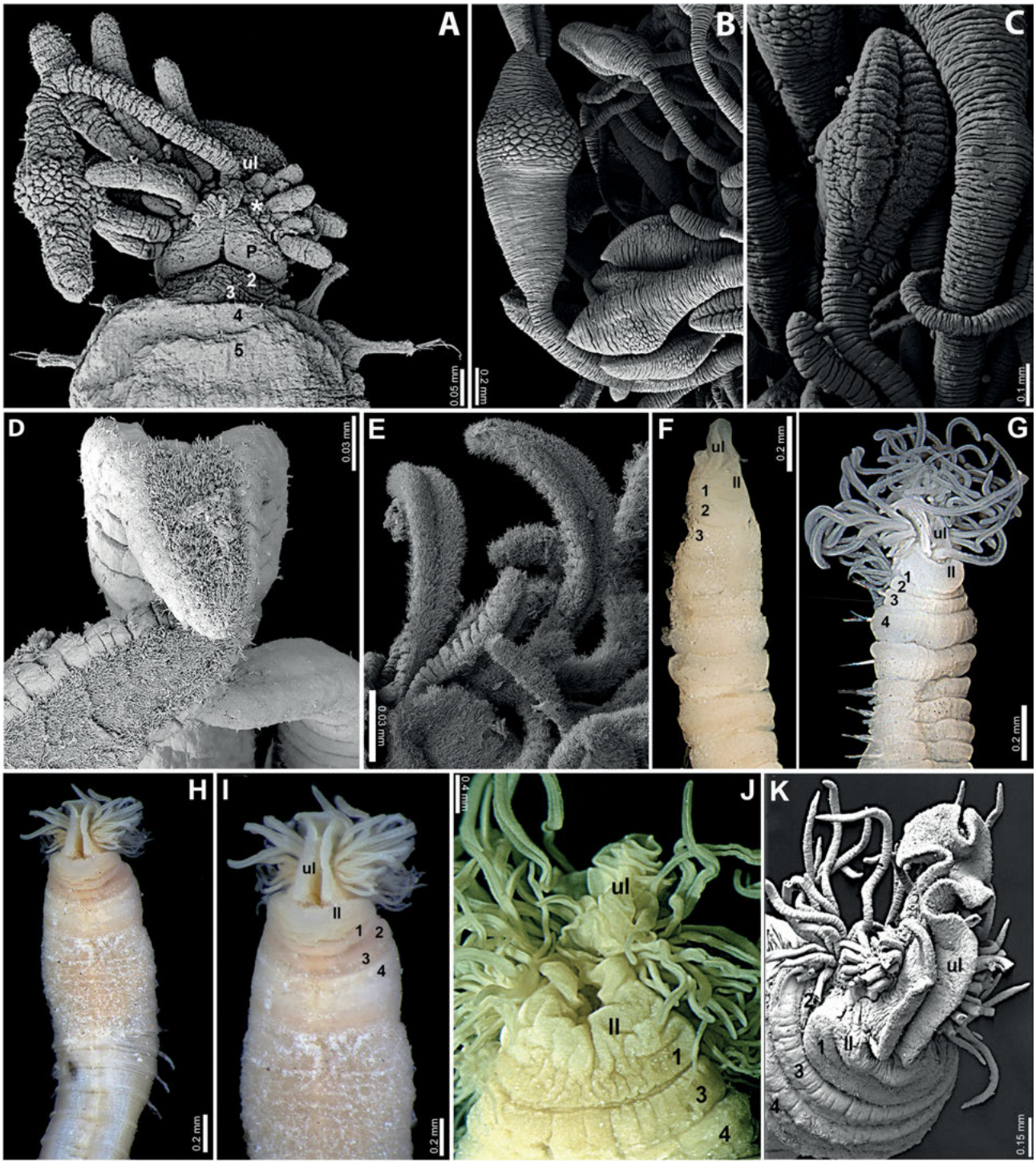


Fig. 7.7.3.4: Anterior ends: A, *Polycirrus cruciformis*, dorsal view; F, *Parathelepus macer*, ventrolateral view; G, *Parathelepus oculeus*, ventrolateral view; H, I, *Rhinothelepus mexicanus*, ventral views; J, *Rhinotelepus lobatus*, ventral view; K, *Rhinothelepus occabus*, ventral view. Buccal tentacles: B, C, *Amaeana occidentalis*; D, *Polycirrus minutus*; E, *Trichobranchus hirsutus*. Numbers refer to segments; *, distal part of prostomium; ll, lower lip; P, basal part of prostomium; ul, upper lip.

Fitzhugh et al. 2015). The peristomium of this family is usually restricted to the lips, but sometimes it extends laterally from the mouth, and more rarely forms a complete ring around the body.

Telothelepodinae has an elongate and narrow upper lip, the margins of which may be convoluted, and a large segment-like to cushion-like lower lip (Figs. 7.7.3.4F–K, 7.7.3.5A, B, D–F). The basal part of the prostomium

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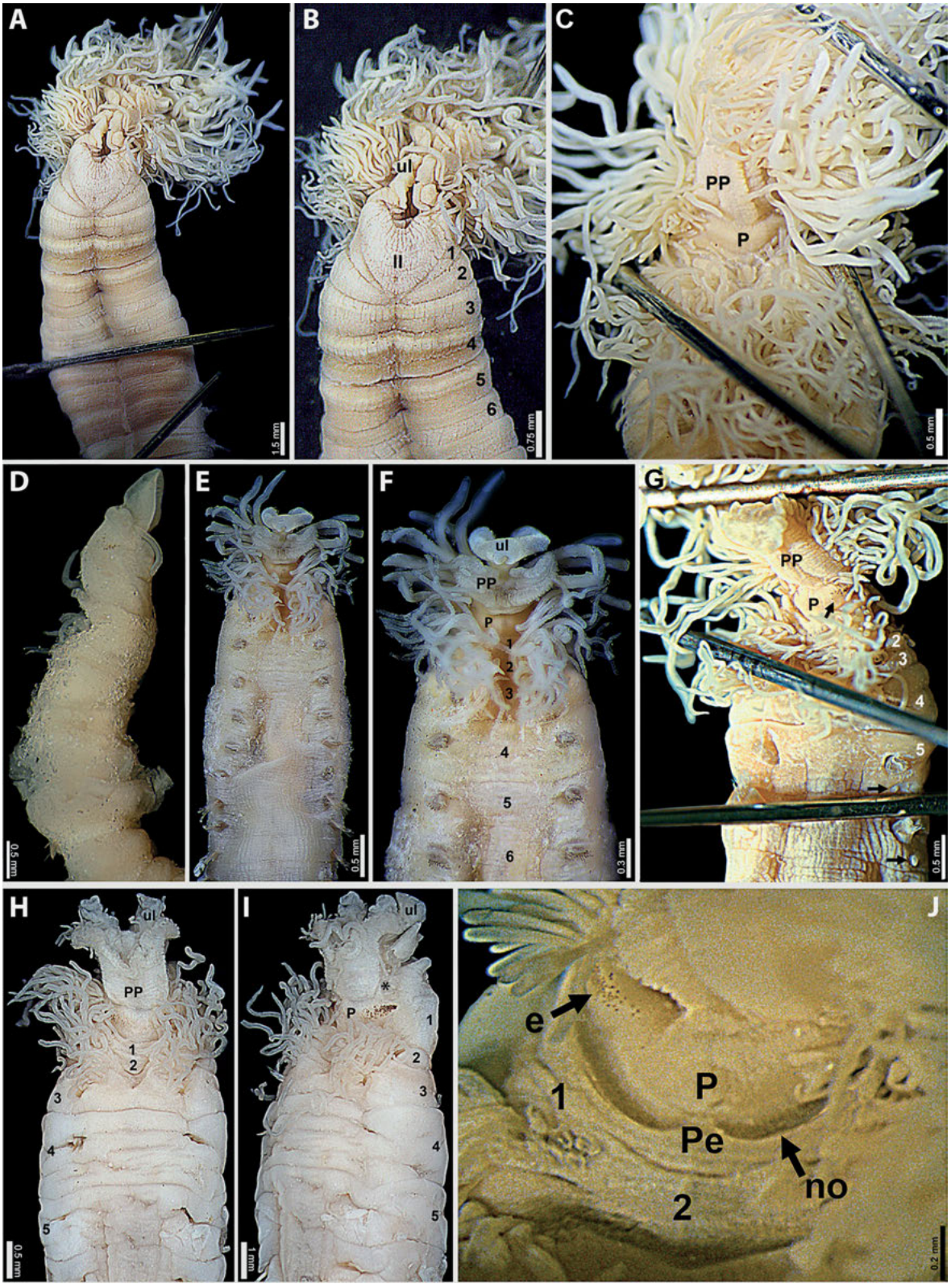


Fig. 7.7.3.5: Anterior ends: A–C, *Telothelepus capensis*, two ventral views and a dorsal view, respectively; D, *Parathelepus macer*, lateral view; E, F, *Rhinothelepus mexicanus*, dorsal views; G, *Rhinothelepus occabus*, dorsal view; oblique arrow points to eye spots and horizontal arrows point to papillae; H, I, *Parathelepus scutatum*, dorsal and dorsolateral views, respectively; J, *Rhinotelepus lobatus*, dorsal view, close-up of nuchal organs. Numbers refer to segments; *, distal part of prostomium; e, eye spots; ll, lower lip; no, nuchal organ; P, basal part of prostomium; Pe, peristomium; PP, prostomial process; ul, upper lip.

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forms a thick crest, usually with eye spots in dorsolateral clusters, and the distal part may have a middorsal process with a large free, tongue-like lobe, or it is distally bilobed (Fig. 7.7.3.5C–J). The peristomium usually continues dorsally, frequently forming a complete ring around the body, but dorsally it is narrow, with one pair of nuchal organs as pits on the border with the prostomium (Fig. 7.7.3.5C, D, G–J) (Nogueira et al. 2010). The buccal tentacles are usually uniformly cylindrical, with slightly expanded tips, and frequently two types of tentacles are present, differentiated mostly by length and thickness (Figs. 7.7.3.4G–K, 7.7.3.5A–C, E–J) (Fitzhugh et al. 2015, Hutchings et al. 2015), one of these types originating from the prostomial process and another from the remaining of the distal part of prostomium (Nogueira et al. 2018).

The upper lip of Thelepodidae is small, about as long as wide, similar to that of Terebellidae *sensu stricto*, and the lower lip is variable in structure, usually button-like and restricted to the oral area, or expanded and covering segment 1 (Fig. 7.7.3.6A–C, F, G, I–K). Species of *Euthelepus* frequently have the lower lip forming a ventral lobe around the mouth (Figs. 7.7.3.6A, B, 7.7.3.8A). In most species, the peristomium does not continue dorsally, but in some species it forms a complete ring around the body, with one pair of ciliated dorsolateral nuchal organs on the border with the prostomium (Fig. 7.7.3.6D–J) (Nogueira et al. 2010). All thelepodids have a single type of buccal tentacles, which are typically uniformly cylindrical, although some species, such as *Pseudostreblosoma brevitentaculatum* Nogueira & Alves, 2006, have tentacles that are distally expanded; the tentacles are frequently deeply grooved with flaring margins and the ciliated groove extends along the entire length of the tentacles (Fig. 7.7.3.6A–H).

In Terebellidae *sensu stricto*, the basal and distal parts of the prostomium are either almost undifferentiated or, more commonly, the distal part is developed to form a shelf-like process from which the buccal tentacles arise (Figs. 7.7.3.7A–I, 7.7.3.8G, 7.7.3.9C, D), and this seems to become more visible with increasing size of the animal and associated maturity. In the genus *Artacama*, the shelf-like distal part of prostomium is bilobed and the lower lip is developed to form a large papillated process (Fig. 7.7.3.7D–G), which has been considered in the literature as a proboscis (Malmgren 1866, Hartman 1967), but it is not a true proboscis, as it is not retractable (Nogueira et al. 2010). This structure caused the genus to be placed in the subfamily Artacaminae; although the validity of this subfamily was questioned several times (Hessle 1917, Day 1967), the subject remained open until McHugh (1995) undertook a detailed phylogenetic study and showed that the genus belongs to Terebellidae *sensu stricto* (as Terebellinae), as the uncini are arranged in double rows on some segments, the defining character for this family. The peristomium is typically restricted to the lips (Figs. 7.7.3.7A, D, 7.7.3.8G, 7.7.3.9D), but in some terebellids it extends laterally from the mouth to a variable degree, terminating dorsolaterally, fused dorsally to segment 1 or forming a complete ring around the body. Most terebellids have only one type of buccal tentacles, although species of *Artacama* have two types, both usually short, with the longer ones being distally expanded and the shorter ones uniformly cylindrical (Fig. 7.7.3.7E, G). The buccal tentacles are frequently colorless in preserved material (Figs. 7.7.3.7E, G, 7.7.3.8B, D, E, J), but in life they may be bright white, coloured, striped, or speckled with iridescent spots (Fig. 7.7.3.7J–M).

Nogueira et al. (2010) indicated that the above interpretations are largely based on external morphology of adults and need to be confirmed or rejected based on larval developmental studies, which are very limited in this group (Heimler 1983, Bhaud and Grémare 1988, Blake 1991, Garraffoni and Lana 2009). The prostomial origin of the buccal tentacles of Terebellidae *sensu lato* has been confirmed by studies of Orrhage (2001) and Orrhage and Muller (2005) on the patterns of innervation of these structures.

Lobes and crests. There has been considerable confusion in the literature, with some workers referring to the peristomium as segment 1 in Terebellidae *sensu lato*, as many species were described as having peristomial lobes (Hutchings and Glasby 1988, McHugh 1995, for example), when they are in fact on segment 1 (Nogueira et al. 2010, 2013). Garraffoni and Lana (2004, 2008) correctly coded the peristomium and the first segment as separate structures in their phylogenetic studies, but they considered the papillated process of *Artacama* as originating from segment 1, whereas it clearly is an expanded lower lip, as discussed above. This confusion has considerable implications for the taxonomy of this family, as the segments on which the notopodia, neuropodia and branchiae start are currently used to define the genera.

Many genera of Terebellidae *sensu stricto* and some Thelepodidae have glandular lobes on anterior segments and they are typically referred to as lateral lobes in the literature (Holthe 1986b, Hutchings and Glasby 1988, among many others). However, as some of these lobes arise ventrally or dorsally, Nogueira et al. (2010) suggested that the term 'lateral lobe' should be replaced with 'lobe' only and that their exact position, orientation, and shape should be provided in taxonomic descriptions. Although most of these lobes are large flaps of tissue that may cover parts of the preceding segment, some are reduced to thickened ridged structures (Figs. 7.7.3.6A, B, 7.7.3.7A–C, H, I,

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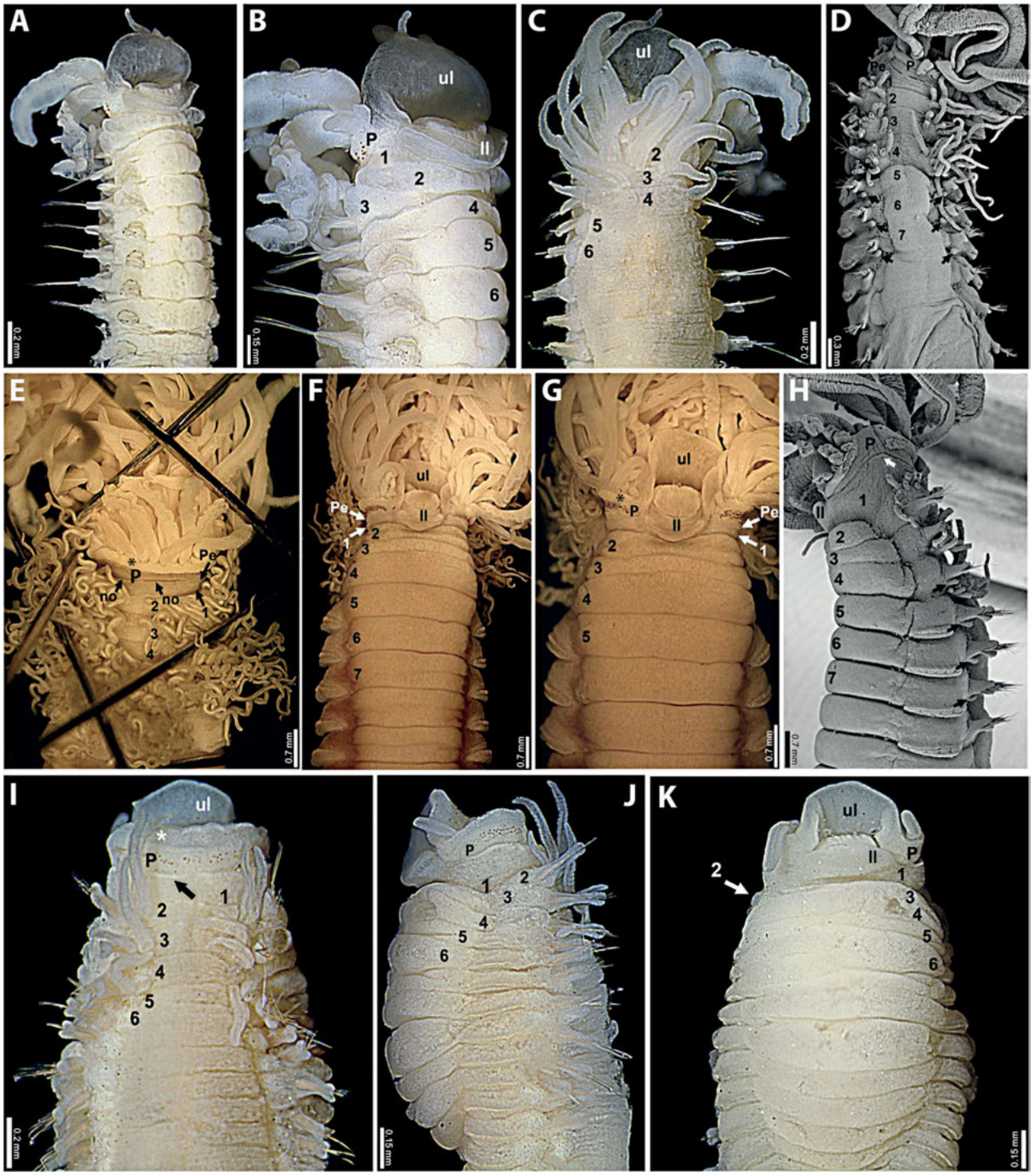


Fig. 7.7.3.6: Anterior ends: A–C, *Euthelepus aserrula*, two ventral views and a dorsal view, respectively; D–H, *Streblosoma patriciae*, two dorsal views, two ventral views, and a lateral view, respectively; I–K, *Streblosoma curvus*, dorsal, lateral, and ventral views, respectively. Numbers refer to segments; unspecific arrows point to nuchal organs; *, distal part of prostomium; ll, lower lip; no, nuchal organ; P, basal part of prostomium; Pe, peristomium; ul, upper lip.

7.7.3.8A–L, 7.7.3.9A–D). In addition, raised crests may also be present on anterior segments (Figs. 7.7.3.4F–K, 7.7.3.5A, B, D, H, I, 7.7.3.6A, B, F–H, J, K, 7.7.3.8D, F, H, I, 7.7.3.9.C–D), and although they have not been described in most taxonomic papers, they are sometimes conspicuous and should be included. As lobes and crests may occur on

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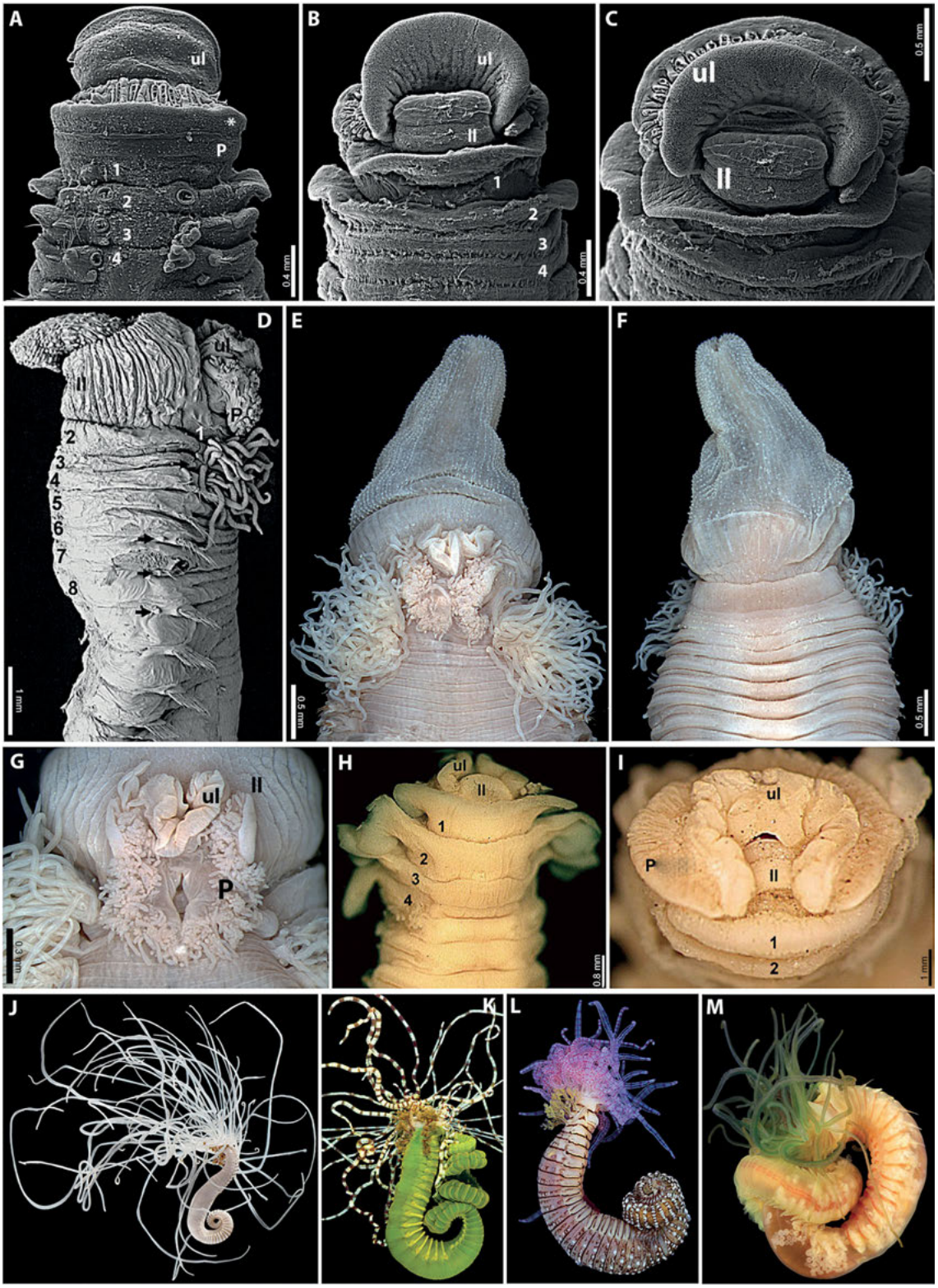


Fig. 7.7.3.7: Anterior ends: A–C, *Eupolymnia corae*, dorsal and two ventral views, respectively; D, *Artacama proboscidea*, lateral view, arrows point to papillae; E–G, *Artacama benedeni*, dorsal and ventral views and close-up of prostomium, respectively; H, I, *Scionella japonica*, ventral and frontal views, respectively. Entire worms, alive: J, *Reteterebella lirrf*; K, *Lanice viridis*; L, *Loimia tuberculata*; M, *Pista chloroplokamia*. Numbers refer to segments; *, distal part of prostomium; ll, lower lip; P, basal part of prostomium; ul, upper lip.

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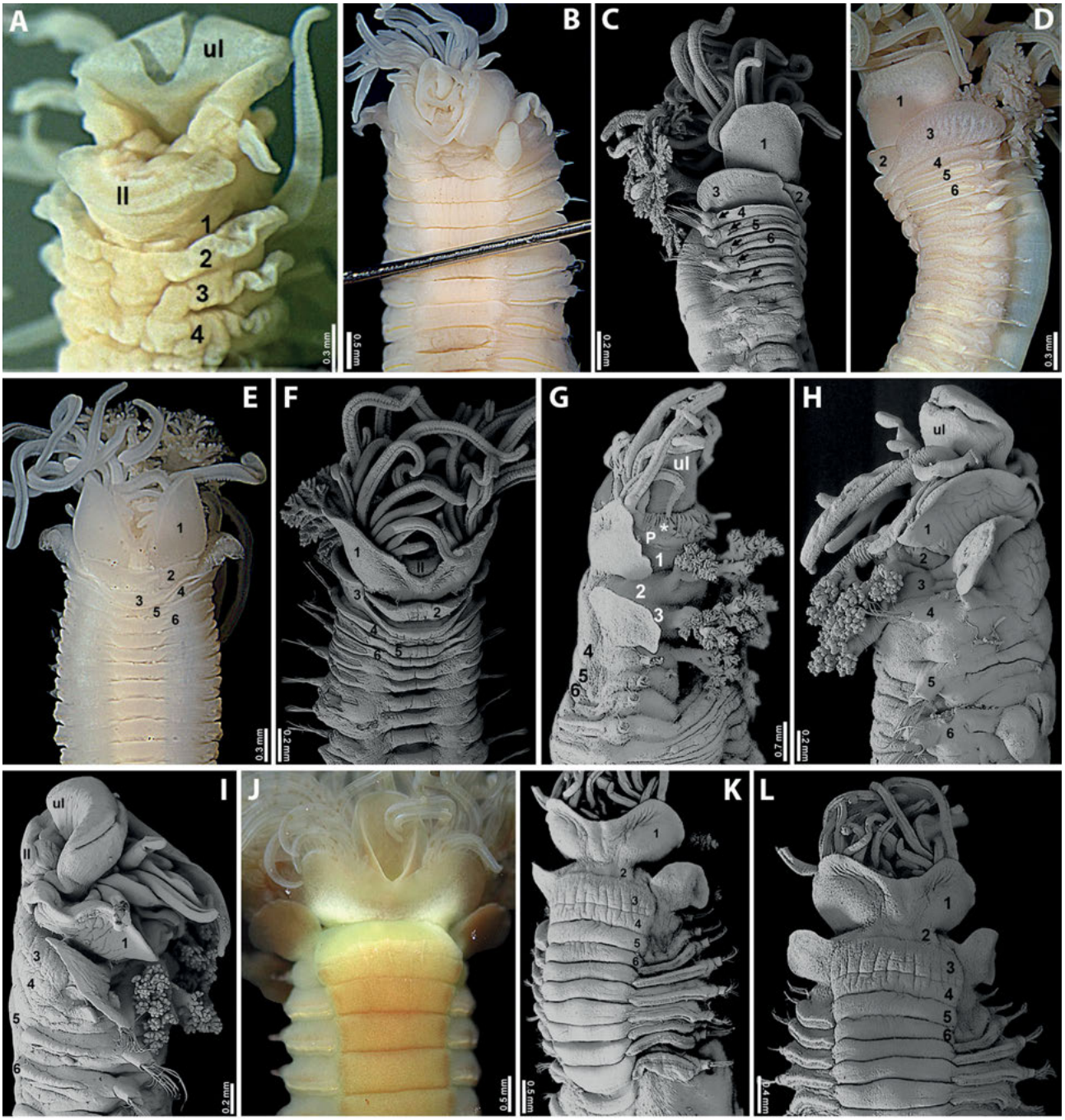


Fig. 7.7.3.8: Anterior ends: A, *Euthelepus serratus*, ventrolateral view; B, *Loimia pseudotriloba*, ventral view; C–E, *Pista chloroplokamia*, two lateral views and a ventral view, respectively; F, *Pista kristiani*, ventral view; G, K, L, *Loimia tuberculata*, a lateral and two ventral views under different angles, respectively; H, I, *L. pseudotriloba*, two lateral views; J, *Loimia brasiliensis*, ventral view. Numbers refer to segments; ll, lower lip; P, basal part of prostomium; ul, upper lip.

the same segment, Nogueira et al. (2010, 2013) regarded them as separate structures. Nogueira et al. (2010) defined lobes as structures that cover at least some portion of the preceding segment and crests as structures that arise from the surface of the segment and just protrude beyond the alignment of the segments, although when lobes are reduced to short thickened structures they may be difficult to distinguish from crests. These lobes and crests are

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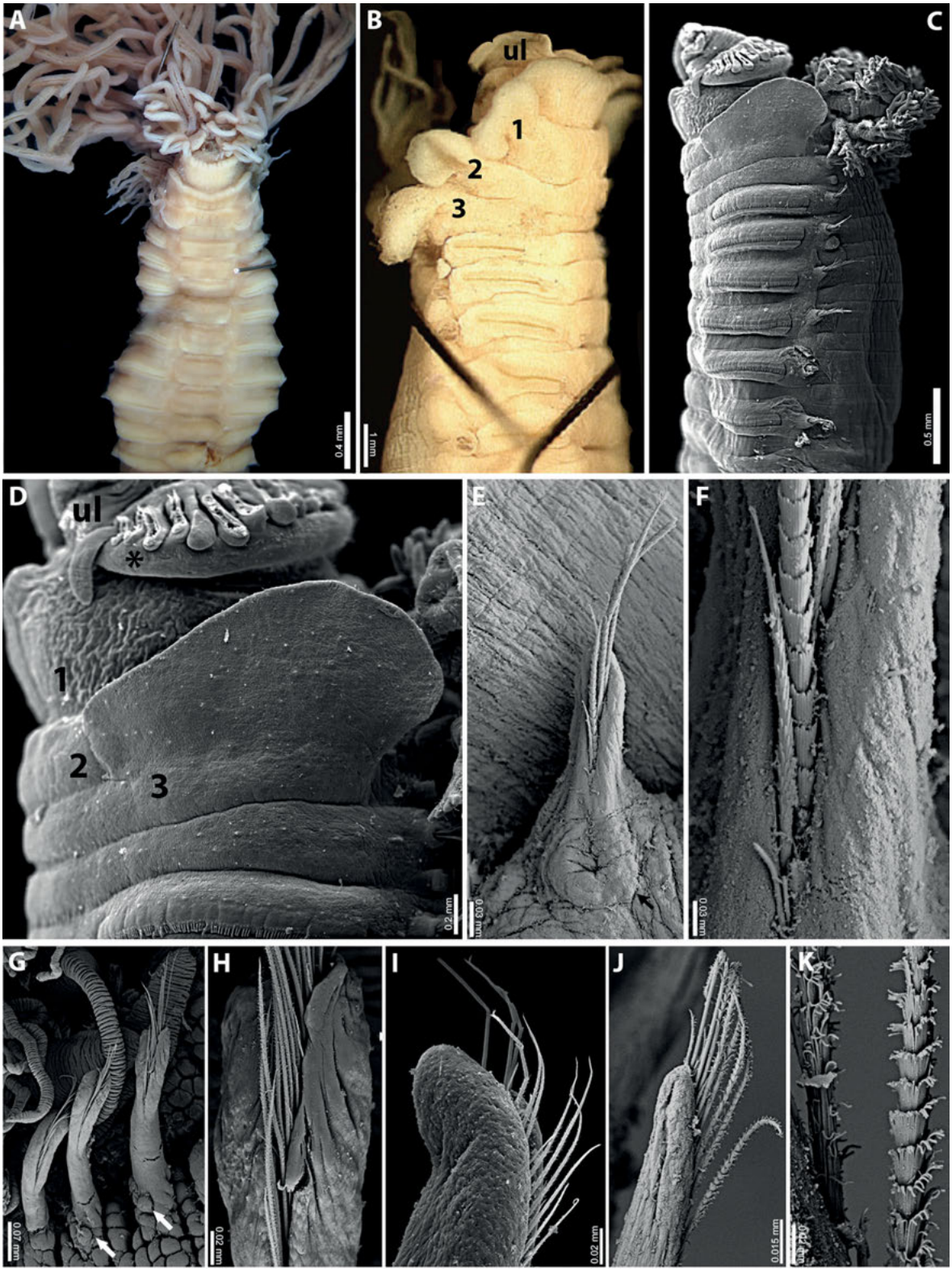


Fig. 7.7.3.9: Anterior ends: A, *Amphitrite cirrata*, ventral view; B, *Scionella japonica*, ventrolateral view; C, D, *Lanicola hutchingsae*, lateral views. Notochaetae: E, F, *Polycirrus* sp., anterior parapodium; G, H, *Amaeana occidentalis*, notopodia of segments 3 to 5 and notochaetae of segment 5, respectively, arrows in G point to nephridial papillae; I, *Amaeana brasiliensis*, notopodium, segment 9; J, K, *Amaeana hsiehae*, notochaetae, segment 7. Numbers refer to segments; *, distal part of prostomium; ul, upper lip.

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mainly restricted to the one to four anterior segments, and their morphology needs to be precisely documented and illustrated for taxonomic purposes.

Segment 1 is reduced in trichobranchids and conspicuous only ventrally. In *Trichobranchus* (Fig. 7.7.3.1B; 2E, F) and *Octobranchus* Marion & Bobretzky, 1875, segment 1 terminates dorsolaterally, not continuing dorsally and not forming a complete ring around the body, whereas in *Terebellides* it is more developed ventrally but does continue dorsally, although much shorter than segment 2 (Fig. 7.7.3.2H). *Trichobranchus* also has a large eversible ventral process on segment 1, which when retracted lies between segments 1 and 2, and segment 1 has a pair of lobes inserted laterally (Fig. 7.7.3.2E, F), which disappear when the ventral process is everted, as they are part of the same structure (Nogueira 2008). Previously, specimens were identified as belonging to the genus *Trichobranchus* when this eversible process was retracted, and as *Artacamella* Hartman, 1955, when the process was everted. Hartman (1955) placed *Artacamella* in the subfamily Artacaminea within Terebellidae *sensu lato*. Later, both Holthe (1977) and Hutchings (1977) independently suggested that *Artacamella* should be placed in Trichobranchidae, as this expanded structure was fully retractable, different from the lower lip of *Artacama*, and the structure of the thoracic neurochaetae was similar to those of trichobranchids. Garraffoni and Lana (2004) subsequently synonymized *Artacamella* with *Trichobranchus* based on a phylogenetic analysis. Trichobranchids typically have lobes on anterior segments forming low collars covering the posterior margin of the preceding segment, extending until segments 7 to 10. These lobes may be only ventral, terminating laterally (Figs. 7.7.3.1B, 7.7.3.2H), or extend all around, completely encircling the body (Fig. 7.7.3.2E, F).

Among the remaining Terebellidae *sensu lato*, lobes of any nature are completely absent in polycirrids, but a crest on segment 3 is frequently present, at least ventrally, and crests on some other anterior segments can also be found (Figs. 7.7.3.1E, F, 7.7.3.2B, I, 7.7.3.3C–F, H, J, L, 7.7.3.4A). Telothelepodids have crests on the anterior margins of all anterior segments until around segment 6 or more posteriorly, which frequently protrude laterally on first segments, as low and thick lobes (Figs. 7.7.3.4F–K, 7.7.3.5A, B, D, H, I). Among thelepodids, lobes are only present in members of *Euthelepus* (Figs. 7.7.3.6A, B, 7.7.3.8A) and *Pseudostreblosoma brevitentaculatum* (Fig. 7.7.3.10E), whereas crests are widespread in this family, frequently at least ventrally on segment 2 (Fig. 7.7.3.6A, B, F–H, J, K). In Terebellidae *sensu stricto*, lobes and crests are widespread and frequently are diagnostic for the genera (Figs. 7.7.3.7A–D, F–I, K–M, 7.7.3.8B–L, 7.7.3.9A–D).

Parapodia: notopodia and notochaetae. Information regarding the morphology of notochaetae and neurochaetae has recently been considerably expanded, as species are increasingly being examined under scanning electron microscopy (SEM), which has revealed previously unseen structures and considerably expanded our interpretations of chaetal morphology.

Some of the most important taxonomic characters of Terebelliformia are related to the notopodia and associated chaetae. The segment on which the notopodia begin is an important generic character and fixed in many genera, as well as the number of pairs of notopodia, which may be a generic or species-specific character; in addition, the type of notochaetae is a critically important generic and species character. Typically, the notopodia are all of the same size and vertically aligned, although the first pairs are usually aligned more dorsally than subsequent notopodia, and first ones may be shorter and/or with shorter notochaetae. Notopodia may be elongate, with prechaetal and postchaetal lobes, as in polycirrids and thelepodids (Figs. 7.7.3.1A, D, I, 7.7.3.2I–N, 7.7.3.3A–C, H, J, L, 7.7.3.4A, 7.7.3.6A–D, H–J, 7.7.3.9E–J, 7.7.3.10E–K), or more compact, conical, barely protruding from the body wall, as in the members of the other families of Terebellidae *sensu lato* (Figs. 7.7.3.1B, C, H, J–L, 7.7.3.2A, E, F, H, 7.7.3.4F–H, 7.7.3.5D–I, 7.7.3.7D, 7.7.3.8C, D, F–I, K, L, 7.7.3.9C, 7.7.3.10I, 7.7.3.11G, I, L, 7.7.3.13G, H).

Notochaetae are arranged in two rows in all Terebelliformia, the posterior row typically the longest (Figs. 7.7.3.9E, G, I, J, 7.7.3.10A, C, E–J, 7.7.3.11A, D, E, G–I, L, N). Chaetae may be similar throughout or vary along the body, as in several abranchiate terebellids (Figs. 7.7.3.11D–H, 7.7.3.13G, H), although for many species the structure of the notochaetae has not been examined in detail along the entire body. Glasby and Hutchings (2014), in their revision of *Polycirrus*, described the chaetae of anterior and posterior rows of anterior and posterior parapodia for all species and found that it was a useful specific character, as also did Garraffoni and Lana (2008).

Notochaetae in Terebelliformia have been traditionally recorded as either distally smooth or distally serrated (e.g., Fauchald 1977, Hutchings and Glasby 1986a, b, c, 1987, 1988, 1990, McHugh 1995, Garraffoni and Lana 2008). However, Glasby et al. (2004) suggested that serrated notochaetae consist of more than one type and this has been confirmed by SEM examination. Nogueira et al. (2010) proposed a new classification, those with tips distally winged or distally serrated, and each of these then being subdivided.

Distally winged notochaetae have limbation extending to the tips of the chaetae, except for a few taxa in

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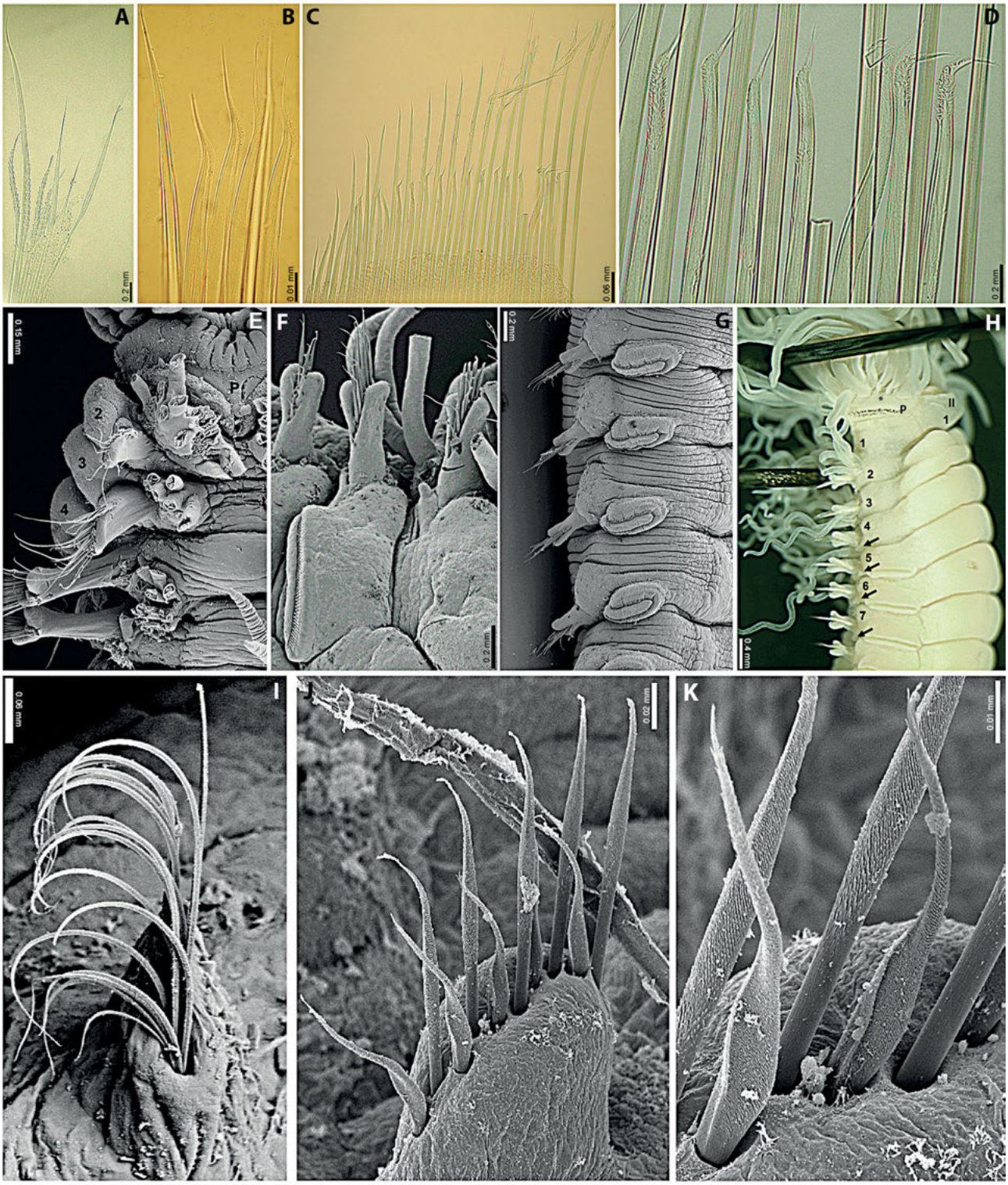


Fig. 7.7.3.10: Notopodia and notochaetae: A, *Polycirrus bicrinalis*, segment 13; B, *Parathelepus collaris*, segment 5; C, D, *Rhinothelepus lobatus*, segment 5; E, *Pseudostreblosoma brevitentaculatum*, anteriormost notopodia; F–H, *Streblosoma porchatensis*, segments 4 to 6, midbody parapodia and anterior end, ventrolateral view, respectively, arrows in H point to papillae; I, *Terebellides anguicomus*, segment 4; J, K, *Streblosoma oligobranchiatum*, general and close-up on notochaetae from anterior row. Numbers refer to segments; *, distal part of prostomium; P, prostomium; ll, lower lip.

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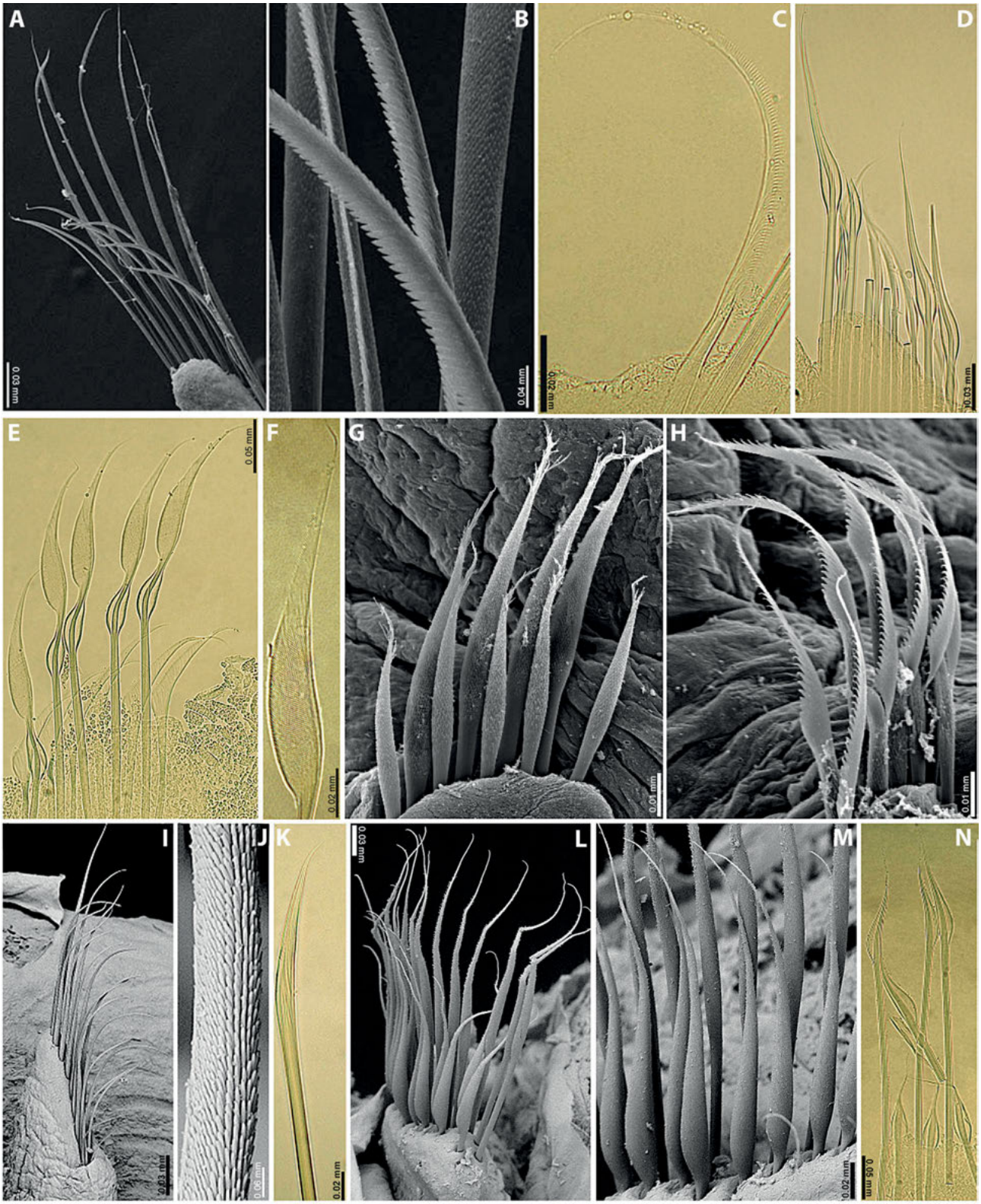


Fig. 7.7.3.11: Notochaetae: A, B, *Pseudostreblosoma brevitentaculatum*, midbody parapodium; C, *Euthelepus serratus*, notochaeta from anterior row, segment 35; D–F, *Spinoshpaera barega*, segments 6 and 20 and tip of *Spinosphaera*-chaeta, respectively; G, H, *Articulatia aberrans*, segments 6 and 11, respectively; I, J, *Eupolymnia koorangia*, segment 8 and close-up of limbation, respectively; K, *Laphania boecki*, notochaeta from posterior row, segment 7; L, M, *Artacama proboscidea*, segment 6 and close-up of chaetae of anterior row; N, *Leaena ebranchiata*, segment 6.

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which the limbation terminates subdistally and the rest of the chaeta has a smooth alimbate tip. Whereas species of *Proclea* Saint-Joseph, 1894, have hirsute limbation, the rest have distally winged capillaries with smooth to striated limbation under light microscopy, but appearing uniformly minutely denticulate along the entire length of the limbation when examined under SEM (Figs. 7.7.3.10I–K, 7.7.3.11B, G, I, J, L, M). These chaetae are divided into subtypes depending on the length and width of the limbation, and those from the posterior row also by the point at which the limbation begins, as chaetae from the anterior tier, have limbation present from the base or near it.

Distally serrated notochaetae are characterized by having teeth along the cutting edge of the blade. These are further subdivided depending on the presence or absence of a limbate area below the serrated blade, the angle between the serrated blade and the shaft, and whether or not there are some differentiated areas below or at the serrated blade.

All trichobranchids have distally narrowly winged capillary notochaetae in both rows (Fig. 7.7.3.10I), and genera differ in the number of pairs of notopodia and the segment on which they begin.

Only four genera of polycirrids possess notopodia: *Amaeana* Hartman, 1959, *Enoplobranchus* Verrill, 1879, *Lysilla* Malmgren, 1866, and *Polycirrus*, and in all of them, the notopodia begin on segment 3. Notopodia are typically restricted to the anterior part of the body, except for *Enoplobranchus* and some species of *Polycirrus*, in which they extend more posteriorly, sometimes almost to the pygidium. Notochaetae are either distally winged, with limbation extending for most of the length, or pinnate (Fig. 7.7.3.9E–K). This latter type is unique to this family and is characterized by the chaetae having circular to oblique transverse bands of spines all along their extension (Fig. 7.7.3.9E, F, J, K). Distally winged notochaetae may be acicular, with remarkably narrow wings, inconspicuous under light microscopy, but visible under SEM as fine denticulation; this occurs mostly in some species of *Amaeana* and *Lysilla*. Notochaetae with broader wings of variable width occur in most species of *Polycirrus*. Two types of notochaetae may occur in the same podia, one in each row, or only a single type is present throughout, and these characters are critically important in distinguishing species (Nogueira et al. 2010, 2015a, b).

Telothelepodids also have notopodia typically beginning on segment 3, although one recently found and described Brazilian species, *Parathelepus praecox* Nogueira, Carrerette, Hutchings & Fitzhugh, 2018, has notopodia beginning from segment 2 (Nogueira et al. 2018). Only narrowly winged chaetae are found in this family, but most species have the unique bayonet-like chaeta, which has sinuous limbation on one side only, terminating in a bulbous hirsute 'head', followed by an alimbate tip (Fig. 7.7.3.10B–D). The bayonet-like chaetae are only present on the anterior row and usually only on anterior thoracic segments, being replaced by regular narrowly winged chaetae from the midthorax until the termination of notopodia.

Notopodia of thelepodids begin either on segment 2 or 3 and continue for a variable number of segments, in some cases almost to the pygidium. The notochaetae are mainly narrowly winged in both rows, with the extension of limbation varying between genera. Some species of *Streblosoma* Sars, 1872 have notochaetae, especially those in the anterior row, with limbations as broad as the width of the shaft on either side, or broader, and under SEM appear lanceolate with twisted tips (Fig. 7.7.3.10J, K). Alimbate and serrated notochaetae are present in *Pseudostreblosoma* Hutchings & Murray, 1984 (Fig. 7.7.3.11B) and some species of *Euthelepus* McIntosh, 1885 (Fig. 7.7.3.11C), usually on anterior row only and frequently only on posterior notopodia (Nogueira and Alves 2006, Nogueira et al. 2010, 2013, Hutchings et al. 2015).

Terebellids usually have 17 pairs of notopodia, beginning on segment 4, although some have them from segments 2 to 5. The exceptions include *Varanusia quasimodo* Nogueira, Hutchings & Carrerette, 2015c, which has 9 pairs only, species of *Leaena* Malmgren, 1866, which have 10 to 11 pairs of notopodia, and some species of *Terebella*, which may have them continuing almost to the pygidium. The notochaetae exhibit a tremendous variation in distally winged and distally serrated chaetae, and Nogueira et al. (2010) proposed three categories of distally winged and four types of distally serrated chaetae.

Distally winged chaetae include narrowly winged chaetae (Figs. 7.7.3.11G, I–M, 7.7.3.12A, C, E), broadly winged chaetae (Figs. 7.7.3.11L–N, 7.7.3.12B), and hirsute chaetae (Fig. 7.7.3.12D, F). These wings appear as hyaline and uniform structures under the compound microscope but are minutely denticulate under SEM, and these denticulations differ from those occurring on serrated chaetae, as they occur in several rows, all around the chaeta (Fig. 7.7.3.11G, I–M). The limbation may be of even width around the blade or wider on one side, in which case they appear geniculate at the base of the limbation wing (Figs. 7.7.3.11L–N, 7.7.3.12C, E). Narrowly winged chaetae are the most common type, with a long narrow limbation extending to the tip (Figs. 7.7.3.11G, I–M, 7.7.3.12A, C, E). Broadly winged chaetae resemble narrowly winged chaetae, but with a limbation that is at least the same width as the shaft on one or both sides [Figs. 7.7.3.11L, M (anterior row), N (both rows), 7.7.3.12B] (for more details,

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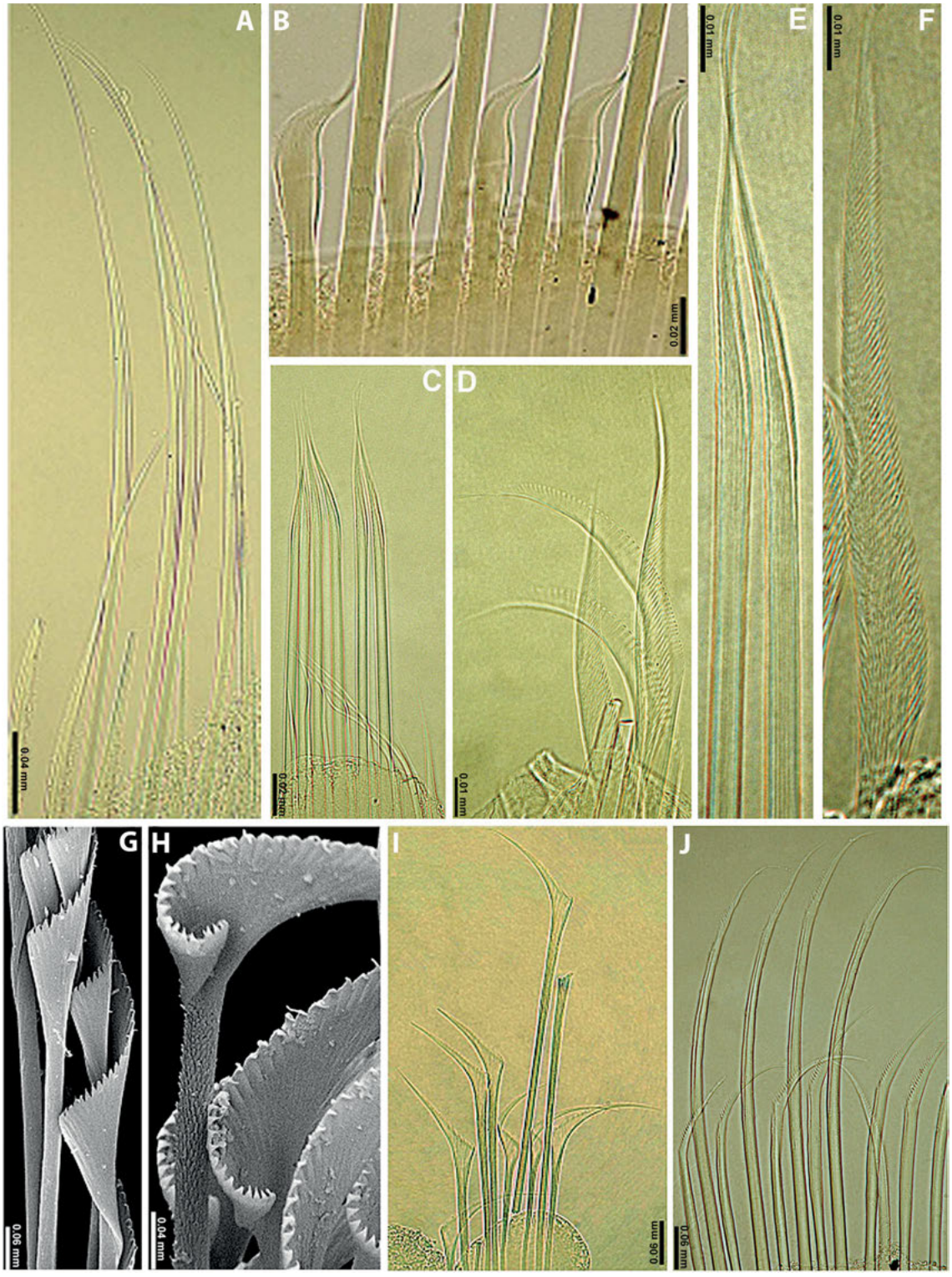


Fig. 7.7.3.12: Notochaetae: A, *Streblosoma acymatum*, segment 26; B, *Laphania boecki*, notochaetae from anterior row, segment 7; C–F, *Proclea malmgreni*, segments 5 and 13, notochaetae from posterior row of segment 5 and notochaeta from posterior row of segment 13; G, H, *Baffinia biseriata*, posterior segments; I, *Hutchingsiella cowarrie*, segment 17; J, *Hadrachaeta aspeta*, anterior segment.

see Nogueira et al. 2010, 2013). Hirsute chaetae are only found in species of *Proclea* Saint-Joseph, 1894, and they are broadly winged, sometimes geniculate, with the limbation strongly hirsute, resembling distally serrated chaetae but with hairs all around the limbation (Fig. 7.7.3.12D, F).

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Distally serrate chaetae consist of four types (Nogueira et al. 2010). Alimbate and serrated chaetae, which have an alimbate shaft and long serrated blade, which may be aligned with the shaft [Figs. 7.7.3.12D, 7.7.3.13G, H (posterior row)], or at an angle to it [Figs. 7.7.3.11E (anterior row), 7.7.3.12G–I]. Most commonly, this type of chaetae is present in the anterior row of posterior notopodia but occurs also in the posterior row of some species and in both rows in posterior notopodia of other species, such as *Hutchingsiella cowarrie* (Hutchings, 1997b) (with Londoño-Mesa 2003, erecting the genus) (Fig. 7.7.3.12I) and *Baffinia biseriata* Hutchings & Glasby, 1988 (Fig. 7.7.3.12G, H); in some parapodia, chaetae have a remarkably narrow wing on shaft, visible under SEM as minute denticulations (Fig. 7.7.3.12H), but as those denticulations are not visible under compound microscopy, we considered them as typical alimbate and serrated chaetae, as also occurs in *Terebella lapidaria* Linnaeus, 1767 (Fig. 7.7.3.13C, D). In contrast, in species of *Phisidia* Saint-Joseph, 1894 (Fig. 7.7.3.13G, H) and *Morgana* Nogueira & Amaral, 2001, they occur from the anterior notopodia onward. McHugh (1995) named these chaetae as 'saw-like chaetae' and suggested that they were a synapomorphic character for the genus *Proclea*, where they occur in the anterior row of

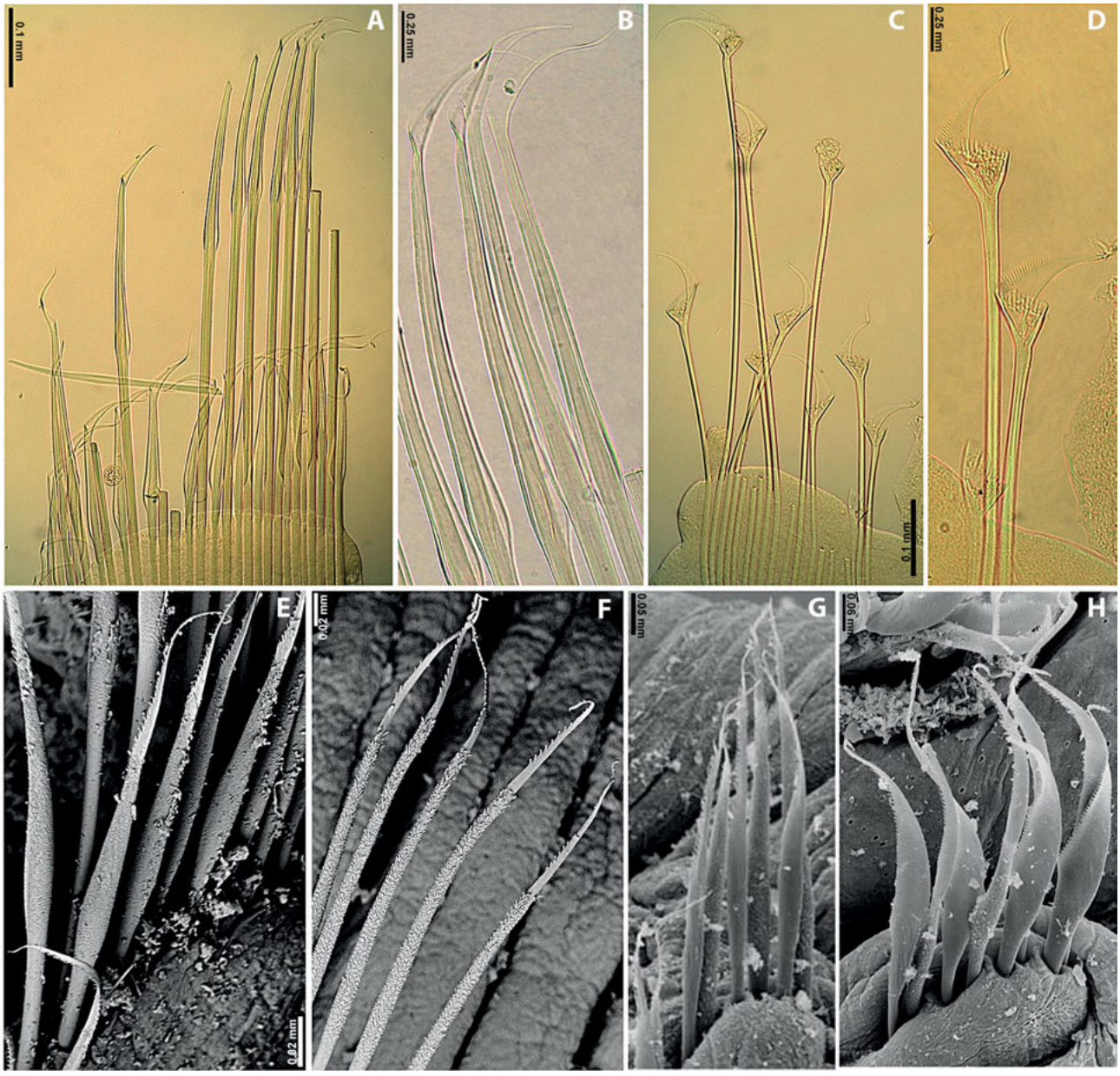


Fig. 7.7.3.13: Notochaetae: A–D, *Terebella lapidaria*, segment 17, notochaetae from posterior row of segment 17, segment 46, and notochaetae from posterior row of segment 46; E, *Longicarpus modestus*, notochaetae from anterior row of segment 7; F, *Terebella pappus*, notochaetae from posterior row of posterior segment; G, H, *Phisidia rubra*, segments 6 and 15.

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posterior notopodia (Fig. 7.7.3.12D), but they occur also in several other genera of Terebellidae *sensu stricto*.

The second type is the limbate and serrated chaeta, which has a limbate shaft with the limbation terminating subdistally, followed by a serrated blade, aligned with the shaft [Figs. 7.7.3.11H (posterior row), 7.7.3.12J (posterior row), 7.7.3.13E, F, H (anterior row)] or at an angle [Figs. 7.7.3.12J (anterior row), 7.7.3.13A, B]. The limbation may be narrow or wide, and restricted to a short swelling, or occupy a relatively large extension of the shaft (Figs. 7.7.3.11H, 7.7.3.12J, 7.7.3.13A, B, E, F, H). The blade may be long or short in relation to the length of the shaft. In those cases where the blade is at an angle to the shaft, they have previously been referred to as 'flail-tipped capillaries' (Hutchings and Glasby 1988); in cases where the teeth are minute and only visible under SEM or oil immersion, they have been referred to as 'finely denticulate capillaries' (Day 1967, Hutchings and Glasby 1988), but Nogueira et al. (2010) suggested a gradation and they all should be referred to as 'limbated and serrated chaetae'.

The third type is the deep-cut chaeta, which has a limbate shaft with a broad limbation and a serrated blade articulated with the shaft by a deep cut at the base of the blade (Fig. 7.7.3.11H). These chaetae are restricted to the anterior row of posterior notopodia of *Articulatia aberrans* Nogueira, Hutchings & Amaral, 2003, and this represents a possible synapomorphy for this currently monotypic genus.

The fourth type, which is referred to as '*Spinosphaera*-chaetae', has a shaft with a broad limbation at midlength followed by a hirsute process and a finely serrated blade [Fig. 7.7.3.11E, F (posterior row)]. They are present in the posterior row of some species of *Spinosphaera* (see Londoño-Mesa 2003, Nogueira and Hutchings 2007). If this type of chaetae is shown to represent a synapomorphy for that genus, some species currently assigned to *Spinosphaera* will need to be allocated to another genus, as they lack these chaetae and only have 'limbate and serrated chaetae'.

Arranooba Hutchings & Glasby, 1988 has some capillary chaetae, which differ from those observed in all other taxa of Terebellidae *sensu lato*. Those chaetae are restricted to segment 15, and they are alimbate and flattened, with smooth margins inwardly curved to form a quill-shaped structure (see Hutchings and Glasby 1988, fig 3).

In the taxa that have a transition in the types of notochaetae present in one or both rows along the body, this is often abrupt and occurs at segment 11 or near it (Figs. 7.7.3.11D–H, 7.7.3.12C–F, 7.7.3.13A–D), whereas, in others, such as species of *Phisidia* Saint-Joseph, 1894, it occurs gradually with those on anterior segments with limbation terminating subdistally, followed by a blade with fine spines to the tip, which gradually become thicker over several segments until around segment 11, where a well-formed serrated blade is present (Fig. 7.7.3.13G, H).

Parapodia: neuropodia and neurochaetae. These characters are important for diagnosing families and genera and include the segment on which the neuropodia first occur, their morphology, and the arrangement and morphology of their uncini.

Trichobranchidae have neuropodia as sessile ridges on those segments with notopodia and raised, rounded to leaf-shaped pinnules with uncini on the distal margin, on segments lacking notopodia (Figs. 7.7.3.1B, C, 7.7.3.2F, 7.7.3.14A–E). Abdominal uncini are attached by ligaments to the internal skeletal shafts of the neuropodia (Fig. 7.7.3.16E, H, J, L) and these skeletal shafts have been referred to as ligaments by some authors (Hilbig 2000) or regarded as part of the uncini. Nogueira et al. (2010) showed that these shafts are part of the podia and not part of the uncini.

In Polycirridae, neuropodia are absent in *Hauchiella*, *Enoplobranchus*, and *Lysilla* but are present in the other genera. The neuropodia may be sessile and restricted to posterior segments, as in *Amaeana*, or form raised pinnules, as in *Biremis*, where they are bilobed (Polloni et al. 1973), and on the abdominal chaetigers of *Polycirrus* (Figs. 7.7.3.1A, 7.7.3.16F, G). Nogueira et al. (2015a) observed considerable variation on the segment on which neuropodia began among species of *Polycirrus*, and four patterns were identified: neuropodia beginning from anterior segments with notopodia, on the last first to three segments with notopodia, immediately after notopodia terminate, or only present on posterior segments. Although abdominal neuropodia of species of *Polycirrus* are raised pinnules, with internal skeletal shafts, they are always sessile ridges when notopodia are present (Figs. 7.7.3.1A, 7.7.3.9E, 7.7.3.16F, G).

Telothelepodidae have the neuropodia of biramous segments as sessile ridges (Figs. 7.7.3.1H, 7.7.3.4G, 7.7.3.14F, G), and after the termination of the notopodia, they become slightly elevated but still much lower than in the other families of this group, except for some terebellids. Despite being short, abdominal neuropodia of telothelepodids have internal skeletal shafts.

Thelepodidae usually have neuropodia of biramous segments as fleshy ridges, which then become pinnules once the notopodia terminate (Figs. 7.7.3.6A, B, D, F–H, J, K, 7.7.3.10F–H, 7.7.3.14I–L). Internal skeletal shafts are present after the termination of notopodia.

Terebellidae *sensu stricto* have neuropodia as low ridges on biramous segments, which may be slightly

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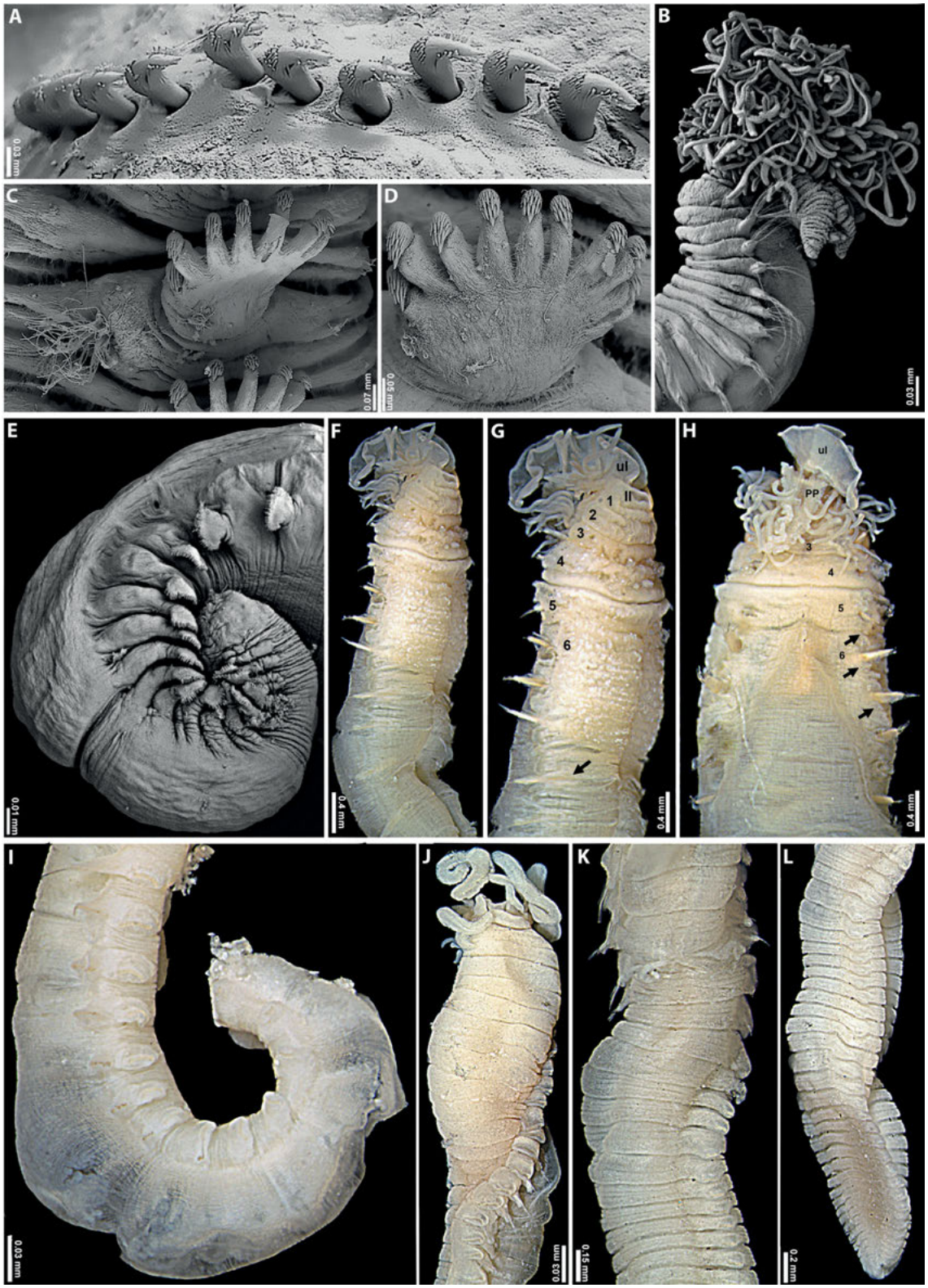


Fig. 7.7.3.14: Neuropodia and neurochaetae: A, C, D, *Trichobranchus hirsutus*, segment 6 and two views of a neuropodium of segment 21; B, E, *Terebellides akares*, lateral views of the anterior and posterior ends; F–H, *Rhinothelepus buku*, two ventrolateral and one dorsal views, arrow in G points to first neuropodium and arrows in H point to papillae; I, *Euthelepus aserrula*, lateral view of posterior end of fragment; J–L, *Thelepus paiderotus*, ventral views of anterior end, midbody at termination of notopodia and posterior end. Numbers refer to segments; ll, lower lip; PP, prostomial process; ul, upper lip.

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fleshy but not as prominent as seen in Thelepodidae (Figs. 7.7.3.7D, F, H, K–M, 7.7.3.8B–L, 7.7.3.9A–D, 7.7.3.15B–D). Once the notopodia terminate, the neuropodia become raised pinnules with internal chitinous shafts in most species (Fig. 7.7.3.15A–C, E), but in species where the notopodia continue almost to the pygidium, and also in a few others with a restricted number of pairs of notopodia, the neuropodia are similar throughout, as sessile ridges, decreasing in size posteriorly (Fig. 7.7.3.15F), and they bear uncini in double rows (see below) until near the pygidium. Species with neuropodia as raised pinnules often have a dorsal papillae on neuropodia, and in *Artacama*, there are distally pointed structures or large 'ear-shaped' lobes (Fig. 7.7.3.15A, B).

All these families, except for the genus *Amaeana* in Polycirridae, have neurochaetae as uncini. *Amaeana* has short peg- or spine-like chaeta, present in low numbers, which are diagnostic for the species (Nogueira et al. 2015b) (Fig. 7.7.3.15G–J).

Various terminologies have been used for describing the structure of the uncini (see Discussion and fig. 37 in Nogueira et al. 2010, which illustrate the various parts, and this terminology is used in this paper). In addition to the morphology of each part of the uncinus, at least two morphometric measurements are important, the height (He) of the uncinus measured from the tip of the crest to the lowest part of the base, including the heel (handles excluded), and the length (L), measured from the anterior tip of the uncinus to the posterior tip.

The uncini of Polycirridae are classified into two types, 'type 1 uncini' *sensu* Glasby and Glasby (2006) and 'type 2 uncini' *sensu* Glasby and Glasby (2006). 'Type 1' uncini are shorter than 'type 2' and are characterized by being longer than high, with a flat base, a short triangular heel directed posteriorly, a short back, and a reduced dorsal button, which is situated closer to the base of the main fang than to the tip of the elongated prow (Fig. 7.7.3.16A–C, E–G). 'Type 2' uncini are about as long as high and have a flat base, frequently oblique, an elongated heel directed downward, an elongate back, a reduced or inconspicuous dorsal button, situated at the base of the main fang, and an elongate prow (Fig. 7.7.3.16D, H–J). Usually, the type of uncini present is consistent throughout the body, but several species of *Polycirrus* have a transition of the types of uncini from biramous chaetigers to uniramous segments after the notopodia terminate (Fig. 7.7.3.16F, G, I); a few species of *Polycirrus* have uncini that look somewhat intermediary between types 1 and 2 (Glasby and Hutchings 2014, Nogueira et al. 2015a).

Telothelepodidae have uncini either as high as long or higher than longer, in both cases with a wide and slightly curved base, a short triangular heel, and a crest of two to three rows of secondary teeth above the main fang (Fig. 7.7.3.16K, M). The only exceptions are *Parathelepus ocellatus* (Hutchings, 1977) and *Mesopothelepus macrothoracicus* (Mohammad, 1980), which have longer than high uncini, with a narrow base (Fig. 7.7.3.16L). A short dorsal button is present nearly at midlength of the uncinus, which is closer to the tip of the prow than to the base of the main fang (Fig. 7.7.3.16K–M). At least in *Rhinothelepus occabus* Hutchings, 1990, the dorsal button is internal and not protruding through the integument, so not visible under SEM, but whether this is consistent for other members of this family in not known, as this is the only species of Telothelepodidae examined under SEM (Nogueira et al. 2010).

Thelepodidae have uncini that are typically longer than high, with the lower margins of the base curved and rounded, strongly convex. The prow is reduced to a short knob or absent, and the main fang has a few transverse rows of secondary teeth, the second row usually with much smaller teeth than the basal row (Fig. 7.7.3.17B, D). The dorsal button is present on the anterior margin of the upper surface of the uncinial base or close to it; under SEM, this appears to be a circular patch of densely packed bristles (Figs. 7.7.3.17BD, 7.7.3.18J, K). However, in *Pseudostreblosoma* (Fig. 7.7.3.17A) and several species of *Streblosoma* Sars, 1872, the uncini are similar to those of telothelepodids, about as high as long, with slightly curved base and dorsal button distant from the anterior margin of the uncini, leaving a conspicuous prow.

In Thelepodidae, the uncini are typically arranged in single straight rows, but there some species in which they occur in curved, C- or U-shaped rows (Figs. 7.7.3.1D, 7.7.3.17C), or even loops, from the midbody onward (Day 1955, Hutchings 1990, Hutchings and Glasby 1990, Hutchings and Smith 1997, Nogueira et al. 2004, Hutchings et al. 2015).

Terebellidae *sensu stricto* exhibit the greatest variation in the structure of uncini and these may also vary along the body. Typically, the uncini are higher than long and have the dorsal button distant from the anterior margin of the uncinus, in most species on the middle or posterior third of the upper surface of the base, closer to the base of main fang (Fig. 7.7.3.17E–L, N–P). A heel is present, but its extension and angle of orientation are highly variable. Above the main fang, a variable number of secondary teeth arranged in transverse rows are present, except in species of *Loimia*, which have the teeth arranged in a single vertical row (Figs. 7.7.3.17E–L, N–P, 7.7.3.18A, B, D–I).

Anterior uncini can be long-handled (Fig. 7.7.3.17H, I, N, O) or short-handled (Fig. 7.7.3.17E–G, J–L), depending on the presence of a handle originating from the heel,

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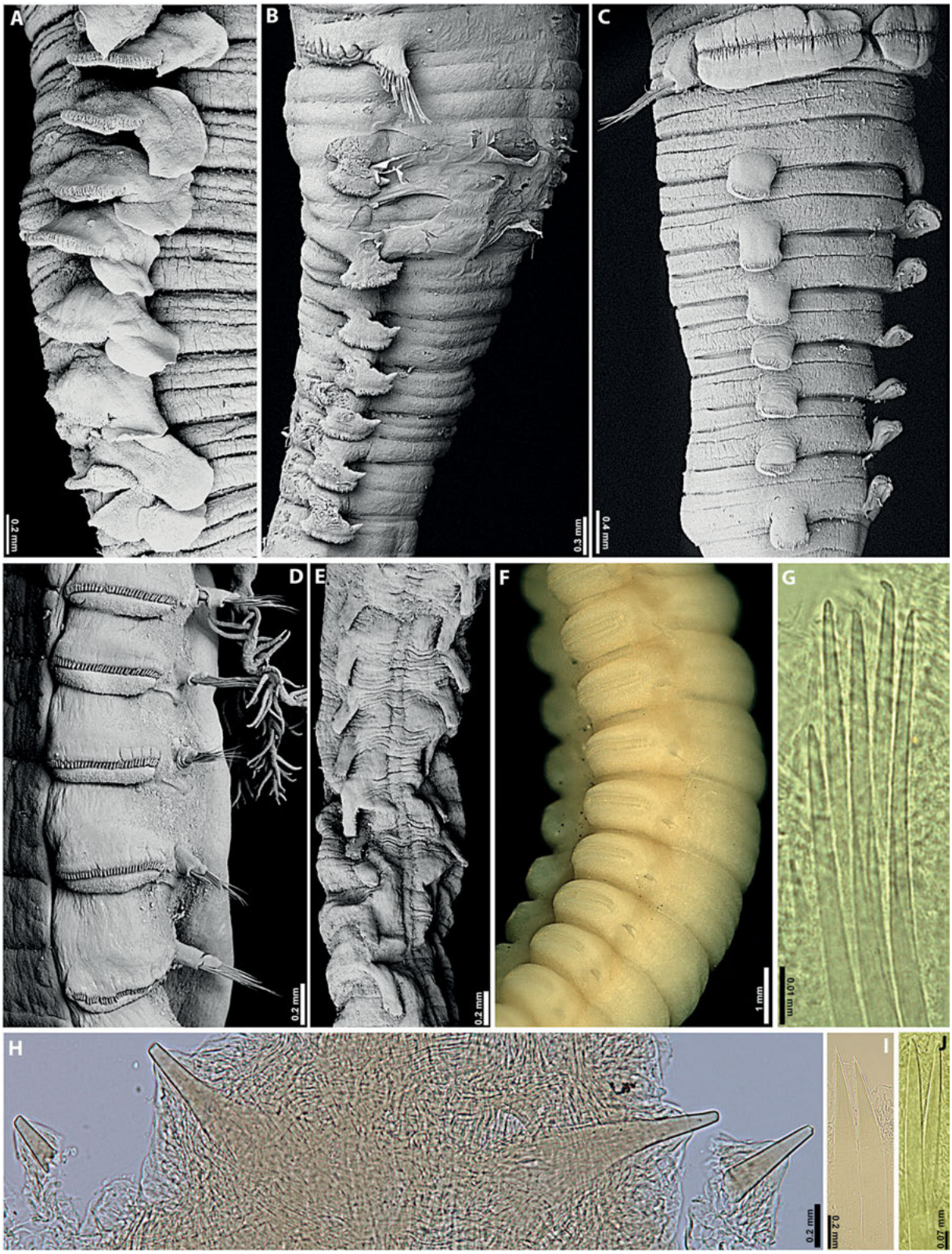


Fig. 7.7.3.15: Neuropodia and neurochaetae: A, *Artacama benedeni*, abdominal neuropodia; B, *Artacama proboscidea*, transition between the thorax and the abdomen, segments 20 to 27; C, *Loimia ingens*, transition between the thorax and the abdomen, segments 20 to 27; D, E, *Amphitrite lobocephala*, thoracic parapodia and abdominal neuropodia; F, *Terebella* cf. *verrilli*, posterior body parapodia; G, *Amaeana breviachaeta*, segment 27; H, *Amaeana crassispinulata*, posterior segments; I, *Amaeana apheles*, posterior segment; J, *Amaeana hsiehae*, segment 24.

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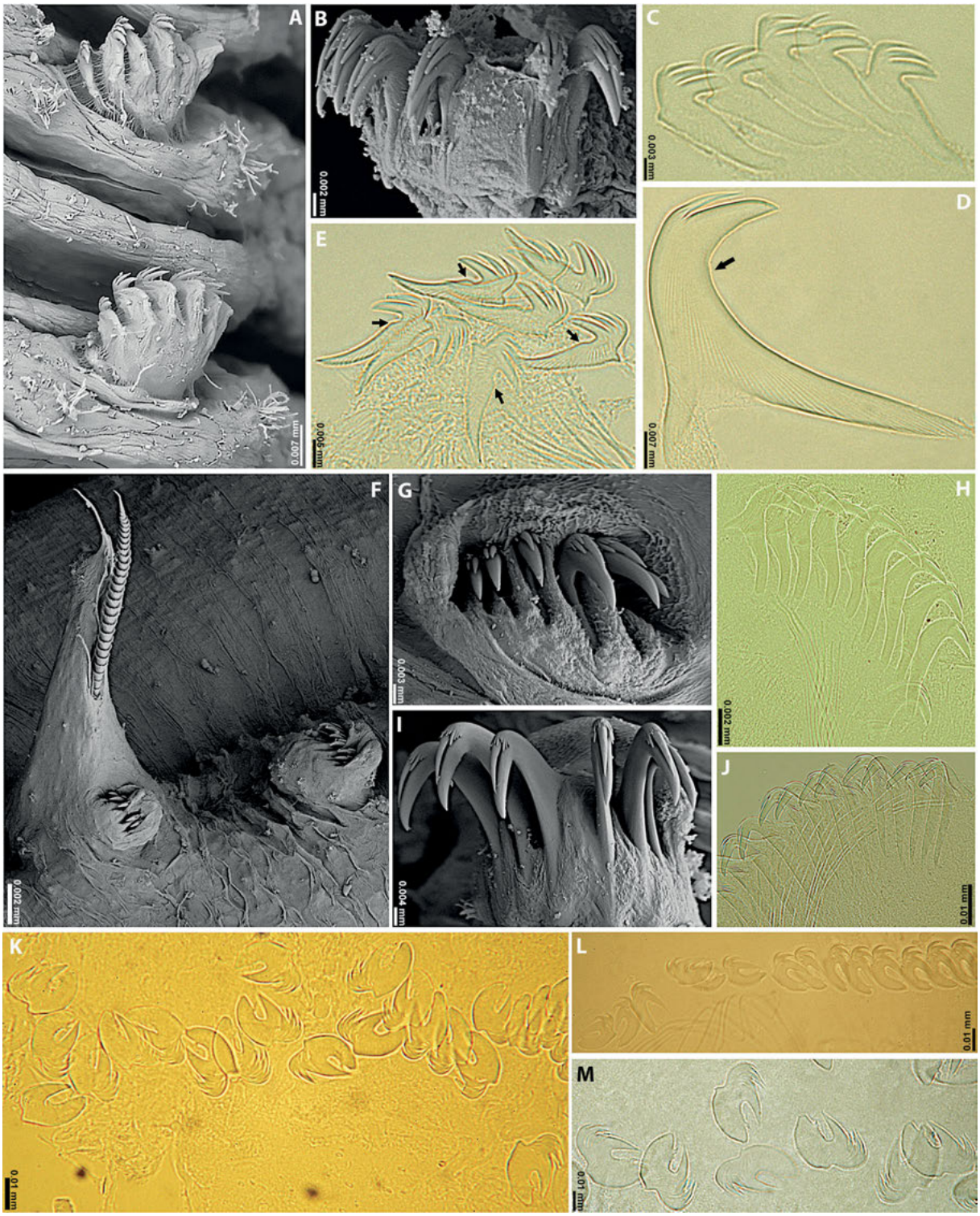


Fig. 7.7.3.16: Neuropodia and neurochaetae: A, *Polycirrus minutus*, abdominal neuropodia; B, *Polycirrus rubrointestinalis*, segment 13; C, E, *Polycirrus bicrinalis*, abdominal uncini, arrows point to dorsal buttons; D, *Polycirrus disjunctus*, abdominal uncinus, arrow points to dorsal button; F–I, *Polycirrus papillatus*, transition between the thorax and the abdomen (segments 13 and 14), segments 11, 18, and 15, respectively; J, *Polycirrus glossochelius*, posterior segment; K, *Parathelepus collaris*, segment 13; L, M, *Mesopothelepus macrothoracicus*, abdominal uncini.

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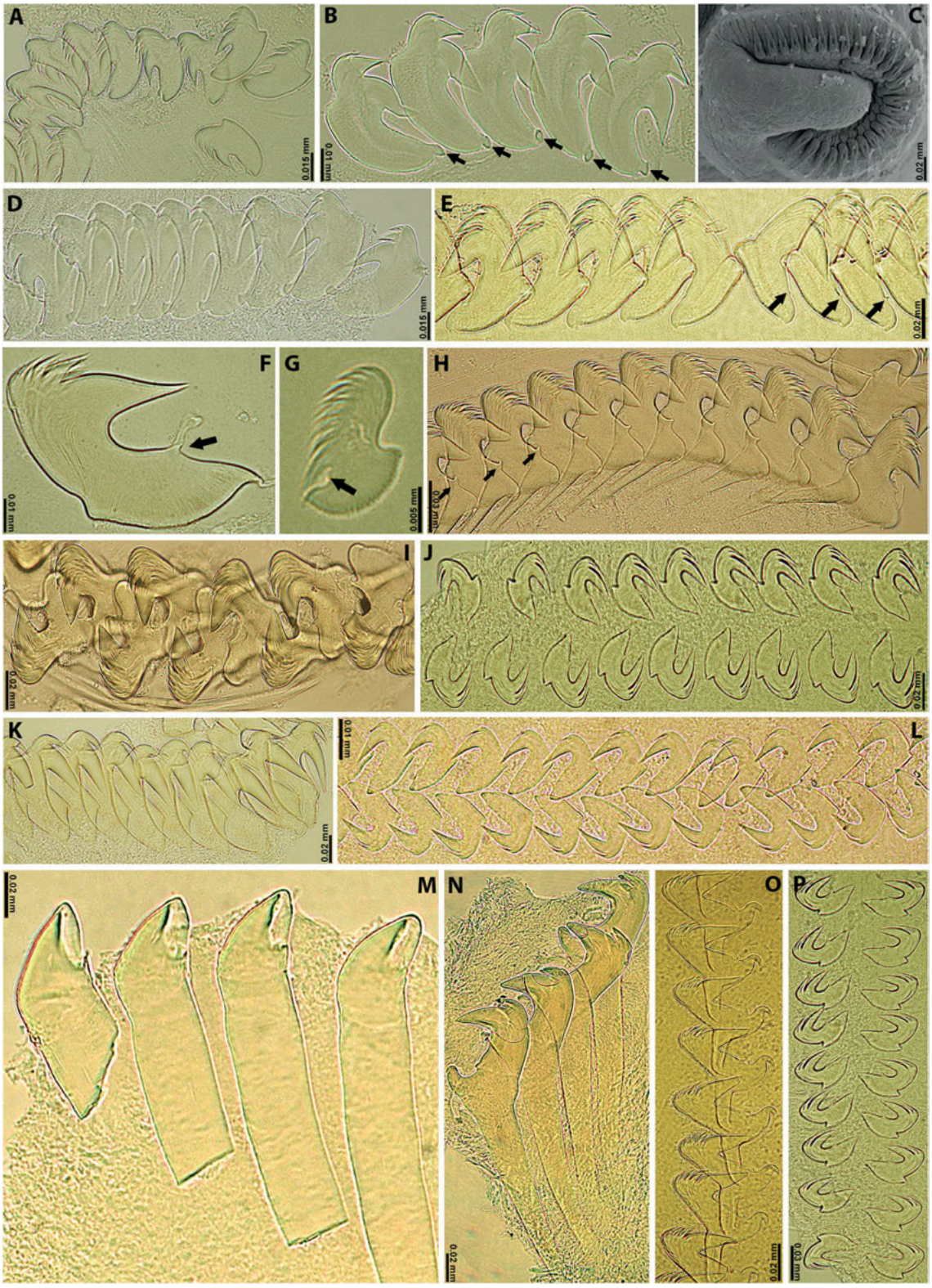


Fig. 7.7.3.17: Neurochaetae: A, *Pseudostreblosoma serratum*, segment 14; B, C, *Streblosoma porchatensis*, posterior uncini and posterior neuropodium; D, *Thelepus cincinnatus*, segment 5; E, *Amphitrite lobocephala*, segment 10; F, *Amphitite cirrata*, thoracic uncinus; G, *Proclea malmgreni*, uncinus, segment 6; H, I, *Pista cristata*, segments 10 and 14; J, *Terebella* cf. *lapidaria*, segment 33; K, *Reteterebella queenslandia*, segment 6; L, M, *Hadrachaeta aspeta*, segments 17 and 8; N, *Betapista dekkerae*, segment 5; O, P, *Longicarpus modestus*, segments 9 and from midbody. Arrows point to dorsal buttons.

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which in some species may be expanded to occupy the entire base of the uncinus. Species with long-handled uncini only have them on anterior neuropodia and they are replaced by short-handled uncini subsequently and the segment on which this replacement occurs is species specific. As already mentioned, the uncini of *Loimia* are unique within the family, as they are pectinate, with teeth arranged in a single row, although Garraffoni and Lana (2009) have shown that, during their early development, they have a main fang with several transverse rows of minute secondary teeth, but this changes to the pectinate structure as the worm matures. Nogueira et al. (2015d) have shown that, in some species of *Loimia*, there is a fringe of bristles at each side of the pectinate row of teeth (Fig. 7.7.3.18B, E).

The main fang is always clearly visible in all genera, including *Loimia* (Figs. 7.7.3.17E–L, N–P, 7.7.3.18A, B, D–I), although in some species of this latter genus the difference in size between the main fang and following teeth is not as marked as in most other species of this family. Uncini from biramous parapodia have a dorsal button as a tuft of elongate bristles surrounding the tip of the main fang, which may be protective (Figs. 7.7.3.17E–L, N–P, 7.7.3.18A, D, G–I). The button is best developed in some taxa with long-handled uncini, and in most species, it is situated midway between the base of main fang and the tip of the prow (Fig. 7.7.3.17F, H, I), but in some it is closer to the anterior margin of the uncini (e.g., *Hadrachaeta aspeta* Hutchings, 1977 and on anterior chaetigers of *Longicarpus modestus* (Quatrefages, 1866)) (Fig. 7.7.3.17E, K, L, O), whereas in others it is situated closer to the base of main fang (Figs. 7.7.3.17G, J, P, 7.7.3.18A). The prow varies in shape, from those that are distally pointed (Fig. 7.7.3.17E–G, J–L, O, P) to those that are more distally rounded (Fig. 7.7.3.17H, I); ligaments and muscles are attached to the prow, and these may be thick. The back of the uncini is usually short and slightly convex (Fig. 7.7.3.17E, F, H–L, N–P), but a few taxa, such as species of *Proclea*, have a higher back, strongly bent backward, with crest with many rows of secondary teeth and an almost inconspicuous dorsal button, at the base of main fang (Fig. 7.7.3.17G).

Short-handled uncini typically have a short triangular heel directed posteriorly (Fig. 7.7.3.17E–G, J–L, P), and in some species of genera such as *Lanice* and *Amphitrite ornata* (Leidy, 1855), the heel forms a triangular projection (Nogueira 2008; Nogueira et al. 2010).

Long-handled neurochaetae have a downwardly directed handle, which has been called a shaft (Day 1967, Hutchings and Glasby 1988, Hutchings 1997a, b). Nogueira et al. (2010) differentiated them into two types: thin-handled uncini, with handles originating from the heel, such as among members of some species of *Pista* (Fig. 7.7.3.17H, I), *Longicarpus modestus* (Fig. 7.7.3.17O) and *Lanicides bilobata* Grube, 1877, and those where the handle originates from the entire base or at least from most of its extension (thick handled uncini), such as in *Betapista dekkerae* Banse, 1980 (Fig. 7.7.3.17N), *Lanicides lacuna* Hutchings & Glasby, 1988, and *Lanicides rubra* Nogueira, Hutchings & Carrerette, 2015d. In all genera with long-handled uncini, they are consistent within a genus, except in *Lanicides* and *Pista*, where both types are present, thin-handled and thick-handled, suggesting that revisions of these genera are needed to confirm if they are monophyletic (Nogueira et al. 2010).

In some genera, the long-handled uncini of anterior segments are more heavily chitinized than subsequent ones (*Longicarpus modestus*, *Betapista dekkerae*, and some species of *Lanicides*). In *Hadrachaeta aspeta*, the neurochaetae of the first four pairs of neuropodia, aside from being more heavily chitinized than subsequent ones, also differ in structure, and they are stout scoop-shaped chaetae, which is unique to this monospecific genus (Figs. 7.7.3.17M; 7.7.3.18C). Whereas Holthe (1986a) and Glasby et al. (2004) considered the neurochaetae of segments 5 to 8 as acicular chaetae, Nogueira et al. (2010) rejected this concept and any similarity between the anterior neurochaetae of *Hadrachaeta* and the acicular uncini of trichobranchids, as those authors had suggested.

Trichobranchidae have acicular thoracic uncini (Fig. 7.7.3.19A, C–E, G, H) and avicular abdominal uncini (Fig. 7.7.3.19B, F, K, L). The thoracic uncini may have a hood below the main fang, which appears as a tuft of bristles under SEM (Fig. 7.7.3.19C–E), whereas the abdominal uncini have secondary teeth on top and laterally to the main fang (Fig. 7.7.3.19B, F, K, L), instead of only on the top, as happens with the avicular uncini of the other families of Terebellidae *sensu lato*. Species of *Terebellides* have the first one to two pairs of neuropodia with acicular, distally bent spines instead of acicular uncini (Fig. 7.7.3.19I, J).

Two taxa of terebellids have unique uncini. Species of *Reteterebella* Hartman, 1963 have uncini that superficially resemble those of 'type 1' of species of *Polycirrus* in being elongate, with an almost flat base, and angular, with sharp corners (Fig. 7.7.3.17K). *Hadrachaeta aspeta*, in addition to the spoon-shaped neurochaetae present on segments 5 to 8, has short and thin uncini from segment 9, with a few rows of secondary teeth (Fig. 7.7.3.17L), and those on the posterior body have a crest with a fringe of flattened, distally rounded bristles arranged in a single transverse row (Fig. 7.7.3.18D).

Terebellidae *sensu stricto* is characterized by having some thoracic segments with uncini in double rows (Figs. 7.7.3.17I–J, L, 7.7.3.18F–H), usually from around segment 11, for a variable number of segments, and then reverting to single rows, which continue to the pygidium.

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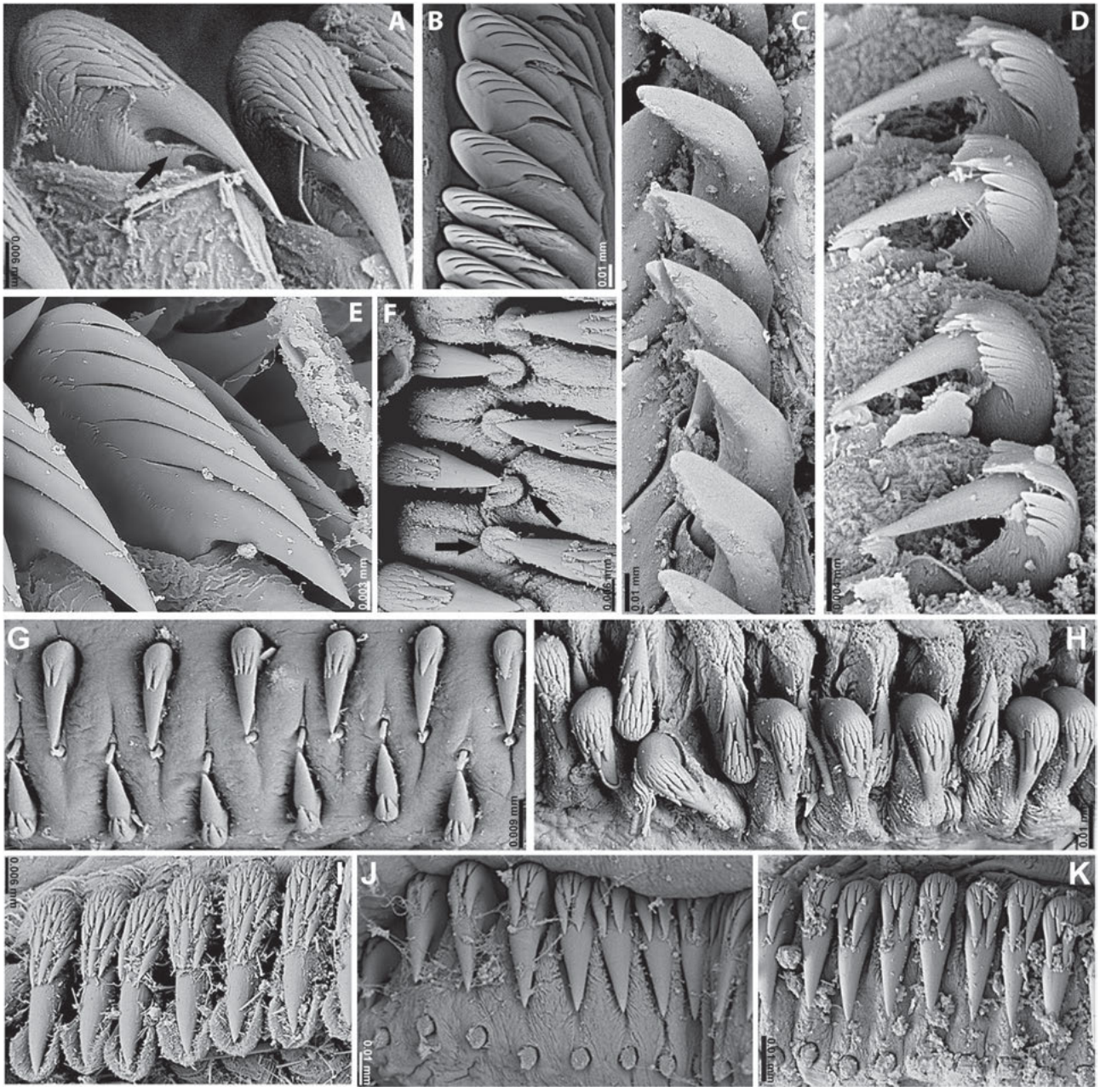


Fig. 7.7.3.18: Neurochaetae: A, *Artacama proboscidea*, abdominal uncini; B, *Loimia keablei*, abdominal uncini; C, D, *Hadrachaeta aspeta*, segments 6 and posterior abdominal; E, *Loimia pseudotriloba*, segment 16; F, *Pista* sp., segment 12, arrows point to dorsal buttons; G, *Nicolea amnis*, segment 11; H, *Terebella tantabiddycreekensis*, midabdominal segment; I, *Lanicides lacuna*, segment 6; J, K, *Thelepus paiderotus*, segments 7 and 26.

Typically, double rows continue to the end of the notopodia, although occasionally they continue for some segments after the termination of the notopodia (e.g., species of *Axionice* Malmgren, 1866 and *Phisidia*), and in some genera, they may continue almost to pygidium, such as in the genera *Hadrachaeta* Hutchings, 1977, *Longicarpus* Hutchings & Murray, 1984, *Amphitritides* Augener, 1922, and many species of *Terebella*. In a few other species, usually very small forms, the double rows of uncini terminate slightly before the termination of notopodia, as occurs in some species of *Spinosphaera* (see Nogueira and Hutchings 2007).

The rows of uncini are well separated, arranged back to back, or beak to beak (main fang to main fang) (Fig. 7.7.3.17J), or they are partially to completely intercalated (Figs. 7.7.3.17I, 7.7.3.18F, G) or partially back to back (Fig. 7.7.3.18H), and this is usually consistent within a genus (see Nogueira et al. 2010 for more details). Studies

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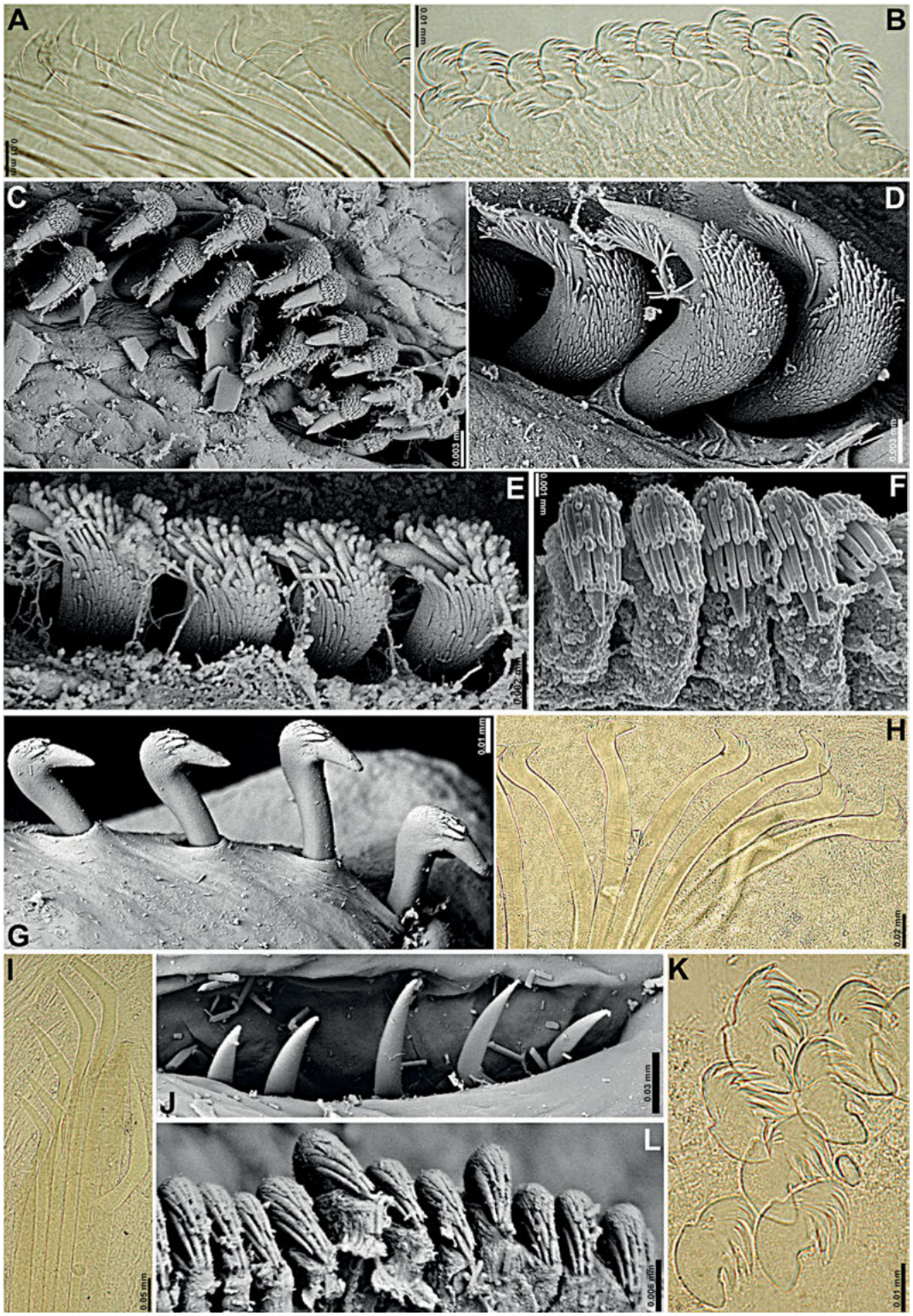


Fig. 7.7.3.19: Neurochaetae: A–D, *Trichobranchus bunnabus*, segment 9, abdominal uncini and two views of uncini of segment 17; E, F, *Trichobranchus dibranchiatus*, segment 19 and abdominal uncini; G–L, *Terebellides anguicomus*, two views of thoracic uncini, two views of neuropodial spines of segment 8, and two views of abdominal uncini.

on the ontogenetic development of these double rows have shown that, during the early stages, the uncini are arranged in single rows on all neuropodia and then, as the animal matures, some chaetoblasts invert their position and produce uncini in an inverted direction, forming the second row of uncini (Wilson 1928, Bhaud 1988,

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Bhaud and Grémare 1988, Blake 1991, Garraffoni and Amaral 2009, Garraffoni and Lana 2009). Whereas Garraffoni and Lana (2009) suggested that 'uncini in inverted rows' would be a better name for uncini in double rows, Nogueira et al. (2010), while accepting this reflects the ontogenetic development of this character, considered that it is still misleading, as the term 'inverted rows' could mean that uncini are arranged in single rows with the main fangs pointing posteriorly (inverted because the uncini are typically arranged with main fangs pointing anteriorly, whenever a single row is present, among all families of Terebellidae *sensu lato*) instead of two rows being present. Nogueira et al. (2010) suggested that the term 'uncini arranged in double rows' should be retained until an alternative name, which reflects all aspects of this character, is found.

Terebellidae *sensu lato* exhibits a tremendous variety of chaetal types and Woodin and Merz (1987) investigated the functional relationships of some of these types. For example, they measured the forces that needed to be applied to remove the worm from the tube and also mimicked the effects of a predatory fish trying to extract the worm from the tubes. They found that the uncini are orientated to resist such removal. Following on from these studies, they proposed a phylogeny for the group, which Fitzhugh (1991) rejected, after examining their data.

Branchiae. In Terebellidae *sensu lato*, branchiae are present in all families, except for Polycirridae and some genera of Terebellidae *sensu stricto*. They are paired structures situated dorsolaterally to dorsally on anterior segments, except in *Terebellides* (Trichobranchidae), which has a single middorsal structure, due to the fusion of two pairs of branchiae (see below). They vary from single filaments to complex, arborescent, or spiraled structures. Typically, they arise from consecutive segments, but members of *Terebellobranchia natalensis* Day, 1951, *Polymniella aurantiaca* (Verrill, 1900), and a few species of *Terebella* have branchiae present on discontinuous segments.

Among trichobranchids, variation exists between genera in the number and shape of branchiae. *Trichobranchus* has two to three pairs of simple branchiae beginning from segment 2, each consisting of one long thick filament on either side of the pair (Figs. 7.7.3.1B, 7.7.3.20A–C). *Octobranchus* has four pairs, on segments 2 to 5. In *Octobranchus myunus* Hutchings & Peart, 2000, each pair of branchiae consists of one long, thick, unbranched filament on each side of the body, but Hutchings and Peart (2000) stated that different types of branchiae are found in other species of this genus, ranging from digitiform to foliaceous structures. *Terebellides* has two pairs of lamellate branchiae fused in a four-lobed lamellate structure, inserted dorsally on a stalk, on segments 2 to 4, frequently with ciliated papillae near tip of lamellae (Figs. 7.7.3.14B, 7.7.3.20D–K). These four lobes are arranged in two pairs, with the first pair, or superior (=dorsal) branchial lobes, much larger (see blood vascular system section). Parapar and Hutchings (2014) showed, for the neotype of *Terebellides stroemii* Sars, 1835, that a large anterior branchial projection is present, projecting anteriorly to the main stalk, which they refer to as the 'fifth lobe', but we considered this 'fifth lobe' as an anterior extension of the superior pair of lobes rather than a truly separate lobe. The stalk comprises a musculoepidermal wall surrounding the four parallel stems of the branchiae (Jouin-Toulmond and Hourdez 2006), contradicting many earlier studies (Fauvel 1927, Day 1967, Fauchald 1977), which suggest a single middorsal stalked structure on segments 2 to 4 or on segment 3 (Holthe 1986a, b, Garraffoni and Lana 2003) or segments 3 to 4 (Hutchings and Peart 2000). Jouin-Toulmond and Hourdez (2006) observed live material and provided detailed illustrations of these four parallel stems. These very distinctive branchial structures have led to the widespread misidentification of a supposedly single species reported worldwide, *T. stroemii*. However, recent studies have shown that *T. stroemii* represents a suite of species, and the structure of the distinctive branchiae actually differs between species (Williams 1984, Hutchings and Peart 2000, Parapar and Hutchings 2014, Hutchings et al. 2015, Nygren et al. 2018, Lavesque et al. 2019).

Polycirrids are characterized by the complete absence of branchiae (Figs. 7.7.3.2I–N, 7.7.3.3A, B, E), which may be the plesiomorphic condition for this group, as that family is the basal-most of the whole Terebelliformia, according to Nogueira et al. (2013). Telothelepodids and thelepodids share similar branchial morphology, with multiple single, unbranched filaments on either side of pairs, originating from a large area of the body wall, often from raised glandular areas (Figs. 7.7.3.1H, 7.7.3.4G–K, 7.7.3.5A–J, 7.7.3.6A–J, 7.7.3.10E, H, 7.7.3.14F–H); two pairs are present in telothelepodids, two or three in thelepodids (although some species were originally described as abranchiate, but we suspected that this is an artifact, due to the loss of branchiae in the type specimens), beginning from segment 2 in both families. Hutchings and Glasby (1987) recorded examples of branchial regeneration in these groups.

The greatest variation on branchial shape is found in Terebellidae *sensu stricto*, from absent in some species to large arborescent, plumous, or pectinate structures, originating from basal stalks on either side of pairs or as unbranching filaments originating all together, from a single point on body wall on either side (Figs. 7.7.3.1J, K,

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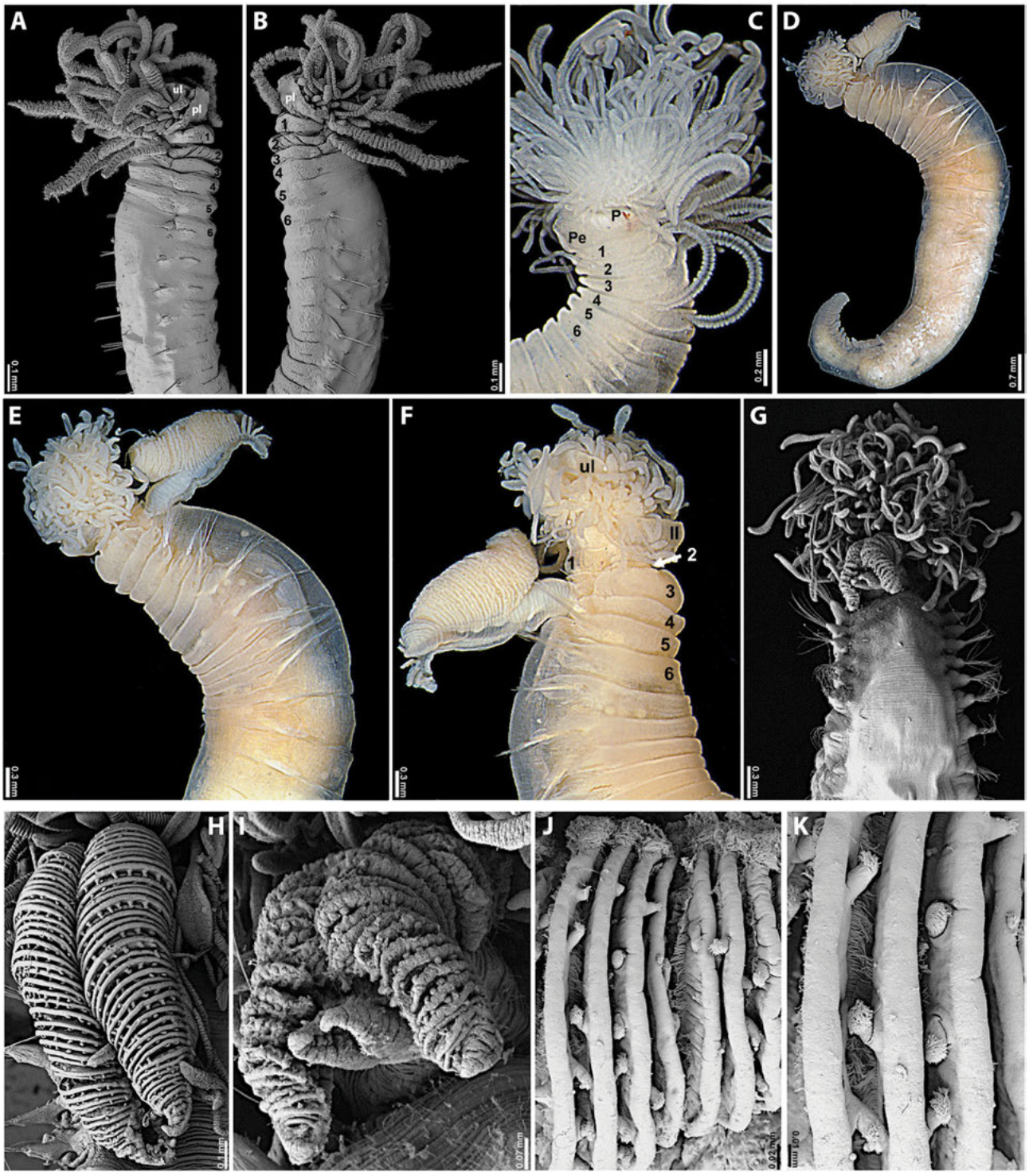


Fig. 7.7.3.20: Branchiae: A–C, *Trichobranchus hirsutus*, lateral views of anterior end; D–K, *Terebellides akares*, entire worm in lateral view, two lateral views of anterior end, one dorsal view of anterior end, and four close-ups of the branchia. Numbers refer to segments; ll, lower lip; P, basal part of prostomium; Pe, peristomium; pl, peristomial lobes; ul, upper lip.

7.7.3.2A, 7.7.3.7A, D–G, J–L, 7.7.3.8C–I, 7.7.3.9A–C, 7.7.3.21A–L, 7.7.3.22A–H). Hutchings and Glasby (1988) suggested that the number and/or size of the branchiae may increase with age, or at least with the size of the animal, and may also be modified by habitat. Fourteen genera of terebellids are abranchiate and have been considered by some authors as polycirrids due to the absence of branchiae (Fauvel 1927, Day 1967), until McHugh (1995) verified that Terebellidae

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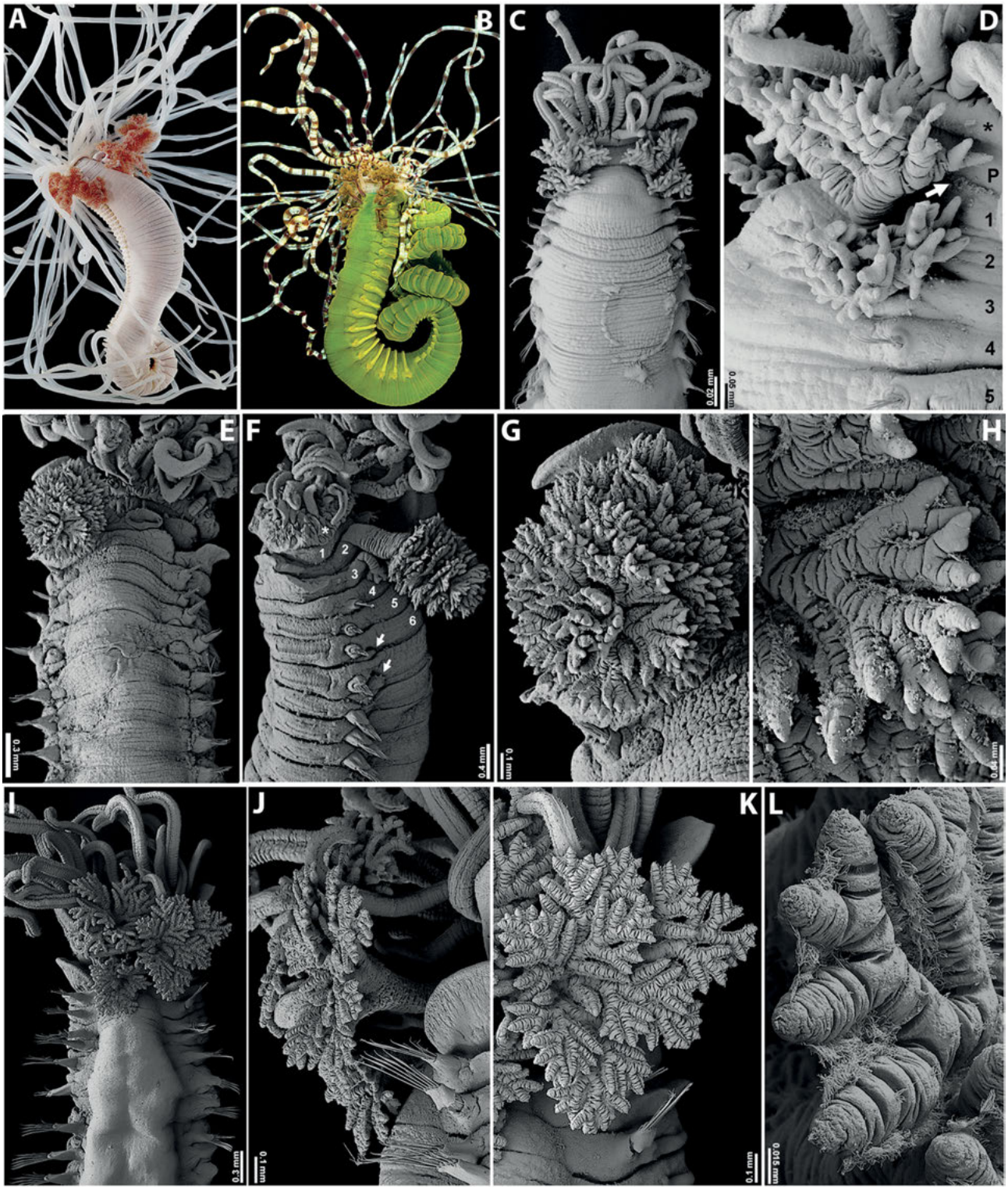


Fig. 7.7.3.21: Entire worms: A, *Reteterebella lirrf*, alive, dorsal view; B, *Lanice viridis*, alive, dorsolateral view. Anterior ends: C, D, *Nicolea vaili*, dorsal views, general view and close-up of right branchiae; E–H, *Pista anneae*, dorsal and lateral views and two close-ups of one branchia; I–L, *Pista chloroplokamia*, dorsal view and three close-ups of branchiae. Numbers refer to segments; *, distal part of prostomium; P, basal part of prostomium.

was defined by the presence of uncini in double rows at least on some segments, as discussed above; therefore, the absence of branchiae is a secondary loss that apparently has occurred independently in several lineages of Terebellidae *sensu stricto* (McHugh 1995, Nogueira et al. 2013).

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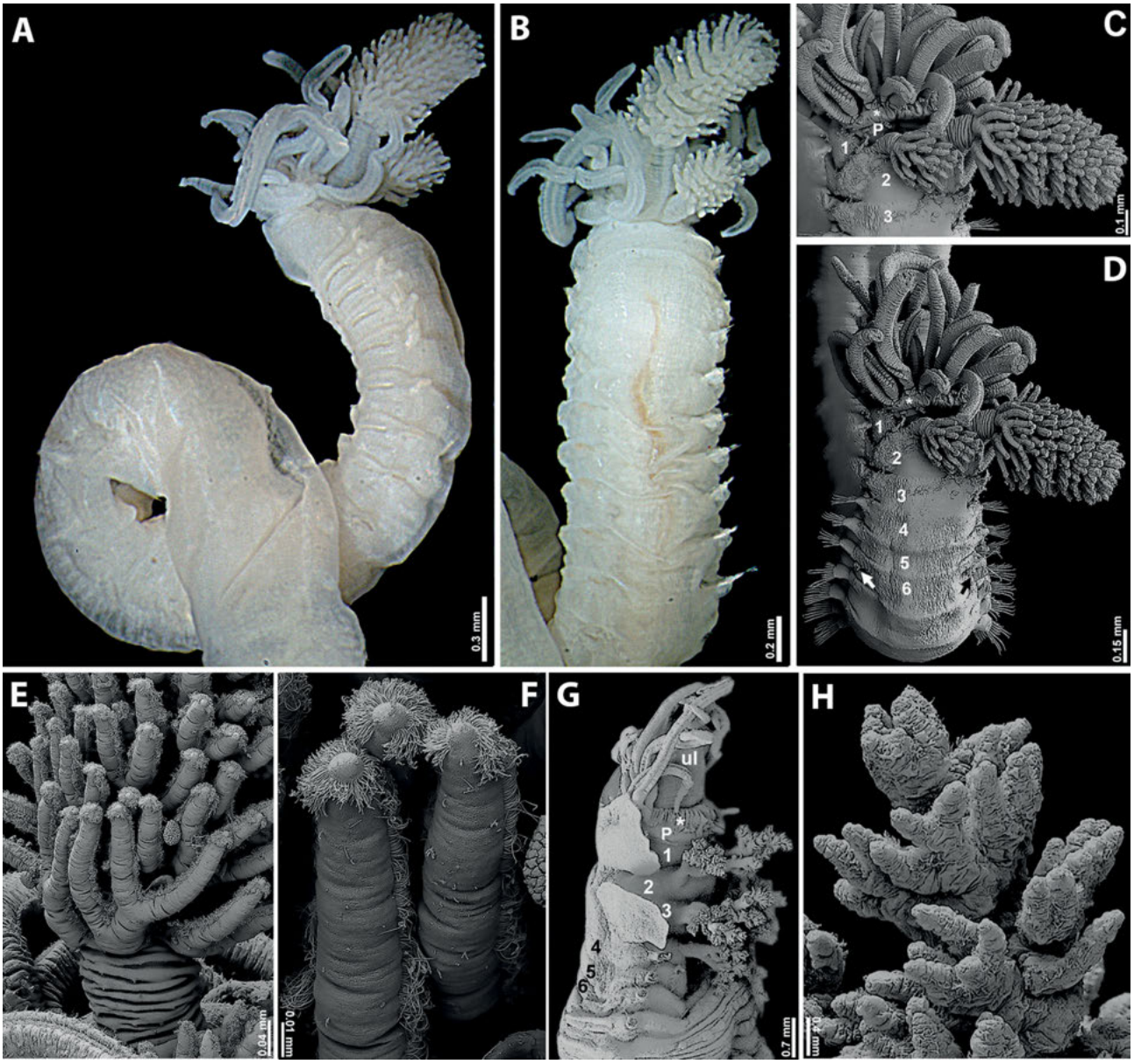


Fig. 7.7.3.22: Branchiae: A–F, *Pistella franciscana*, lateral and three dorsal views of anterior end and two close-ups of one branchia; G, H, *Loimia tuberculata*, lateral view of anterior end and close-up of one branchia. Numbers refer to segments; *, distal part of prostomium; P, basal part of prostomium; ul, upper lip.

Most genera of terebellids have two to three pairs of branchiae, and a few have a single pair; the number of pairs of branchiae is frequently fixed within a genus. In most species, branchiae begin on segment 2, but *Scionella* Moore, 1903 has a single pair on segment 4 (Fig. 7.7.3.9B). Branchiae of terebellids typically have a basal stalk, originating from a single point on the body wall on each side, in contrast to those of telothelepodids and thelepodids that have filaments originating independently from multiple points on the body wall. Branchial filaments have ciliary tracks that promote the circulation of water (Figs. 7.7.3.21C–L, 7.7.3.22C–H), increasing the efficiency of gas exchanges; usually, there is a blood sinus at the base of the branchiae, pumping high-pressure blood into the branchial filaments. At least some genera of terebellids appear to frequently loose and regenerate their branchiae, as they may present a remarkable difference in size from one side to another within a pair (Figs. 7.7.3.21E, 7.7.3.22A–D) (Nogueira et al. 2015d). It is also common that when two or three pairs of branchiae are present, these pairs differ in size (Fig. 7.7.3.21A–D, I).

In species of *Artacama* (Fig. 7.7.3.7D–G), *Scionella* (Fig. 7.7.3.9B), and *Amphitrite* Müller, 1771, among others, there are long unbranching filaments that originate from

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very short basal stalk; frequently, the stalk is almost inconspicuous, but those filaments clearly originate all together, from a restricted area of the body wall on either side of pairs, different from those of telothelepodids and thelepodids. Most species of terebellids, however, have large arborescent, plumous, or pectinate structures, with secondary stalks and distal filaments originating in a spiral, dichotomously or in a pectinate pattern (Figs. 7.7.3.8C–I, 7.7.3.9C, 7.7.3.21A–L, 7.7.3.22A–H). Frequently, the morphology of branchiae is similar within a genus, but in some cases, such as in *Pista*, species exhibit a considerable degree of variability.

Nogueira et al. (2010) recognized three major types of branchiae in Terebellidae *sensu stricto*: (1) unbranching branchiae characterized by long, unbranched filaments originating from a short to inconspicuous common stalk, as occurs, for example, in *Amphitrite cirrata* Müller, 1771 in 1776, species of *Artacama* (Fig. 7.7.3.7D, E, G), *Thelepides koehleri* Gravier, 1911, and *Scionella japonica* Moore, 1903 (Fig. 7.7.3.9B); (2) branching branchiae characterized by branches originating from a common stalk with variable number of ramifications and terminating in either short, thick, flattened filaments or cylindrical filaments of variable length, as in species of *Nicolea* Malmgren, 1866 or *Loimia* (Figs. 7.7.3.1J–K, 7.7.3.2A, 7.7.3.7J–L, 7.7.3.8C–I, 7.7.3.9C, 7.7.3.21A–D, I–L, 7.7.3.22G, H); and (3) plumous branchiae characterized by branchial filaments originating in a spiral around the common stem, which is typically long, and this type occurs in several species of *Pista* (Fig. 7.7.3.21E–H) and in *Pistella* Hartmann-Schröder, 1996 (Fig. 7.7.3.22A–F). A fourth type of branchiae, pectinate, with one long main stem and branches coming off along one axis, is found in *Pista pectinata* Hutchings, 1977.

In most branchiate terebellids, all the pairs of branchiae are either vertically aligned or the branchiae are progressively arranged more laterally from the first to last pair. All these branchiae, if present, are well supplied with blood, as are the lobes. In abranchiate species, gas exchange must occur across the body wall, and this probably also occurs in branchiate species. We suggest that the expanded upper lip present in polycirrids may also facilitate oxygen uptake.

Ventral pads. Among Terebellidae *sensu lato*, in addition to the glandular lobes and crests, which are commonly present on anterior segments, the ventral surface of the anterior body is also highly glandular, except for species of trichobranchids (Fig. 7.7.3.2F, H), several telothelepodids (Fig. 7.7.3.5A, B), and *Thelepus australiensis* Hutchings & Smith, 1997. It seems likely that these glandular areas are used in the construction of tubes, and in the case of polycirrids that lack tubes, they secrete large amounts of mucus, which allow the worms to glide through the substrate. Typically, the glandular region is followed by a midventral groove with small shields inside, which extends to the pygidium.

In polycirrids, paired and sometimes highly papillate ventrolateral pads are present on anterior segments and the midventral groove extends from about segment 3 to the pygidium (Figs. 7.7.3.1A, E, F, 7.7.3.3C, D, F, H, J). Garraffoni and Lana (2008) have suggested that the shields inside the midventral grove are ventral pads, homologous to those present in Terebellidae *sensu stricto*; however, Nogueira et al. (2010) have rejected these homologies.

In both Thelepodidae and Telothelepodidae, discrete ventral pads are absent; instead, the entire ventrum is glandular. In most species of telothelepodids, these glandular ventral surfaces are poorly developed in comparison to the other families of Terebellidae *sensu lato* (Figs. 7.7.3.1H, 7.7.3.4F–K, 7.7.3.5A, B, D), similar to trichobranchids, whereas in other species the glandular region is well developed. In contrast, thelepodids have the glandular ventral surfaces of the anterior segments as usually well-developed, cushion-like, and sometimes corrugated (Figs. 7.7.3.1I, 7.7.3.6A, B, F–H, J, K, 7.7.3.8A, 7.7.3.10H, 7.7.3.14J).

In Terebellidae *sensu stricto*, the glandular epithelium is limited to rectangular to trapezoidal midventral shields, which extend from the anterior segments to the posterior part of the region with biramous parapodia, decreasing in size posteriorly (Figs. 7.7.3.1L, 7.7.3.2A, 7.7.3.7F, H, 7.7.3.8B, E, F, J–L). Although Londoño-Mesa (2003, 2006, 2009) and Londoño-Mesa and Carrera-Parra (2005) provided detailed descriptions of the segments on which ventral pads begin and finish and discussed their usefulness in distinguishing between species, for most species, such information has not been included in the descriptions.

Nephridial and genital papillae. The gular membrane is present in all Terebellidae *sensu lato* (see Rouse and Fauchald 1997), between segments 4 and 5, dividing the coelomic cavity into an anterior section with excretory functions and a posterior one, where gametes develop and where septa between segments along the body are absent or incomplete (Zhadan and Tzetlin 2003). As the internal openings of the nephridia are situated in the segment anterior to the nephridiopores, the papillae up to segment 5 are assumed to be excretory (nephridial papillae), and those from segment 6 onward are assumed to be genital papillae (gonoducts) through which gametes are released (Smith 1992, 1994). Hessle (1917) suggested a classification of Terebelliformia based on the distribution of nephridia, which requires the dissection of material. This classification has

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rarely been followed; in fact, most species descriptions lack information about these papillae, especially the older ones. Museum collection managers are unwilling to allow the type material to be dissected to reveal these structures. Modern techniques, such as the micro-computed tomography, allow the visualization of internal structures without dissection of the specimens and will hopefully provide useful information on the nephridial organization of several species in the near future (Faulwetter et al. 2013, Parapar and Hutchings 2014, Paterson et al. 2014, Parapar et al. 2016).

Nephridial papillae are typically found on segments 3 and 4, with those on segment 3 usually the largest. Genital papillae can occur dorsal to notopodia, aligned with the notopodia and posterior to them, or inserted between the parapodial lobes (notopodium and neuropodium). The number of genital papillae visible may be a function of the sexual maturity of the animal.

In trichobranchids, Hessle (1917) reported that nephridia were present on segments 3 and on segments 6 to 7. Jouin-Toulmond and Hourdez (2006, see fig. 5B) confirmed this and stated that the first and last pairs have excretory functions, whereas the one on segment 6 is used to discharge gametes. In *Terebellides narribri* Hutchings & Peart, 2000, the papillae on segment 3 are large, digitiform, and positioned above the notopodia, whereas in *Terebellides anguicomus* Müller, 1858, which is one of the few species of this genus with notopodia beginning on segment 4, the papillae are vertically aligned with the notopodia (Fig. 7.7.3.2H). In both species, the papillae on segments 6 to 7 are much shorter, especially the last pair, and are located posteriorly to the notopodia (Nogueira et al. 2010). In *Trichobranchus*, nephridia are present on segments 3 and 7 (Jouin-Toulmond and Hourdez 2006), although Nogueira et al. (2010) failed to observe papillae on species of this genus they examined, which may indicate that papillae only become conspicuous when individuals are mature.

Species of Polycirridae typically have nearly spherical nephridial and genital papillae, anterior and slightly ventral to bases of notopodia (Fig. 7.7.3.3L). Three patterns of distribution of papillae are observed among polycirrids. These may be present (1) only on a few anterior segments, (2) on a larger number of anterior segments but terminating well before the termination of notopodia, or (3) at bases of all notopodia, except, sometimes, for the last one to two pairs (Fitzhugh et al. 2015, Nogueira et al. 2015a, b). Some species of polycirrids appear to lack nephridial or genital papillae, although nephridia can often be seen through the transparent body wall.

Most Thelepodidae and Telothelepodidae have one or two pairs of nephridial papillae on segments 4 and 5 and two pairs of genital papillae on segments 6 to 7, always immediately posterior to bases of notopodia, with the genital papillae frequently larger than the nephridial papillae. Typically, species of Telothelepodidae have papillae on segments 5 to 7 (Fig. 7.7.3.14H), whereas those of Thelepodidae have papillae on segments 4 to 7 (Fig. 7.7.3.6D, H), but in both families there are several cases of species with inconspicuous or not visible papillae.

In Terebellidae *sensu stricto*, nephridial papillae are not visible in several species, although they must actually be present to discharge excretory products. If visible, they occur on segment 3 or segments 3 and 4, inserted laterally to the branchiae, or in cases where large lobes are present they typically are found between the bases of the branchiae and the lobes, at each side. The distribution of genital papillae varies between taxa (Figs. 7.7.3.2A, 7.7.3.7D, 7.7.3.8C) (Nogueira et al. 2010, 2013).

All the above information regarding the distribution of these papillae is based on observations of the external morphology and not on dissections.

According to Goodrich (1945), members of Terebellidae *sensu lato* have mixonephridia with anterior ducts excretory and posterior ones functioning as gonoducts. Smith (1988) rejected this terminology, arguing that the excretory organs are metanephridia based on his studies of two species, *Lanice conchilega* (Pallas, 1766) and *Eupolymnia nebulosa* (Montagu, 1819), as the ciliated funnels contain two distinctly different tissues. Smith's studies supported those of earlier studies by Meyer (1887), who suggested that the ciliated funnels of the segmental organs have this dual composition and therefore are nephromixia and not mixonephridia as suggested by Goodrich (1945), who did not refer to the studies of Meyer (1887). However, Rouse and Fauchald (1997) suggested that the metanephridia of terebellids are not similar to those found in some other polychaete families, including Syllidae and Hesionidae; obviously, more work is needed to clarify the situation in terebelliforms. Hessle (1917) investigated 11 species of *Pista* (summarized by Smith 1992, tab. 1) and reported some variation as to the segments on which nephridiopores were present. Smith (1992) described several types of nephromixia within the genus *Pista* and suggested that the genus, and also other genera, could be split using these characters, supporting Hessle's (1917) view of the usefulness of nephridia as taxonomic characters. Smith (1992) found three nephromixial patterns in species currently assigned to *Pista* and suggested that this is the first example of intrageneric nephromixial variation to be reported within Terebellidae *sensu stricto*, although we should mention that most genera have not been investigated in detail. Certainly, a revision of *Pista* is needed, as several types of long-handled uncini have been

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recorded, and the nephromixial patterns may be another useful character in this revision.

To date, no detailed studies have been undertaken on the osmoregulatory abilities of terebelliforms, although they occur primarily in fully saline conditions, which suggests that they may have limited abilities.

Posterior segments and pygidium. In most Terebellidae *sensu lato*, the pygidium is terminal and smooth to crenulated, but in some the anus is surrounded by soft anal papillae of variable size, ranging from short and rounded to digitiform, and there are also some species with more elongate, distally pointed cirri (Figs. 7.7.3.1A, B, D, F, I, 7.7.3.23A–N).

The proliferation of segments continues throughout life but decreases with age, and posterior segments are always strongly compacted.

Anatomy

Integument. The epidermis of specimens of Terebellidae *sensu lato*, which lies on a thin fibrous extracellular layer, is monolayered and consists of supportive, ciliary, secretory, and sensory cells covered by a thin cuticle. Supportive cells vary in shape, and they are long and may reach up to 70 µm in some regions of the body in *Lanice conchilega* (see Storch 1988). Storch (1988) provided a schematic representation of the epidermis and the cuticle of *L. conchilega*. Unlike most polychaetes, the collagen is not laid down regularly and the cuticle is up to 10 µm thick. Secretory cells are important in tube construction, which has been studied in detail by Bielakoff et al. (1975) for *L. conchilega*, in terms of the histology and histochemistry of secretions; they recognized 14 types of cells responsible for tube construction. Some terebellid larvae also construct tubes while they are in the plankton. Tiberi and Vovelle (1975) found that the dorsal gland of *L. conchilega* was the main site responsible for the secretions used in building these larval tubes.

Members of Terebellidae *sensu lato* have longitudinal and circular muscle bands (Storch 1968, Tzetlin and Filippova 2005). They may have either a firm muscular body, such as in many species of terebellids, or a flaccid body, as in many species of polycirrids.

Blood vascular system. Members of Terebellidae *sensu lato* have a well-developed blood system, often with a conspicuous heart-body (Meyer 1887, Picton 1899, Kennedy and Dales 1958). Wirén (1885) carried out a detailed morphological study on the circulatory system of several terebellids. Friedman and Weiss (1980) have investigated the production of hemoglobin in *Amphitrite ornata*, and Mangum et al. (1975) investigated the functioning of coelomic and vascular hemoglobin in three species of the group. The heart-body, which is located within the supraesophageal dorsal blood vessel, is cylindrical with thin highly corrugated walls (Friedman and Weiss 1980). Blood is pumped around the body by both the dorsal vessel and the general muscular movement. Although the blood lacks corpuscles, it has high molecular weight respiratory pigments dissolved in the plasma, and although this is typically hemoglobin, some Australian thelepodids have the green pigmented chlorocruorin instead, and the branchiae in live animals appear bright green. Hemoglobin, as well as being present in the blood, is also found in the coelomic cells of some species (Mangum et al. 1975, Friedman and Weiss 1980); however, considerable differences in the oxygen affinity occur between vascular and coelomic hemoglobins. The relatively high molecular weight of vascular hemoglobin means that it has relatively low oxygen affinity and transport oxygen primarily to coelomic fluid rather than deep into the tissue. In contrast, the coelomic hemoglobin has a high oxygen affinity and is responsible for 30% to 55% of the total oxygen consumption both, at high tide, when oxygen transport is their main function and, at low tide, when oxygen storage predominates. Mangum et al. (1975) also suggested that the major target organ for the oxygen transported by the vascular system is not muscle, nerve, nephridia, or other internal organs but rather the metabolically active coelomic cells and gametes. It is unknown whether this pattern is uniform across these animals regardless of whether they occur intertidally or subtidally.

Recently, detailed studies on the molecular structure of the hemoglobin of several terebellids have been undertaken (Serrano et al. 2010, Barrios et al. 2014, McCombs et al. 2016), showing not only their ability to absorb oxygen but also biologically relevant peroxidase activity. For a recent review of these hemoglobin dehaloperoxidases, see Franzen et al. (2015).

Jouin-Toulmond and Hourdez (2006) observed blood circulation in live *Terebellides* and found the branchial organ to consist of two pairs of lamelliform branchiae, an anterior pair, also called superior branchial lobes (lobes 1 and 2 according to Hutchings and Peart 2000, Garraffoni and Lana 2004), covering a second pair of reduced branchiae, or inferior branchial lobes (lobes 3 and 4), posterior to the first ones. Each branchia is made of lamellae inserted on a muscular stem surrounding a coelomic cavity, which contains the blood vessels. The blood contains amaebocytes, and the water currents on the gill surface, created by the cilia of the lamellae (see above), form countercurrents stream to the direction of blood flow. Jouin-Toulmond and Hourdez (2006) also suggested that, although the branchiae are primarily respiratory organs, they may also participate in the collection of particles for feeding or tube building.

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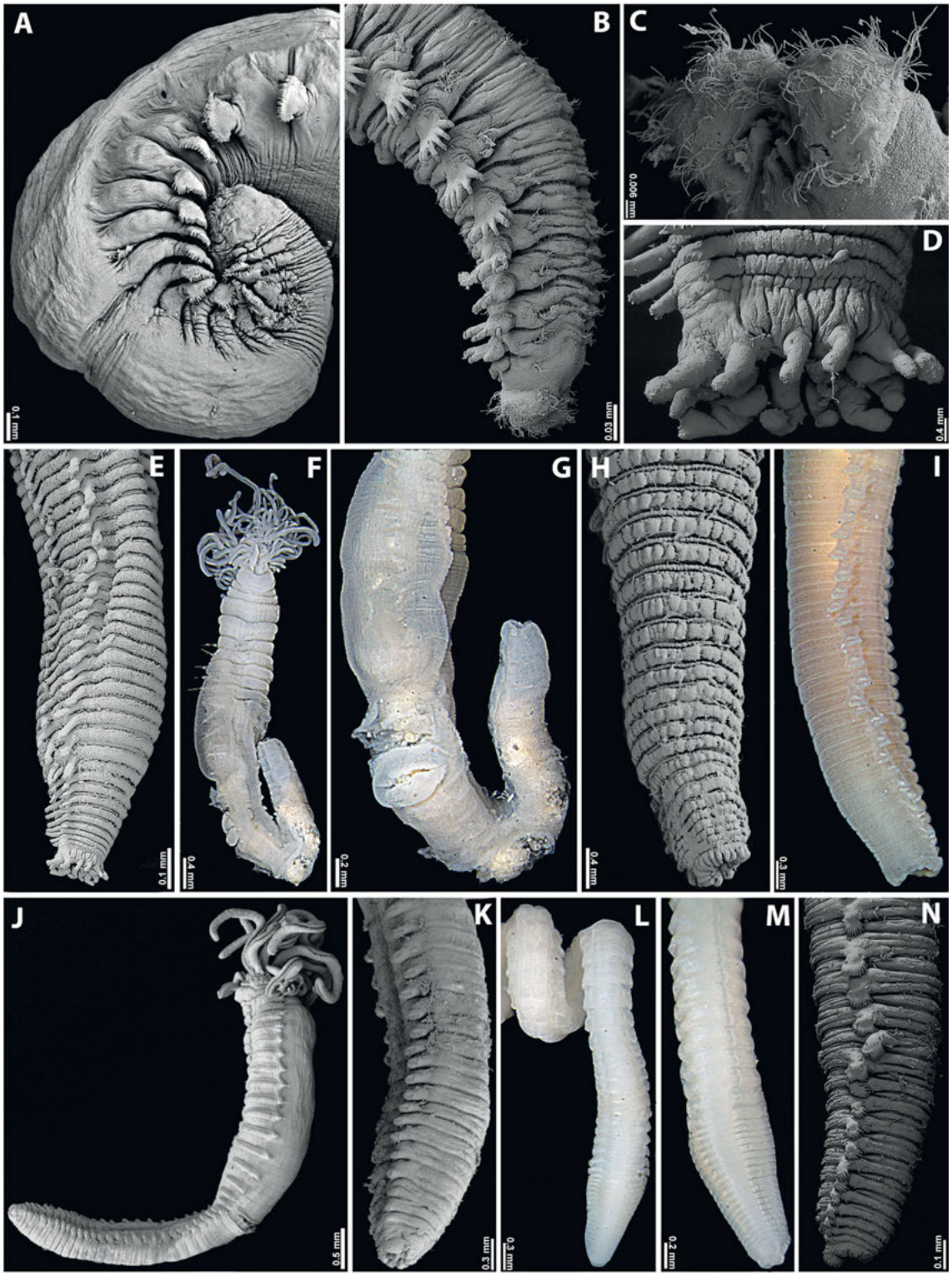


Fig. 7.7.3.23: Posterior ends: A, *Terebellides akares*, lateral view; B, C, *Trichobranchus hirsutus*, lateral and frontal views; D, E, *Loimia pseudotriloba*, close-up and lateral view; F, G, *Parathelepus oculeus*, entire worm and lateral view; H, *Loimia keablei*, dorsal view; I, *Pista chloroplokamia*, lateral view; J, K, *Nicolea murrayae*, entire worm and lateral view; L–N, *Pistella franciscana*, dorsal, ventral, and lateral views.

Sensory organs. A number of sensory organs have been reported in terebellids. A single pair of statocysts has been reported in subepidermal vesicles, which link to the exterior via ciliated canals (Storch and Schlötzer-Schrehardt 1988). The receptor epithelium of these statocysts is composed of supporting and sensory cells, with cilia

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that lack rootlets; gland cells are absent (Heimler 1983). The statocysts present in *Lanice conchilega* develop from epidermal invaginations of the first segment on the metatrochophore.

The chemosensory nuchal organs are usually present, but in some cases they are indistinct or absent, in which cases they are presumed to have been lost (Heimler 1983, Rouse and Fauchald 1997). In contrast, McHugh (1995) suggested that they are completely absent in Terebellidae *sensu stricto* and Polycirridae; obviously, this needs further investigation. We have seen nuchal organs as dorsolateral ciliated slits in many species of Telothelepodidae and some of Thelepodidae and Terebellidae *sensu stricto* (Nogueira personal observations). Nuchal organs are present in species of *Trichobranchus* (see McHugh 1995) but not in *Terebellides*, according to Rullier (1951), and no species of *Octobranchus* has been examined in detail (Rouse and Fauchald 1997).

Multiciliate solitary sensory cells are present in the tentacular epithelium of *Lanice conchilega* (see Schulte and Riehl 1976) and may be involved in the feeding process. Trochophores of *L. conchilega* have apical organs consisting of numerous primary sensory cells, which probably are either mechanoreceptors or chemoreceptors (Heimler 1981). These cells have a few long cilia with a 9+2 microtubule pattern and long rootlets and are connected to the neuropil of the brain.

Reproduction and development

Most terebellids are dioecious with no morphological differences between genders, except at the time of breeding, when the mature gametes typically differ in color and gonopores may be enlarged. Females at this time may be pinkish or greenish, and males are cream colored. A few taxa, such as several species of *Nicolea* Malmgren, 1866, have sexual dimorphism of the genital papillae (Fig. 7.7.3.2A) and distribution of glandular areas (Nogueira 2008). No evidence of asexual reproduction has been recorded, although these animals are capable of regenerating posterior ends, branchiae, and buccal tentacles.

Gametes are proliferated from patches on germinal epithelium often associated with the nephridia and released into the coelomic cavity, where vitellogenesis and spermatogenesis occur (Eckelbarger 1975). Detailed studies of the ultrastructure of spermatids and spermatozoa in *Ramex californiensis* Hartman, 1944 and *Nicolea zostericola* Örsted, 1844 (Terebellidae *sensu stricto*) have been undertaken by Rouse and McHugh (1994). The ultrastructure of the coelomic amoebocytes plays an important role in nutrient storage, and Eckelbarger (1976) suggested that they supply developing oocytes with the necessary nutrients for oogenesis. The way in which the coelomocytes obtain the nutrients is unknown, although Dales (1957, 1961) suggested that fats are synthesized by the cells or taken directly from body fluids. Later, Dales (1964) found amoebocytes with pseudopodial contacts with the gut wall and the outer walls of blood vessels, although he was unable to document any transfer of nutrients from the amoebocytes to the developing oocytes.

Ripe gametes are shed from the body cavity through the gonoducts (reproductive nephridia). Spawning in *Lanice* was studied in detail by Smith (1989a, 1989b), who found that the surface of the oocytes becomes reticulate at maturity, and suggested that this may be a way in which to ensure that only mature oocytes are shed externally through the nephridia. Bhaud (cited in Smith 1989b) reported a similar change to the surface of the oocytes in *Eupolymnia nebulosa*. Much earlier, Scott (1911) had suggested that the ciliated funnels of the nephridia in *Amphitrite ornata* only accept mature oocytes. All these species exhibit external fertilization. McHugh (1993) stated that there is no evidence of self-fertilization, and hermaphrodites have rarely been reported. Typically, populations of terebelliforms have a sex ratio of 1:1. Some species live for several years and may spawn several times. Spawning varies from a discrete period of several months to only 1 or 2 days. For example, *Thelepus crispus* Johnson, 1901, spawns over a 6-month period, whereas *Ramex californiensis* produces cocoons throughout the year (McHugh 1993). Eckelbarger (1975) investigated gametogenesis in *Nicolea zostericola*, which is monotelic and spawns two to five times over a 2-week period, at the end of its life of 12 months. Others, such as *Neoleprea streptochaeta* (Ehlers, 1897), are polytelic and spawn annually over its 5-year life span (Duchêne 1980).

Currently, no studies on the endocrine system controlling breeding has been undertaken on any Terebelliformia; however, given the variety of reproductive patterns demonstrated in the few species that have been examined in detail, several patterns may occur.

Terebellids exhibit diverse reproductive strategies. Wilson (1991) reviewed the seven species of Terebellidae *sensu stricto* and Thelepodidae, which had been studied by that time, and McHugh (1993) provided additional data on another two species of terebellids. Currently, these animals range from free spawning, with a lecithotrophic larvae, to others that brood eggs within their tubes or with embryos developing within a gelatinous mass and released as lecithotrophic larvae. Others brood encapsulated embryos that undergo direct development inside the parent tube. Specimens of *Terebellides* sp. investigated by Thorson (1946) had embryos developing directly in a

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gelatinous mass [identified as *T. stroemii*, but unlikely to be that species, as it is restricted to northern Norway, and Thorson's material was from Denmark (see Parapar and Hutchings 2014, Nygren et al. 2018)].

Few studies on the development of terebellids have been carried out (McHugh 1993) and range from those that mass spawn and produce a benthonic larva, which after about 7 days settles as a 5-chaetiger juvenile, to those that are brooded only until a 1-chaetiger stage and then spend 1 day in the plankton before settling as juveniles with eight chaetigers. Another species that McHugh (1993) studied has direct development within a cocoon, and larvae are released at the 11-chaetiger stage. Bhaud (1991) investigated spawning in *Eupolymnia nebulosa* and suggested that it was related to lunar phases; this species has eggs that develop in a mucous sac and a feeding benthonic larval stage of about 15 days, but this is controlled by temperature and food supply.

Studies by Schüller and Hutchings (2012) on deep-sea populations of *Terebellides gingko* Schüller & Hutchings, 2012, separated by distances of 4150 km, verified that they are connected genetically and suggested that the hydrographic structure of the two basins in which they are found (Argentine and Brazilian basins) allows for some exchange of larvae between these populations.

Biology and ecology

Distribution

The group is widespread from the intertidal to deep water. Whereas many genera occur worldwide, others are currently known only from very restricted areas. For instance, *Reteterebella* is currently restricted to Australia, Hong Kong, and Solomon Islands (Hutchings et al. 2015). Of the 72 genera of Terebellidae *sensu lato*, 27 are currently monospecific and some are known only from the type specimens.

Species range from supposedly widespread to those with very restricted distributions. Increasingly, some widely spread species such as *T. stroemii* are being shown to represent suites of species (Williams 1984, Hutchings and Peart 2000, Parapar and Hutchings 2014, Lavesque et al. 2019). Other species, such as *Thelepus setosus* (Quatrefages, 1866), have been recorded from many parts of the world, with the original descriptions being very brief and often without a type having been deposited; until these species are redescribed based on material from the type localities, the true identity of material from outside the type localities cannot be determined. That is the case of many Arctic species that have been reported in the Antarctic (Hartman 1966), as until the original Arctic species are redescribed, the Antarctic material cannot be identified, especially because it seems biologically very unlikely these species have such discontinuous distributions (Hutchings in preparation). Recently, the distributions of *Loimia medusa* and *Polycirrus medusa* Grube, 1850 have been redefined (Hutchings and Glasby 1995 and Glasby and Hutchings 2014, respectively), with neotypes being designated from their respective type localities or close areas.

The biogeography of Australian terebellids was discussed by Hutchings and Glasby (1991), with some species having a wide distribution within Australia, others have either a southern or a northern one, and some species have very restricted distributions.

Ecology

Terebellids are widespread in the marine environment. The spatial and temporal effects of terebellid tubes in soft sediments were investigated by Trueblood (1991). He found that terebellids *sensu stricto* actively avoid tentacles of neighboring worms, supporting an earlier study by Anderson and Kendziorek (1982), who worked on *Thelepus crispus* and postulated that this was caused by competition for food or space. Although tubes of terebellids have a limited role in influencing temporal patterns in soft-bottom communities (Trueblood 1991), they do have some impact on the spatial patterns of recruitment of capitellids and dorvilleids, perhaps by modifying the hydrodynamics of the area or by interactions between recruiting infaunal species.

Feeding. All terebellids are surface deposit feeders, and studies by Dales (1955, 1963, fig. 6) on *Amphitrite johnstoni* Malmgren, 1866 and *Terebella lapidaria* showed how this occurs. The highly mobile and extensile buccal tentacles are inverted U-shaped in cross-section; those tentacles are spread out over the surface of the sediment, with the ciliated margins of the groove directing fine particles into the bottom of the groove (Fauchald and Jumars 1979, Jumars et al. 2015). Dales (1963) found that the entire tentacle surface is provided with mucous cells, and about half of them are ciliated; the ciliated side is commonly inrolled so as to form a groove in which the cilia beat toward the mouth. Trapped sediment in this groove is then wrapped in mucous and moved along the highly muscular tentacle by peristalsis toward the mouth. At the base of the tentacles, the muscular lips surrounding the mouth sort the particles into those for ingestion and tube building, and those that are too large are then ejected by contraction of these lips (see fig. 1.222 in Hutchings 2000, after Dales 1955). Leaving a terebellid in a Petri dish with a fine layer of sediment overnight will leave a clear circle around the worm, as it vacuums all the sediment within the range

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of the tentacles. Some species such as *Reteterebella lirrf* Nogueira, Hutchings & Carrerette, 2015 and *Reteterebella queenslandia* Hartman, 1963, have extremely long tentacles that may extend for 1 to 2 m across the coral substrate; these tentacles will rapidly retract back into the burrow if touched, deep down in the crevices of the coral, and we suggest that they are unpalatable to other organisms.

Meyer (1887) suggested that the movement of the buccal tentacles is controlled by four conical pouches on the gular membrane and that fluid from these sacs is forced into the tentacles. Dales (1955) showed that even if the anterior coelom is opened the buccal tentacles are still highly mobile; he suggested that the extension of the tentacles is due to ciliary creep. The tentacles roll over and open out the ciliary groove, thus presenting a flat ciliated surface on the substrate and crawling very much like a planarian. The curling and rolling movements of the tentacles are controlled by their complicated musculature, which consists of transverse and oblique muscles, together with individual muscle fibers located along the edge of the inverted U-shaped groove, causing the groove edges to undulate, which facilitates the transport of food particles along the groove to the mouth.

Alimentary canal and nutrition. The morphology of the alimentary canal has been investigated in several species of terebellids by Wirén (1885). The mouth leads into a long narrow esophagus that opens into a wide thin-walled forestomach followed by a hind stomach that has a well-developed muscle layer (Dales 1955). The movement of food along the gut is probably via a muscular action. The pH of the esophageal contents is lower than the surrounding seawater, suggesting that some enzymes are secreted in the posterior part of the esophagus as well as in the stomach. The acidity of the gut fluids increases toward the hind-intestine, and digestion is probably entirely extracellular, with absorption taking place in the foreintestine and in the anterior part of the hind-intestine (Dales 1955).

The fine particles that are ingested are covered with diatoms and bacterial films, which provide the nutrients to the worms (Self and Jumars 1978, 1988). They can be selective as to which particles they retain, and this can occur along the feeding tentacle based on elegant field experiments with glass beads coated in amino acids.

Tubes. Terebellids that possess tubes need to maintain those throughout life and also extend them as the animal grows. The tubes often have a mucous fibrous lining, and we suspect that they rapidly decompose when the animal dies, as empty tubes are rarely found (Nogueira personal observations). The anterior ends of tubes can be repaired if predators attempt to extract the animal, and live specimens of several species form thin, transparent mucous tubes in a matter of minutes when removed from their tubes and relaxed in menthol solution in a Petri dish (Nogueira personal observations). However, under natural conditions, these animals probably would not be able to build a new tube if removed from their original ones, as they are far too vulnerable to predation.

Tubes vary from fine muddy tubes to those ornamented with shell fragments/sponge spicules; they are flexible and always longer than the body of the worm, so they can retract deep into the tube if disturbed. Some species live with tubes freely in the sediment, whereas others are attached to the undersurface of rocks, shells, or wood fragments or lying in among the bases of seagrass blades or in among kelp holdfasts.

Although terebellids are often a conspicuous member of benthic communities, they are rarely present in large numbers. An exception is *Nicolea uspiana* (Nogueira, 2003), which is extremely abundant in Brazil, on rocky shores off southeastern and northeastern Brazil. Some benthic Antarctic habitats also have large numbers of specimens of a species of *Thelepus* (Hutchings personal observations).

Symbiosis. Some parasites have been found in terebellids, such as unencysted metacercariae of digenetic trematodes, which have been reported from the metanephridial sacs of *Amphitrite ornata*, and those feed on the tissues of the metanephridia and perhaps also on the vascular hemoglobin (Vandergon et al. 1988). Gregarines are commonly seen in the coelomic fluid of terebelliforms. Some species of terebelliforms have also been reported as intermediate hosts for trematodes, with the final host being a fish (Koie and Petersen 1988), and the parasites appear to be species specific with regard to their hosts.

Recent studies have shown that two species of Terebellidae *sensu stricto*, *Reteterebella aloba* Hutchings & Glasby, 1988 and *Longicarpus modestus*, are intermediate hosts of the trematode *Cardicola forsteri*, whose final host is the southern bluefin tuna (Cribb et al. 2011). Subsequent studies by Shirakashi et al. (2016) in Japan found that the intermediate host for this trematode was another terebellid, *Nicolea gracilibranchis* (Grube, 1878), or a species of *Amphitrite* sp. Another study from Japan on the same species of trematode by Sugihara et al. (2013) found the intermediate stages in a species of *Terebella*, indicating that this animal can use several species of Terebellidae *sensu stricto*, belonging to several genera, as an intermediate host. Some of the larger species often have commensal polynoids within their tubes, although the nature of this relationship is not known. Dales (1955) found that the scale worm *Gattyana cirrhosa* (Pallas, 1766), which lives in tubes of *Amphitrite johnstoni*, moves forward in the

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burrow as irrigation movements are reduced, ingestion begins, and takes food away from the terebellid, making the host restart the movements. Pinnotherid (pea crabs) are also commonly found in tubes of the larger terebellids (Hutchings personal observations).

Fossil records. As all terebellids are soft-bodied animals, they do not readily fossilize. Some types of fossilized worm tubes have been found in the Erins Vale Formation (Late Permian), Southern Sydney Basin, New South Wales, Australia. These tubes have been studied by Pickett (1972), who suggested that they belong to terebelliforms. Howell (1953) described a genus of terebellids based on the construction of fossil tubes, ranging in age from the Cambrian to the Recent.

Some other terebellid-like burrows have been recorded in northwest Russia, Estonia, Baltica, and North America, occurring in the Middle Ordovician and in Silurian (Thomas and Smith 1998, Vinn and Toom 2014).

Phylogeny and taxonomy

Phylogeny

Whereas the close relationship among the families of Terebellidae *sensu lato* has never been doubted, the relationship of the group to the other polychaete families has been much debated.

Grube first formally recognized the polychaetes as a uniform group in 1850 and then divided them into two suborders, Rapacia and Limivora, to reflect their modes of feeding. Most members of Rapacia included what Audouin and Milne Edwards (1834) had been calling 'errant' polychaetes, whereas Limivora included mostly the 'sedentary' polychaetes [see Read 2019 (A History of Annelida Research) and Struck 2019 (Phylogeny) in Volume 1 of the Handbook]. Later, Quatrefages (1865) designated a subdivision originally proposed by Blainville (1825), in which 'sedentary' polychaetes had distinctly regionalized bodies, in contrast to the 'errants' that lack such regions. Benham (1894, 1896) removed some of the 'sedentary', including Sabellidae, Serpulidae, and Sabellariidae, and formed the order Cryptocephala, and all other polychaetes were placed in the order Phanerocephela; however, this revised classification was not adopted by later workers. About the same time as Benham, Hatschek (1893) divided the polychaetes into another two groups, Cirrifera and Acirra, and the terebellids, together with Drilomorpha and serpulimorphs, belonged in Acirra. Although these two terms of Hatschek have been disregarded by most later workers, the names Terebellomorpha and Spiomorpha have been used by many later workers, with roughly the composition that Hatschek gave them. Interestingly, the first major cladistics analyses of the polychaetes by Rouse and Fauchald (1997) does in part recognize the concepts of the two groups originally proposed by Hatschek (1893).

During the twentieth century, various classifications were proposed; however, the system proposed by Quatrefages (1865) was adopted by Fauvel (1923, 1927, 1953), Ushakov (1955), Day (1967), and Hartmann-Schröder (1971), and the terms 'sedentaries' and 'errants' became entrenched in the literature, although Day (1967) and Hartman (1968) complained about the limitations of this classification. Dales (1962, 1963, 1977) proposed an alternative classification based on the structure of the buccal organs, and Terebellidae *sensu lato* was placed in a group with noneversible buccal organs, although this scheme has not been widely used (Hutchings 2000, Hutchings and Glasby 2000).

Later, Fauchald (1977) defined 17 orders based on a combination of characters, although most were defined on anterior characters and similar to Dales (1963) classification. Both organized their groups in a hierarchical structure, so a higher classification could be assumed. Subsequently, individual families were subjected to cladistic analyses all based on morphological characters (e.g., Rouse and Fitzhugh 1994 on sabellids and Glasby 1991, 1993, 1999 on nereidids), and McHugh (1995) investigated the relationships within Terebellidae *sensu stricto* (as the so-called subfamily Terebellinae) and confirmed the placement of abranchiate terebellids within Terebellidae.

In a major cladistic analysis of polychaetes, Rouse and Fauchald (1997) proposed that Polychaeta were split into Scolecida and Palpata. Scolecida comprised Arenicolida, Capitellida, Opheliida, Orbiniida, Paraonidae, and Cossuridae (fig. 6.1E in Rouse and Fauchald 1997); the name for these earthworm-like taxa is derived from the Greek word 'scolex' for worm. Palpata was further divided into Canalipalpata and Aciculata, with Canalipalpata comprising Chaetopterida, Oweniida, Sabellida, Spionida, and Terebellida and the remaining Cirratulida. Terebellidae *sensu lato* was supported by the presence of multiple prostomial buccal tentacles (palps), although the support was not high. They were sister to a clade containing Alvinellidae, Ampharetidae, and Pectinariidae, which have lateral organs and multiple peristomial palps. This now classical study of Rouse and Fauchald (1997) then allowed various hypotheses to be tested using both morphological and molecular data.

Colgan et al. (2001) used five gene segments and found that Alvinellidae belongs to a clade within Terebellidae *sensu lato*, which contradicts morphological studies. They found that Terebellidae *sensu stricto* was

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paraphyletic with respect to Polycirrinae (now Polycirridae), suggesting their morphological simplicity is derived. Later studies by Colgan et al. (2006) found that Echiura formed the sister group to Trichobranchidae. Studies by Hall et al. (2004) found no support for the expansion of Terebelliformia proposed by Rouse and Fauchald (1997) to include the families Acrocirridae, Cirratulidae, and Flabelligeridae, and the morphological studies of Glasby et al. (2004), in general, supported the traditional concept of Terebelliformia, and they also found that, depending on the coding of a few characters, Alvinellidae may be a discrete family, sister to the Ampharetidae, or embedded within Terebellidae *sensu lato*.

Another morphological study by Garraffoni and Lana (2008), based on 94 species, found that Polycirrinae, Terebellinae, and Trichobranchinae (now all elevated to family by Nogueira et al. 2013) were monophyletic, and they further suggested that Thelepodinae is not monophyletic, which was later supported by Nogueira et al. (2013), who split them into two families, although the reasons that led Garraffoni and Lana (2008) to that conclusion are different from those of Nogueira et al. (2013).

In contrast, Rousset et al. (2003) undertook a molecular and morphological study and found well-supported monophyletic clades for Trichobranchidae and the remaining Terebellidae *sensu lato*, and they suggested that the traditional view of these two groups may be based on plesiomorphic similarities rather than homologous characters. They also inferred a sister-group relationship between Alvinellidae and Trichobranchidae. However, these results cannot be substantiated, as they only used a single species of Trichobranchidae (*Terebellides* spp., from a variety of regions of the world), which means that they did not test for monophyly of this family, and they also only used three species of Terebellidae *sensu stricto* (*Eupolymnia nebulosa*, *Lanice conchilega*, and *Neomphitrite edwardsi*) and one species of Thelepodidae (*Thelepus cincinnatus*), but no representatives of Telothelepodidae or Polycirridae were included. Thus, that study cannot provide any support for family monophyly, including the 'subfamilies' of Terebellidae *sensu lato*, now raised to families.

Struck has recently published the *Phylogeny of Annelida* (Struck 2012, 2019) in this series and has comprehensively summarized the numerous studies that have attempted to resolve the relationship of this group. Based on molecular analyses from several studies, Struck (2019) has proposed a new classification of Annelida (fig. 6.2 in Struck 2019), which is an alternative to the classification proposed by Rouse and Fauchald (1997, see fig. 73), based only on morphological data. He resurrected the classical classification of Annelida in Errantia and Sedentaria, which contains Terebelliformia (as Terebellida). The most derived position within Sedentaria is occupied by a clade composed of 'Terebellida'/Arenicolida, Opheliida, Capitellida, and Clitellata. The sister group of Clitellata is still not fully resolved; hence, the relationships between this latter and the other four taxa are also still not resolved. Although there is a strong molecular support for the relationship between 'Terebellida' and Arenicolida (Struck et al. 2008, Zrzavý et al. 2009), this relationship is hard to believe considering morphological data. Struck et al. (2008) used one species of Trichobranchidae, one of Polycirridae, and two Terebellidae *sensu stricto* and found a terebellid in the same clade as a *Polycirrus* sp., which was sister to another terebellid, which was sister to a clade consisting of a single species of Ampharetidae and Trichobranchidae, and this entire grouping was sister to a maldanid and an arenicolid based on 18S and 28S rDNA. Again, the representation of the terebelliforms was very limited. Zrzavý et al. (2009), while using more genes, only used two Terebellidae *sensu stricto*, *Lanice* and *Pista*, and two species of Trichobranchidae, *Trichobranchus* sp. (as *Artacamella*) and *Terebellides* sp., so, again, hardly representative of Terebellomorpha.

The new families recently erected by Nogueira et al. (2013), based on 85 taxa, and the subsequent studies of Polycirridae, based on 40 taxa (Fitzhugh et al. 2015), and Telothelepodinae, based on 21 taxa (Nogueira et al. 2017), are based only on morphological characters but represent the most comprehensive phylogenetic studies of the group to date.

In summary, the relationship of the terebelliforms to other polychaete families still has not been resolved, and of course, this is not helped by the lack of any fossil records for the family apart from possible tubes. We should repeat that all of these molecular studies only included a handful of terebelliforms and do not cover the full range of morphological variation found within the group.

Taxonomy

We consider that Terebellidae *sensu lato* consists of five families, Polycirridae Malmgren, 1866, Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013, Terebellidae Johnston, 1846 *sensu stricto*, Thelepodidae Malmgren, 1866, and Trichobranchidae Malmgren, 1866. Of those, Polycirridae is the most plesiomorphic (fig. 1 in Nogueira et al. 2013), although several previous studies have considered it as an apomorphic group within Terebelliformia (Glasby et al. 2004, Garraffoni and Lana 2008). The families Alvinellidae (chapter 7.7.4. pp. 145–162 Jollivet and Hourdez), Ampharetidae (chapter 7.7.2. pp. 50–67 Ebbe and Purschke), and Pectinariidae (chapter 7.7.1. pp.34–50 Hutchings et al.) will be dealt with in other chapters in this volume.

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The most important diagnostic characters to distinguish between these families are the morphology of the prostomium and peristomium, especially the upper lip, insertion of buccal tentacles, morphology of branchiae, when present, morphology of the ventral surface of anterior segments, and types of notochaetae and neurochaetae present.

Although we provide the main references for each of these diagnoses, we supplement it with our own observations based on examination of the type material or material from the type locality, which we used in the coding of taxa for our phylogenetic studies of the group (Nogueira et al. 2013, 2017, Fitzhugh et al. 2015).

Family Polycirridae Malmgren, 1866

Polycirridae counts on six genera, distinguished from each other by the presence of notopodia and neuropodia and the type of neuropodial chaetae. Parapodia are completely absent in *Hauchiella* Levinsen, 1893, whereas *Lysilla* Malmgren, 1866 and *Enoplobranchus* Verrill, 1879 only have notopodia, *Biremis* Polloni, Rowe & Teal, 1973 only has neuropodia, bearing avicular uncini, and both *Polycirrus* Grube, 1850 and *Amaeana* Hartman, 1959 have both notopodia and neuropodia, this last bearing avicular uncini in the former genus and acicular spines in the latter.

Although these genera are well separated morphologically, at least in complete specimens, a recent phylogenetic study on the family based on morphology found that only *Hauchiella* was monophyletic, in a clade inside *Polycirrus*, which is paraphyletic, whereas *Amaeana* and *Lysilla* were mixed up in an apomorphic clade, also nested within *Polycirrus* (Fitzhugh et al. 2015). *Biremis* and *Enoplobranchus* are both monotypic and also come out from within *Polycirrus* radiation (Fitzhugh et al. 2015, see fig. 2). We prefer, however, to keep the traditional genera of Polycirridae at least until more comprehensive studies are available, including molecular data.

Polycirridae Malmgren, 1866

Type genus: *Polycirrus* Grube, 1850, by monotypy

Definition: Frequently nontubiculous terebelliforms, although mucous sheaths are common. Transverse prostomium attached to dorsal surface of upper lip; basal part usually as thick horseshoe-shaped crest, eye spots absent; distal part either as another thick crest, with flaring distal lobes, with or without middorsal process, or extending along upper lip until near anterior margin of lip; prostomium frequently extending ventrally, terminating laterally to mouth. Buccal tentacles of two types at least, short ones thin, uniformly cylindrical, long tentacles stouter, expanded at tips at variable degrees, distally spatulate or more specialized. Peristomium forming lips; lips expanded, upper lip large, frequently circular and convoluted, folded into three lobes; swollen lower lip, only midventral or cushion-like across ventrum, sometimes extending posteriorly for a few segments. Segment 1 reduced, frequently only visible ventrally, sometimes completely hidden; segment 2 distinctly narrower than following segments, constricting body posteriorly to "lips head"; segment 2 usually with rectangular or pentagonal midventral shield at beginning of midventral groove, sometimes extending anteriorly through segment 1 until near posterior margin of lower lip. Anterior segments highly glandular ventrally, frequently papillose or tessellated, with paired ventrolateral pads separated from each other within pairs by midventral groove extending from segments 2 to 4 to posterior body. Branchiae absent. Notopodia, if present, beginning from segment 3, extending for a variable number of segments, usually few; bilobed, elongate notopodia, postchaetal lobes sometimes longer, notochaetae originating between lobes along all extension of notopodia, separating lobes from base on ventral side of notopodia; notochaetae winged and/or pinnate, wings of variable width. Neuropodia, if present, beginning posteriorly to notopodia, frequently from posterior thoracic segments or only on abdomen; neurochaetae as acicular spines or avicular uncini, of two types. Nephridial and genital papillae usually present, at anterior bases of all notopodia, or only the anterior ones. Pygidium smooth or with rounded ventral papilla.

Main references: Nogueira et al. 2013, 2015a, b, Fitzhugh et al. 2015.

Amaeana Hartman, 1959

Type species: *Polycirrus trilobatus* Sars, 1863, by original designation

13 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest; distal part restricted to base of upper lip, with flaring lobes and frequently also a middorsal process; prostomium extending ventrally, terminating laterally to mouth. Buccal tentacles of three types, short tentacles thin, uniformly cylindrical, intermediate ones spatulate, long buccal tentacles spatulate or more specialized, with subdistal cylindrical swelling and pointed to blunt tip; apparently, tentacles with heavily ciliated longitudinal groove only at tips, with peduncle smooth or with poorly developed longitudinal ciliary tract. Peristomium forming lips; upper lip large, frequently circular and convoluted, folded into three lobes, swollen lower lip, midventral and button-like. Segments biannulated throughout, segment 1 reduced, frequently

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visible ventrally and dorsally but laterally hidden by expanded prostomium; segment 2 distinctly narrower than following segments, with rectangular or pentagonal midventral shield at beginning of midventral groove, sometimes extending anteriorly through segment 1 until near posterior margin of lower lip. Body wall papillate throughout, papillae distinctly larger and more abundant on ventrolateral pads of anterior segments; pads usually from segment 2 to last with notopodia. Notopodia extending for a few segments, usually around 10; bilobed, elongate notopodia, lobes about same size; notochaetae throughout usually acicular, with distinctly narrow wings, inconspicuous under light microscopy, only visible under SEM; pinnate chaetae sometimes present. Neuropodia beginning after conspicuous gap of some achaetous segments posterior to termination of notopodia; neurochaetae as distally tapering acicular spines, sometimes specialized at tips. Nephridial and genital papillae present, usually at anterior bases of all notopodia. Pygidium smooth or with rounded ventral papilla.

Main references: Hutchings and Glasby 1986a, Fitzhugh et al. 2015, Nogueira et al. 2015a, b.

Biremis Polloni, Rowe & Teal, 1973

Type species: *Biremis blandi* Polloni, Rowe & Teal, 1973, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as low crest; distal part extending along upper lip until anterior border of lip. Long tentacles expanded at tips, spatulate. Peristomium forming lips; lips expanded, upper lip distinctly large, circular and convoluted, swollen lower lip, cushion-like across entire ventrum. Anterior segments with several annulations, segmentation often obscure; segment 1 visible dorsally and ventrally, laterally covered by expanded upper lip and prostomium; segment 2 conspicuous all around, distinctly narrower than following segments. Smooth, swollen ventrolateral pads present until midbody. Notopodia absent throughout, neuropodia beginning from segment 15, bilobed, both lobes bearing type 1 uncini. Genital papillae on segments 7 to 10, in equivalent position to anterior bases of notopodia, if those were present. Pygidium smooth.

Main references: Polloni et al. 1973, Nogueira et al. 2013, Fitzhugh et al. 2015.

Enoplobranchus Verrill, 1879

Type species: *Chaetobranchus sanguineus* Verrill, 1873, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest; distal part extending along upper lip until near anterior border of lip; prostomium extending ventrally, terminating laterally to mouth. Long buccal tentacles expanded at tips, spatulate. Peristomium forming lips; upper lip large, circular and convoluted, folded into three lobes, swollen lower lip, midventral, roughly rounded to rectangular, protruding, extending posteriorly until anterior margin of segment 3. Segment 1 reduced, visible dorsally and ventrally, laterally covered by expanded prostomium; segment 2 distinctly narrower than following segments, ventrally hidden by expanded lower lip. Notopodia extending to posterior segments, terminating well before pygidium; anterior notopodia conical, distally blunt; midbody notopodia dichotomously branching into as many as ~20 branches, each with two rows of pinnate chaetae at tips; posterior notopodia similar to anterior ones, unbranching. Neuropodia absent throughout. Nephridial and genital papillae absent or not visible. Pygidium with rounded ventral papilla.

Main references: Nogueira 2008, Fitzhugh et al. 2015.

Hauchiella Levinsen, 1893

Type species: *Polycirrus tribullata* McIntosh, 1869, by monotypy

3 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest; distal part as flaring lobes at base of upper lip; prostomium frequently extending ventrally, terminating laterally to mouth. Long buccal tentacles expanded at tips, spatulate, or more specialized, with subdistal cylindrical swelling and pointed to blunt tip. Peristomium forming lips; upper lip large, circular and convoluted, frequently folded into three lobes; swollen lower lip, midventral, button-like. Segments throughout biannulated or with more annulations, segment 1 reduced, usually visible dorsally and ventrally, laterally hidden by expanded prostomium; segment 2 distinctly short, narrower than following segments, usually with rectangular or pentagonal midventral shield at beginning of midventral groove, sometimes extending anteriorly through segment 1 until near posterior margin of lower lip. Body wall with transverse rows of papillae throughout or only anteriorly, papillae distinctly larger and more abundant on ventrolateral pads of anterior segments, usually present from segment 2. Parapodia absent throughout. Genital papillae may be present on some anterior segments, in equivalent position to anterior bases of notopodia, if those were present. Pygidium smooth to crenulate or with rounded ventral papilla.

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Main references: Hutchings and Glasby 1986a, Fitzhugh et al. 2015, Nogueira et al. 2015b.

Lysilla Malmgren, 1866

Type species: *Lysilla loveni* Malmgren, 1866, by monotypy
14 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest; distal part as flaring lobes restricted to base of upper lip, middorsal process sometimes present; prostomium extending ventrally, terminating laterally to mouth. Long buccal tentacles expanded at tips, spatulate, or more specialized, with subdistal cylindrical swelling and blunt tip. Peristomium forming lips; upper lip large, frequently circular and convoluted, folded into three lobes; swollen lower lip, midventral and button-like. Segments throughout biannulated or with more annulations, segment 1 reduced, usually visible dorsally and ventrally, laterally hidden by expanded prostomium; segment 2 distinctly short, narrower than following segments, usually with rectangular or pentagonal midventral shield at beginning of midventral groove, sometimes extending anteriorly through segment 1 until near posterior margin of lower lip. Body wall with transverse rows of papillae throughout or only anteriorly, papillae distinctly larger and more abundant on ventrolateral pads of anterior segments; pads usually from segment 2 to last with notopodia. Notopodia extending for a variable number of segments, usually few; bilobed, elongate notopodia, lobes about same size; notochaetae throughout usually acicular, with distinctly narrow wings, inconspicuous under light microscopy, only visible under SEM; pinnate chaetae sometimes present. Neuropodia absent throughout. Nephridial and genital papillae usually present, at anterior bases of all notopodia, or terminating one to few segments before last pair of notopodia. Pygidium smooth or with rounded ventral papilla.

Main references: Hutchings and Glasby 1986a, Fitzhugh et al. 2015, Nogueira et al. 2015b.

Polycirrus Grube, 1850

Type species: *Polycirrus medusa* Grube, 1850, by monotypy
78 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest; distal part either as flaring lobes at base of upper lip or extending along upper lip until near anterior border of lip; prostomium frequently extending ventrally, terminating laterally to mouth. Buccal tentacles of two types at least, short ones thin, uniformly cylindrical, long tentacles expanded at tips, spatulate, or more specialized, with subdistal cylindrical swelling and pointed to blunt tip. Peristomium forming lips; lips expanded, upper lip large, frequently circular and convoluted, folded into three lobes; swollen lower lip, midventral or cushion-like across ventrum, sometimes extending posteriorly for a few segments. Segment 1 visible all around or reduced to completely hidden; segment 2 distinctly narrower than following segments, usually with rectangular or pentagonal midventral shield at beginning of midventral groove, sometimes extending anteriorly through segment 1 until near posterior margin of lower lip. Body wall papillate throughout, papillae distinctly larger and more abundant on ventrolateral pads of anterior segments; pads usually from segment 2 to last with notopodia, from nearly smooth to highly tessellated. Notopodia extending for a variable number of segments; bilobed, elongate notopodia, postchaetal lobes sometimes longer; notochaetae winged, wings of variable width, usually conspicuous under light microscopy, or pinnate, sometimes both types present on same parapodium, one in each row. Neuropodia present, beginning from anterior segments, from posterior thoracic segments, from one to two last segments with notopodia, or only on abdomen, sometimes with gap of some segments between termination of notopodia and beginning of neuropodia; neurochaetae as avicular uncini of type 1 or 2, rarely both types present, type 1 on thoracic chaetigers and type 2 on abdomen. Nephridial and genital papillae usually present, at anterior bases of notopodia, only on anterior segments or until termination of notopodia or near it. Pygidium smooth or with rounded ventral papilla.

Main references: Glasby and Hutchings 2014, Fitzhugh et al. 2015, Nogueira et al. 2015b.

Family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013

Telothelepodidae is characterized by a narrow and elongate upper lip, distal part of prostomium frequently forming a large middorsal tongue-like process and, in most taxa, a particular type of winged chaetae, the bayonet-like chaetae (Nogueira et al. 2010, 2013, 2018). There are two pairs of branchiae, on segments 2 and 3, each with multiple single and relatively short filaments, originating independently from each other directly from the body wall or from specialized, apparently glandular, dorsolateral cushion-like pads (Hutchings et al. 2015, Nogueira et al. 2018).

The first telothelepodid described was *Thelepides collaris* Southern, 1914, which was described as a new genus, but Southern (1914) did not notice that the generic name was preoccupied by a terebellid, so another generic name was attributed by Caullery (1915), who named that species as *Parathelepus collaris*. Other taxa of this family

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were subsequently described by Day (1955), Hutchings (1974, 1977), Mohammad (1980), Hutchings and Glasby (1986b), Londoño-Mesa (2009), Hutchings et al. (2015), and Nogueira et al. (2018), resulting in 4 genera and 15 currently known species for the group.

Previously, the only character used to distinguish between genera of telothelepodids was the segment on which neuropodia begin, and six genera were valid (Hutchings et al. 2015). However, a recent phylogenetic analysis based on morphological characters suggested a new arrangement for the species in this family, which are now divided into four genera, two of which monotypic (Nogueira et al. 2017, 2018). The segment on which begin is now viewed as a specific character and the genera are separated by the morphology of the lower lip and segment 1 (Nogueira et al. 2017, 2018).

Similar to Polycirridae, nearly all species of telothelepodids have notopodia beginning on segment 3, the exception being *Parathelepus praecox* Nogueira, Carrerette, Hutchings & Fitzhugh, 2018, the members of which have notopodia beginning on segment 2. The number of pairs of notopodia presents little variation in this group; members of most species have 15 pairs, extending until segment 17, but *Rhinothelepus mexicanus* (Hutchings & Glasby, 1986), previously allocated to the monotypic genus *Glossothelepus* Hutchings & Glasby, 1986, and *Parathelepus anomalus* Londoño-Mesa, 2009, previously the type and only species of *Kritzlerius* Londoño-Mesa, 2009, are both known from a few incomplete specimens, with notopodia until the end of fragments, with at least 23 pairs of notopodia in *R. mexicanus* and 17 in *P. anomalus* (Nogueira et al. 2017, 2018).

Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013

Type genus: *Telothelepus* Day, 1955, by original designation (Nogueira et al. 2013)

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots frequently present in one pair of dorsolateral clusters, each with several rows of eye spots; distal part at base of upper lip, frequently with low or erect middorsal tongue-like process, fused to upper lip at variable degrees, with free distal lobe(s), or free from the base. Buccal tentacles of two types, short ones thin, uniformly cylindrical, long tentacles stouter and expanded at tips, slightly spatulate. Peristomium forming lips and continuing dorsally at least for short extension, with dorsolateral nuchal organs at margin with prostomium; lips expanded, upper lip distinctly elongate and narrow, undulated to convoluted; swollen lower lip extending across ventrum, cushion-like or segment-like, frequently deeply grooved. Either segment 1 or 2 reduced, not forming complete ring in many species. Anterior segments glandular ventrally, smooth, discrete shields absent and frequently with glandular regions poorly developed in comparison to other families of Terebellidae *sensu lato*; midventral groove frequently extending from anterior segments. Two pairs of branchiae on segments 2 and 3, each pair with simple thin, curled, and relatively short filaments progressively tapering to tips, originating from raised crests on anterior margins of segments 2 and 3 or from specialized, apparently glandular, dorsolateral cushion-like pads occupying from anterior margins to level of posterior bases of notopodia of those segments. Members of all but one species with notopodia beginning from segment 3, extending for at least 15 segments; notopodia as short cones, notochaetae originating from central core on top, distal lobes absent; notochaetae winged, sometimes with bulbous head and alimbate tips (bayonet-like chaetae), at least in anterior row of anterior thoracic segments. Neuropodia beginning posteriorly to notopodia, usually around segments 8 to 12; neuropodia in conjunction with notopodia as sessile tori, as distinctly low pinnules after notopodia terminate; neurochaetae as avicular uncini about as long as high, with shortly triangular heel directed posteriorly, wide and slightly curved base, and dorsal button near midlength of uncini but closer to anterior margin. Nephridial and genital papillae, if conspicuous, on segments 5 to 7, posterior to bases of notopodia.

Main references: Nogueira et al. 2013, 2017, 2018, Fitzhugh et al. 2015.

***Mesopothelepus* Nogueira, Fitzhugh, Hutchings & Carrerette, 2017**

Type species: *Telothelepus macrothoracicus* Mohammad, 1980, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part at base of upper lip, middorsal process present, basally fused to upper lip with free distal lobe. Buccal tentacles all uniformly cylindrical. Peristomium forming lips and complete annulation; lips expanded, upper lip elongate and narrow, convoluted; swollen lower lip extending across ventrum, cushion-like, deeply grooved. Segments 1 and 2 visible all around, shorter midventrally, partially covered by expanded lower lip. Branchial filaments originating from cushion-like pads. Notopodia extending for 15 segments, until segment 17; only narrowly winged notochaetae. Neuropodia beginning on segment 18, first after termination of notopodia. Nephridial and genital papillae present, on segments 5 to 7.

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Main references: Mohammad 1980, Nogueira et al. 2010, 2013, 2017, 2018.

Parathelepus Caullery, 1915

Type species: *Thelepides collaris* Southern, 1914, by monotypy
8 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present; distal part at base of upper lip, middorsal process distinctly low, almost inconspicuous, or well developed, with elongate free lobe. Buccal tentacles of two types, short ones thin, uniformly cylindrical, long tentacles slightly expanded at tips. Peristomium forming lips and complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, upper lip elongate and narrow, undulated to highly convoluted; swollen, usually cushion-like lower lip, smooth, extending across ventrum. Segment 1 short, visible dorsally and laterally, covered by expanded lower lip ventrally. Branchial filaments originating in a row at anterior margins of segments 2 and 3, or from cushion-like pads, extending from anterior margins to level of notopodia. Notopodia extending for a variable number of segments, frequently 15; notopodia as short cones; narrowly winged and bayonet-like chaetae present. Neuropodia beginning on a thoracic segment. Nephridial and genital papillae, if present, on segments 5 to 7.
Main references: Southern 1914, Caullery 1915, Nogueira et al. 2010, 2013, 2017, 2018.

Rhinothelepus Hutchings, 1974

Type species: *Rhinothelepus lobatus* Hutchings, 1974, by monotypy
5 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present; distal part at base of upper lip, middorsal process present, usually erect, with distally free lobe. Buccal tentacles of two types, short ones thin, uniformly cylindrical, long tentacles slightly expanded at tips. Peristomium forming lips and complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, upper lip distinctly elongate and narrow, usually highly convoluted; segment-like lower lip, extending across ventrum, deeply grooved. Branchial filaments originating from cushion-like pads. Notopodia extending for a variable number of segments, frequently 15; notopodia as short cones; narrowly winged and bayonet-like chaetae present. Neuropodia beginning on segment 8 or 9. Nephridial and genital papillae usually posterior to notopodia of segments 5 to 7.
Main references: Hutchings 1974, Nogueira et al. 2010, 2013, 2017, 2018, Hutchings et al. 2015.

Telothelepus Day, 1955

Type species: *Telothelepus capensis* Day, 1955, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part at base of upper lip, middorsal process present, fused to upper lip along entire length or only basally, with free distal lobe. Buccal tentacles of two types, short ones thin, uniformly cylindrical, long tentacles stouter, expanded at tips, spatulate. Peristomium forming lips and complete annulation; lips expanded, upper lip elongate and narrow, convoluted; swollen lower lip extending across ventrum, cushion-like, deeply grooved. Segments 1 and 2 visible all around, shorter midventrally, partially covered by expanded lower lip. Branchial filaments originating from cushion-like pads. Notopodia extending for 15 segments, until segment 17; narrowly winged and bayonet-like chaetae both present. Neuropodia beginning on segment 18, first after termination of notopodia. Nephridial and genital papillae present, on segments 5 to 7.
Main references: Day 1955, Nogueira et al. 2010, 2013, 2017, 2018.

Family Thelepodidae Hessle, 1917

Thelepodids are a well-known group of Terebelliformia, characterized by the presence of short, hood-like upper lip, about as long as high, usually two to three pairs of branchiae on segments 2 and 3 or segments 2 to 4, each with multiple single and relatively short filaments, frequently curled, originating independently from each other directly from body wall or from specialized, apparently glandular, dorsolateral cushion-like pads. Uncini of thelepodids are also characteristic, usually longer than high, with strongly curved base (convex), and dorsal button as a tuft of bristles at the anterior margin of uncini or near it, although some taxa have uncini similar to those of telothelepodids.

The group was first described by Hessle (1917) and remained under the status of subfamily until Nogueira et al. (2013) raised it to familial level. The authors also restricted the diagnosis of this family, however, to exclude Telothelepodidae Nogueira, Fitzhugh and Hutchings, 2013 after a phylogenetic analysis of Terebelliformia based on morphological data (Nogueira et al. 2013).

As currently conceived, the family counts on five genera, *Euthelepus* McIntosh, 1885, *Pseudostreblosoma*

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Hutchings & Murray, 1984, *Pseudothelepus* Hutchings, 1997a, *Streblosoma* Sars, 1872, and *Thelepus* Leuckart, 1849, distinguished from each other by the presence of lobes on anterior segments, segments on which notopodia and neuropodia begin, and the morphology of notochaetae. The internal relationships within Thelepodidae, however, have not yet been investigated.
Main references: Nogueira et al. 2010, 2013.

Thelepodidae Hessle, 1917
Type genus: *Thelepus* Leuckart, 1849, by original designation (Hessle 1917)
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots frequently present, in short rows at each lateral, or extending transversely across basal part of prostomium, usually progressively more spaced toward dorsal midline, with middorsal gap or not; distal part at base of upper lip, short, from nearly indistinct to shelf-like. Buccal tentacles all uniformly thin and cylindrical to slightly spatulate distally. Peristomium forming lips, sometimes also complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, button-like, midventral lower lip. Segment 1 usually present all around, frequently with ventral lobe marginal to mouth; segment 2 typically with anterior margin as protruding crest, at least ventrally; lobes on following anterior segments sometimes present. Anterior segments highly glandular ventrally, smooth to highly corrugated between neuropodia within pairs, discrete shields absent; midventral groove frequently extending from anterior segments with notopodia. Two to three pairs of branchiae, on segments 2 and 3 or segments 2 to 4, each pair with simple thin, curled, and relatively short filaments progressively tapering to tips, leaving middorsal gap or not between filaments within pairs; branchial filaments originating directly from the body wall or from specialized, apparently glandular, dorsolateral cushion-like pads. Notopodia beginning on segments 2 and 3, usually extending to midbody, at least, sometimes until near posterior end; cylindrical to rectangular, distally bilobed notopodia, notochaetae originating between lobes; most taxa with winged notochaetae only, with wings of variable width, distally serrate notochaetae sometimes also present; bayonet-like and pinnate chaetae both absent. Neuropodia beginning posteriorly to notopodia, on segments 4 to 6, typically on segment 5; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini frequently longer than high, with short triangular heel directed posteriorly, distinctly curved and wide base, and dorsal button near anterior margin of uncini, or within anterior third of distance between anterior margin of uncini and base of main fang. Nephridial and genital papillae usually present, on segments 4 to 7, posterior to bases of notopodia or between parapodial lobes.
Main references: Hutchings and Glasby 1987, Nogueira et al. 2013, Hutchings et al. 2015.

***Euthelepus* McIntosh, 1885**
Type species: *Euthelepus setubalensis* McIntosh, 1885, by monotypy
6 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots frequently present; distal part at base of upper lip, short, from nearly indistinct to shelf-like. Buccal tentacles all uniformly cylindrical to leaf-like, deeply grooved with flaring margins. Peristomium forming lips, sometimes also complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, button-like, midventral lower lip, with ventral lobe marginal to mouth. Segment 1 fused ventrally with lower lip lobe; segments 2 and 3 or segments 2 to 4 with ventrolateral to lateral lobes, typically inserted progressively more laterally. Three pairs of branchiae, beginning from segment 2, each pair with relatively few, thick, and elongate branchial filaments progressively tapering to tips; filaments in continuous row across dorsum, middorsal gap absent or very narrow, at least on segment 2. Notopodia beginning from segment 3, extending for a variable number of segments, terminating well before pygidium; cylindrical to rectangular, distally bilobed notopodia, notochaetae originating between lobes, postchaetal lobe sometimes longer; winged notochaetae in anterior row, posterior row with winged or serrated notochaetae, sometimes changing types from anterior to posterior segments. Neuropodia typically beginning on segment 5, but one species with neuropodia from segment 4 and another from segment 6; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini frequently longer than high, with shortly triangular heel directed posteriorly, distinctly curved and wide base, and dorsal button near anterior margin of uncini, with conspicuous prow. Nephridial and genital papillae usually inconspicuous or absent.
Main references: Hutchings and Glasby 1986c, Hutchings et al. 2015.

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Pseudostreblosoma Hutchings & Murray, 1984

Type species: *Pseudostreblosoma serratum* Hutchings & Murray, 1984, by monotypy

3 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present, from only laterally to across basal part of prostomium, with middorsal gap; distal part at base of upper lip, short, as a thick crest to shelf-like. Buccal tentacles all uniformly cylindrical to leaf-like, deeply grooved with flaring margins. Peristomium forming lips, and usually also complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, button-like, midventral lower lip. Segment 1 usually with ventral lobe marginal to mouth; segments 2 to 4 sometimes with thick and low lateral lobes on anterior margin. Three pairs of branchiae, beginning from segment 2, each pair with relatively few, thick, and elongate branchial filaments progressively tapering to tips; filaments originating directly from body wall or cushion-like pads, dorsally to notopodia, with conspicuous middorsal gap between filaments of each side within pairs. Notopodia beginning on segment 2 and extending to midbody, at least; rectangular notopodia, notochaetae originating between relatively large distal lobes; anterior segments with narrowly winged notochaetae only, from midbody parapodia distally serrate notochaetae also present, in anterior row. Neuropodia beginning on segment 5; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini about as long as high, with short triangular heel directed posteriorly, slightly curved and wide base, and dorsal button at anterior third of distance between anterior margin of uncini and base of main fang, but away from anterior border, with conspicuous prow. Nephridial and genital papillae not visible.

Main references: Hutchings and Murray 1984, Nogueira and Alves 2006.

Pseudothelepus Hutchings, 1997a

Type species: *Pseudothelepus binara* Hutchings, 1997a, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots in continuous transverse row; distal part at base of upper lip, short, nearly indistinct. Buccal tentacles slightly spatulate distally, deeply grooved (few remaining on both known specimens). Peristomium forming lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin straight; swollen, button-like, midventral lower lip. Segment 1 with ventral lobe marginal to mouth; anterior segments with anterior margins as thick, protruding crests laterally and ventrally, segment 6 with dorsal lobe as low collar of uniform length extending across dorsum, segment 7 with low dorsolateral lobes of uniform length. Three pairs of branchiae, on segments 2 to 4, each pair with thin, curled, and relatively short filaments progressively tapering to tips; filaments originating directly from body wall, dorsally to notopodia, those from segment 2 extending laterally to level of notopodia for short extension, with conspicuous middorsal gap between filaments of each side within pairs. Notopodia beginning on segment 3, extending to end of fragments on both known specimens, at least 31 to 32 pairs; rectangular notopodia, notochaetae originating between relatively large distal lobes; narrowly winged notochaetae in both rows. Neuropodia beginning on segment 6; neuropodia in conjunction with notopodia as fleshy, swollen ridges; neurochaetae as avicular uncini as long as high, with short triangular heel directed posteriorly, distinctly curved and wide base, and dorsal button near anterior margin of uncini. Nephridial and genital papillae on segments 4 to 7, posterior to bases of notopodia, between parapodial lobes.

Main references: Hutchings 1997a, Nogueira et al. 2010, 2013.

Remarks: The generic name is preoccupied by *Pseudothelepus nyanganus* Augener, 1918; however, these two species do not belong in the same genus, as *P. nyanganus* is a species of *Streblosoma* (Nogueira personal observations). A new generic name will be provided to *P. binara* by Nogueira and Hutchings (in preparation).

Streblosoma Sars, 1872

Type species: *Grymaea bairdi* Malmgren, 1866, by original designation (Malmgren 1866)

45 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present, from only laterally to across basal part of prostomium, with or without middorsal gap; distal part at base of upper lip, short, from nearly indistinct to shelf-like. Buccal tentacles all uniformly cylindrical to leaf-like, deeply grooved with flaring margins. Peristomium forming lips, and frequently also complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, button-like, midventral lower lip. Segment 1 usually with ventral lobe marginal to mouth;

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other lobes absent, but at least segment 2 with thickened anterior margin as protruding crest, ventrally or all around. Branchiae usually present, two to three pairs, beginning from segment 2, each pair with relatively thin and usually short branchial filaments, progressively tapering to tips; filaments originating directly from body wall or cushion-like pads, dorsally to notopodia, those of segment 2 sometimes extending laterally from notopodia for short extension, with or without conspicuous middorsal gap between filaments of each side within pairs. Notopodia beginning on segment 2, extending for a variable number of segments, at least to midbody; cylindrical to rectangular notopodia, notochaetae originating between relatively large distal lobes; winged notochaetae in both rows throughout, those from anterior row broadly winged in several species, wings somewhat twisted, posterior row with narrowly winged notochaetae. Neuropodia beginning on segment 5; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini about as long as high, with short triangular heel directed posteriorly, usually distinctly curved and wide base, and dorsal button near anterior margin of uncini or at anterior third of distance between anterior margin of uncini and base of main fang, with or without conspicuous prow; uncini usually in straight rows, but some species with some midbody parapodia, at least, with uncini in C-shaped to looped rows. Nephridial and genital papillae usually present, on segments 4 to 7, posterior to bases of notopodia or between parapodial lobes.

Main references: Hutchings et al. 2015, Lezzi and Giangrande 2019, Nogueira 2019.

Thelepus Leuckart, 1849

Type species: *Amphitrite cincinnata* Fabricius, 1780, by original designation

57 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present, from only lateral to across basal part of prostomium, with or without middorsal gap; distal part at base of upper lip, short, from nearly indistinct to shelf-like. Buccal tentacles all uniformly cylindrical to leaf-like, deeply grooved with flaring margins. Peristomium forming lips, and frequently also complete annulation, with dorsolateral nuchal organs as ciliated grooves; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, button-like, midventral lower lip. Segment 1 usually with ventral lobe marginal to mouth; other lobes absent, but at least segment 2 with thickened anterior margin as protruding crest, ventrally or all around. Branchiae usually present, 2 to 3 pairs, beginning from segment 2, each pair with relatively thin and usually short branchial filaments, progressively tapering to tips, leaving middorsal gap or not between filaments within pairs; filaments originating directly from body wall or cushion-like pads, dorsally to notopodia, those of segment 2 sometimes extending laterally from notopodia for short extension, with or without conspicuous middorsal gap between filaments of each side within pairs. Notopodia beginning on segment 3, extending for a variable number of segments, at least to midbody; cylindrical to rectangular notopodia, notochaetae originating between relatively large distal lobes; winged notochaetae in both rows throughout, those from anterior row broadly winged in several species, with somewhat twisted wings, posterior row with narrowly winged notochaetae. Neuropodia beginning on segment 5; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini about as long as high, with short triangular heel directed posteriorly, usually distinctly curved and wide base, and dorsal button near anterior margin of uncini, with or without conspicuous prow. Nephridial and genital papillae usually present, on segments 4 to 7, posterior to bases of notopodia or between parapodial lobes.

Main references: Hutchings et al. 2015, Nogueira 2019.

Family Terebellidae Johnston, 1845

Terebellidae is a well-known group of Terebelliformia, characterized by the presence of short, hood-like upper lip, about as long as high, usually one to three pairs of branching branchiae, originating dorsolaterally from the main stalk or a single point on the body wall, on either side of pairs, and anterior segments that are highly glandular ventrally, with discrete rectangular to trapezoidal midventral shields. Uncini of terebellids are about as long as high, with a slightly curved base, and the dorsal button is as a tuft of bristles usually at about midlength of the distance between the base of main fang and the anterior margin of uncini, in such way that the tuft of bristles holds the tip of main fang possibly to protect the tissues from main fang sharpness; long handles originating from the heel or entire base are present on the anterior tori of several genera. More important than the morphology of the uncini, however, is the fact that they are arranged in double rows from around segments 10 to 11, usually to the termination of notopodia or close to it, which is the most important diagnostic feature of this family.

As currently conceived, Terebellidae counts on about 50 genera, several of which are monotypic. Those genera are distinguished from each other mostly by the

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presence and morphology of lobes on anterior segments, the number of pairs of branchiae and their morphology, the number of pairs of notopodia, the segment of which notopodia and neuropodia begin, and the morphology of notochaetae and neurochaetae. The internal relationships within Terebellidae as currently conceived were studied by McHugh (1995) but with low number of genera and only the type species of each; therefore, the relationships among those genera and their monophyly still remain largely unknown. Nogueira et al. (2013) included a large number of species of terebellids in their phylogenetic analysis of Terebelliformia, but, as the scope of that study was more general, the monophyly of the genera of Terebellidae and the relationships among them still await a more detailed phylogenetic analysis.

Terebellidae Johnston, 1846

Type genus: *Terebella* Linnaeus, 1767, by original designation

Diagnosis: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots frequently present, in short rows at each lateral, or extending transversely across basal part of prostomium, eye spots usually progressively more spaced toward dorsal midline, with middorsal gap or not; distal part at base of upper lip, short, from nearly indistinct to shelf-like. Buccal tentacles all usually uniformly cylindrical. Peristomium usually forming lips only; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, usually button-like and midventral lower lip (distinctly expanded in *Artacama*). Segment 1 terminating laterally to ventrolaterally, partially fused to expanded lower lip, or developed, forming lobes of variable extension and position. Lobes on anterior segments frequently present, of variable length, sometimes extending to segments 5 to 7. Anterior segments highly glandular ventrally, with discrete, smooth to corrugated, rectangular to trapezoidal midventral shields extending from anterior segments until termination of notopodia or near it; midventral groove extending from termination of midventral shields. Two to three pairs of branchiae usually present, but three genera have a single pair and several are abranchiate; branchial filaments originating all together from a single point on body wall, on either side of branchiferous segments, unbranched, or, more frequently, originating from a conspicuous main stalk on either side of pair, branching from one to several levels, in plumose (spiraled), dichotomous, pectinate, or arborescent arrangement. Notopodia beginning on segments 2 to 5, segment 4 in most genera, usually extending to midbody, around segment 20, but sometimes present on fewer segments or extending more posteriorly for variable extension, rarely until near posterior end; first pairs of notopodia inserted dorsolaterally, progressively more laterally, then vertically aligned; cylindrical to rectangular notopodia, notochaetae originating from central core on top, distal lobes absent; notochaetae distally winged, wings of variable length and width, or serrate, sometimes with wings at midlength, basally to a serrated blade; some more specialized types of notochaetae may be present. Neuropodia beginning posteriorly to notopodia, on segments 5 to 9, usually on segment 5; neuropodia in conjunction with notopodia as low, sessile ridges, sometimes continuing posteriorly until pygidium, but most taxa with rectangular to cylindrical or foliaceous neuropodial pinnules after notopodia terminate; neurochaetae as avicular uncini usually as long as high, with short triangular heel directed posteriorly, slightly curved and wide base, and dorsal button as a tuft of bristles at about midlength of the distance between base of main fang and anterior margin of uncini in most taxa; some genera with long-handled uncini on a variable number of anterior segments, handles originating from heel or entire base; uncini arranged in double rows from around segment 11 usually until termination of notopodia, but several genera with double rows extending to posterior body. Nephridial and genital papillae usually present on some anterior segments, posterior to bases of notopodia or between parapodial lobes.

Main references: Hutchings and Glasby 1988, Nogueira et al. 2010, 2013, 2015d.

***Amphitrite* O.F. Müller, 1771**

Type species: *Amphitrite cirrata* O.F. Müller, 1771 *in* 1776, by monotypy

22 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots may be present; distal part shelf-like. Buccal tentacles all usually uniformly cylindrical. Peristomium forming lips and continuing dorsally for short extension, not forming complete ring; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded and slightly undulated; narrow, rectangular, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, ventrally developed, with midventral lobe marginal to mouth. Lobes on anterior segments present, of variable length, usually on segments 2 to 4. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal shields. Two to three pairs of branchiae, usually three pairs, on segments 2 to 4; unbranched branchial filaments originating

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all together from a single point on body wall, on either side of branchiferous segments, or originating from a conspicuous main stalk, branching from one to several levels, in dichotomous or arborescent arrangements. Rectangular to conical notopodia beginning on segment 4, extending for 17 segments in most species, until segment 20, but some taxa with notopodia extending more posteriorly, sometimes for around 40 segments; notochaetae all broadly winged medially and finely serrated distally. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in partially intercalated double rows, with prows aligned, from segment 11 until termination of notopodia. Nephridial papillae on segment 3, genital papillae on some anterior segments, beginning from segment 6, between parapodial lobes.

Main references: Hutchings and Glasby 1988, Londoño-Mesa 2009 (as *Neoamphitrite* Hessle, 1917), Nogueira et al. 2013.

Amphitritides Augener, 1922

Type species: *Terebella gracilis* Grube, 1860, by original designation

7 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots may be present; distal part shelf-like. Buccal tentacles all usually uniformly cylindrical. Peristomium forming lips and continuing dorsally for short extension, not forming complete annulation; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded, slightly undulated; narrow, rectangular, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, ventrally developed, with midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal shields. Two pairs of short, arborescent branchiae, on segments 2 and 3, with short main stalks. Rectangular to conical notopodia beginning on segment 4, extending a variable number of segments; notochaetae all medially winged and finely serrated distally, with basally bulbous wings. Neuropodia beginning on segment 5, as low, sessile ridges throughout; neurochaetae as short-handled avicular uncini, in completely separate double rows, beak-to-beak arrangement, from segment 11 until posterior body. Nephridial papillae on segment 3, genital papillae on some anterior segments, beginning from segment 6, between parapodial lobes or at anterior bases of notopodia.

Main references: Hutchings and Glasby 1988, Nogueira and Hutchings 2007, Nogueira et al. 2013.

Arranooba Hutchings & Glasby, 1988

Type species: *Arranooba booromia* Hutchings & Glasby, 1988, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all missing in only known specimen. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin nearly straight; short, button-like, midventral lower lip, almost completely covered by lobes of segment 1. Segment 1 conspicuous all around, dorsally narrow, with pair of lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip. Lobes on anterior segments present, segment 2 oblique ventrally, covering segments 3 to 4, with low midventral lobe; segment 3 with pair of high lateral lobes, higher dorsolaterally, progressively lower ventrally, terminating ventrolaterally. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Branchiae absent. Rectangular to conical notopodia beginning on segment 4, extending for 17 segments, until segment 20; broadly winged notochaetae, with basally broader wings, and quill-like chaetae; notochaetae of segment 15 distinctly stouter than those of other chaetigers, with similar morphology. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in completely intercalated double rows from segment 11 until termination of notopodia. Nephridial and genital papillae inconspicuous or absent. Pygidium slightly crenulate.

Main references: Hutchings and Glasby 1988, Nogueira et al. 2013.

Artacama Malmgren, 1866

Type species: *Artacama proboscidea* Malmgren, 1866, by monotypy

9 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like and bilobed. Buccal tentacles of two types, both short in comparison to the tentacles of other terebellids, in two lengths, short tentacles thin, uniformly cylindrical, long tentacles spatulate. Peristomium restricted to lips; lips expanded, large upper lip, hood-like, distal margin convoluted; distinctly expanded lower lip, forming

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large conical, distally blunt papillate process. Segment 1 dorsally narrow, ventrally fused to lower lip. Lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular trapezoidal shields. Three pairs of branchiae, on segments 2 to 4; unbranching branchial filaments originating all together from a single point on body wall, on either side of branchiferous segments. Almost rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all broadly winged, with bulbous wings basally. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and large foliaceous pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest and dorsal button at base of main fang, in completely separated double rows, beak-to-beak arrangement, from segment 11 until termination of notopodia. Nephridial papillae on segment 3, genital papillae on segments 6 to 8, between parapodial lobes. Pygidium smooth.

Main references: Holthe 1986b, Nogueira et al. 2013.

Remarks: The above definition varies considerably from Holthe (1986b) and is based mostly on our own observations.

Articulatia Nogueira, Hutchings & Amaral, 2003

Type species: *Articulatia aberrans* Nogueira, Hutchings & Amaral, 2003, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present laterally; distal part nearly indistinct. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin straight; short, button-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Branchiae absent. Conical notopodia beginning on segment 5, extending for a variable number of segments, 12 to 21, until segments 16 to 25; anterior notopodia with broadly winged notochaetae in both rows, posterior notopodia with medially winged and distally serrated chaetae, wings basally bulbous, those from anterior row with deep cut between shaft and blade (deep-cut chaetae). Neuropodia beginning on segment 6, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in partially intercalated double rows, prows aligned, from segment 11 until a few segments before pygidium. Nephridial and genital papillae inconspicuous or absent. Pygidium papillate.

Main references: Nogueira et al. 2003, 2013.

Axionice Malmgren, 1866

Type species: *Terebella flexuosa* Grube, 1860, by original designation

5 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots may be present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded and slightly undulated; button-like, midventral lower lip, almost completely covered by lobes of segment 1. Segment 1 conspicuous all around, dorsally narrow, with pair of lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip. Segment 2 frequently with single, low midventral lobe, segment 3 with pair of large, distally rounded, lateral lobes, segment 4 with pair of low and thick lateral flaps. Anterior segments highly glandular ventrally, with discrete, rectangular to trapezoidal shields; anterior shields corrugated then smooth. Single pair of short, dichotomously branching branchiae, on segment 2, with short main stalks. Approximately rectangular notopodia beginning on segment 4, extending 15 to 16 segments, until segments 18 and 19; narrowly winged notochaetae throughout, wings slightly broader basally. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia, and conical to rectangular pinnules posteriorly; neurochaetae as short-handled avicular uncini, in partially intercalated double rows, prows aligned, from segment 11 until termination of notopodia, or one to two segments before. Nephridial papillae usually present on segment 3, genital papillae on some anterior segments, beginning from segment 6, posterior and dorsal to notopodia. Pygidium with digitiform papillae.

Main references: Holthe 1986b, Nogueira et al. 2013.

Remarks: The above diagnosis differs from Holthe (1986b) and is based mostly on our own observations.

Genus *Baffinia* Wesenberg-Lund, 1950

Type species: *Terebella hesslei* Annenkova-Chlopina, 1924, by monotypy

2 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots may be present; distal part nearly indistinct. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin straight; short, button-like, midventral lower lip. Segment 1 conspicuous all

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around, dorsally narrow, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Branchiae absent. Approximately cylindrical notopodia beginning on segment 4, extending until posterior body, close to pygidium; anterior notopodia with medially winged, distally serrated notochaetae in both rows, posterior notopodia with alimbate, distally serrated notochaetae, with blade at an angle with shaft. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini throughout, in completely separate double rows, beak-to-beak arrangement, from segment 11 until few segments before pygidium. Nephridial and genital papillae, if present, on segments 3 and 6 to 7, genital papillae posterior and dorsal to notopodia. Pygidium smooth to slightly crenulate.

Main references: Fournier and Barrie 1984, Hutchings and Glasby 1988, Nogueira et al. 2013.

Betapista Banse, 1980

Type species: *Betapista dekkerae* Banse, 1980, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, as long as wide to wider than long, distal margin rounded and slightly undulated; button-like, midventral lower lip, almost completely covered by lobes of segment 1. Segment 1 conspicuous all around, dorsally narrow, with pair of lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip. Segment 2 with pair of triangular crests dorsally, segments 3 and 4 with large, distally rounded and progressively shorter pairs of lateral lobes. Anterior segments highly glandular ventrally, with discrete, rectangular to trapezoidal shields; anterior shields corrugated then smooth. Three pairs of progressively shorter branchiae, on segments 3 to 5[1], with long main stalk and short arborescent branches terminating all at same level. Almost rectangular notopodia beginning on segment 4, extending 17 segments, until segment 20; notochaetae all narrowly winged, with wings slightly broader basally. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and conical to rectangular pinnules posteriorly; neurochaetae as avicular uncini with stout handles on segments 5 to 7, originating from almost entire base, short-handled from segment 8; uncini in completely intercalated double rows from segment 11 until termination of notopodia. Nephridial papillae present on segment 3, genital papillae on segments 6 to 9, posterior and dorsal to notopodia, intersegmental. Pygidium unknown.

Main references: Banse 1980, Nogueira et al. 2013.

Eupistella Chamberlin, 1919

Type species: *Eupista darwini* McIntosh, 1885, by original designation

4 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded; button-like, midventral lower lip, almost completely covered by lobes of segment 1. Segment 1 conspicuous all around, dorsally narrow, with pair of triangular ventrolateral lobes extending anteriorly to level of upper lip, probably connected to each other by lower membrane across ventrum, partially exposing lower lip. Segments 2 and 3 each with pair of large, triangular, distally rounded lobes, connected to each other within pairs by membranes across ventrum; lobes originating progressively more laterally, those of segment 2 ventrolateral, lateral lobes on segment 3; segment 4 with paired, thickened dorsolateral crests, connected to each other by low lobe across dorsum. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Two pairs of branchiae, on segments 2 and 3, each with single thick, unbranching filament on either side of pair, basally stouter, abruptly tapering on distal third. Almost rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all narrowly winged, wings slightly broader basally on one side. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and conical to rectangular pinnules posteriorly; neurochaetae as avicular uncini with thin handles originating only from heel, short-handled after notopodia terminate; uncini in completely intercalated double rows from segment 11 until termination of notopodia. Nephridial and genital papillae usually present on segments 3 and 5 to 8, between parapodial lobes. Pygidium with digitiform papillae.

1 Holotype is considered as an abnormal specimen. Specimens belonging to the type and only known species usually have branchiae on segments 2 to 4 and genital papillae on segments 6 to 8 (Leslie Harris, NHMLAC, personal communication).

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Main references: Fauchald 1977, Nogueira et al. 2013.
Remarks: The arrangement of lateral lobes is difficult to observe given the damaged type specimen.

Eupolymnia Verrill, 1900

Type species: *Amphitrite nesidensis* Delle Chiaje, 1828, by original designation
23 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, wider than long, distal margin rounded, frequently undulated; button-like, midventral lower lip, almost completely covered by lobes of segment 1. Segment 1 conspicuous all around, dorsally narrow, with pair of low ventrolateral lobes connected to each other by midventral lobe marginal to mouth. Segments 2 to 4 with pairs of progressively shorter and more laterally inserted lobes, those on segment 2 ventrolateral and frequently connected to each other by low collar-like lobe across ventrum. Anterior segments highly glandular ventrally, with discrete rectangular shields, anterior shields frequently corrugated. Three pairs of branchiae, on segments 2 to 4, each with single short and thick main stalk, dichotomously branching to short distal filaments. Conical to roughly rectangular notopodia beginning on segment 4, extending 17 segments, until segment 20; notochaetae all narrowly winged, wings slightly broader basally on one side. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and conical to rectangular pinnules posteriorly; neurochaetae as short-handled avicular uncini, in completely intercalated double rows from segment 11 until termination of notopodia. Nephridial and genital papillae present, from segments 2 or 3, extending for few anterior segments, between parapodial lobes or equivalent position on anterior segments. Pygidium crenulate to papillate.
Main references: Capa and Hutchings 2006, Carrerette and Nogueira 2015a, Nogueira et al. 2015d.

Hadrachaeta Hutchings, 1977

Type species: *Hadrachaeta aspeta* Hutchings, 1977, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded; rectangular, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, with midventral lobe marginal to mouth. Segment 2 with swollen anterior margin laterally and more pronounced ventrally, cushion-like; segment 3 laterally swollen along all extension, protruding, with pair of short and thick lateral lobes; segment 4 with pair of high, triangular, and distally rounded lateral lobes; segment 5 with pair of low and rounded lateral lobes, with bases broader than those of segment 4. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Three pairs of progressively shorter branchiae, on segments 2 to 4, with unbranching filaments originating in pectinate arrangement from almost inconspicuous main stalk. Almost rectangular notopodia beginning on segment 4, extending 16 segments, until segment 19; notochaetae all medially winged and finely serrated distally, with distinctly narrow wings. Neuropodia beginning on segment 5, as low, sessile ridges throughout; first four pairs of neuropodia, on segments 5 to 8, with much darker neurochaetae, distally rounded, spoon-shaped, main fang absent, and stout handle originating from entire base; from segment 9, remarkably small, short-handled avicular uncini, in partially intercalated double rows, prows aligned, from segment 11 until posterior body; posterior neuropodia with uncini in single rows, with elongate, distally sharp main fang as crest with a single row of flattened spines. Nephridial papillae present on segment 3, genital papillae on segments 6 to 10, between parapodial lobes. Pygidium crenulated.
Main references: Hutchings 1977, Nogueira et al. 2013.

Hutchingsiella Londoño-Mesa, 2003

Type species: *Spinosphaera cowarrie* Hutchings, 1997a, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present laterally; distal part nearly indistinct. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, wider than long; short, button-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, with low and thick midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Roughly cylindrical notopodia beginning on segment 4, extending until near pygidium; anterior notopodia with narrowly winged notochaetae in both rows, posterior notopodia with alimbate, distally serrated notochaetae, with blade at an angle

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with shaft. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in partially intercalated double rows, dorsal buttons aligned, from segment 11 until a few segments before pygidium. Nephridial papillae on segment 3, genital papillae on segments 6 to 10. Pygidium papillate.
Main reference: Nogueira et al. 2013.
Remarks: There are significant discrepancies between the original descriptions of the species and the genus (Hutchings 1997, Londoño-Mesa 2003) and the reexamination of the type material by Nogueira et al. (2013) with regard to the segment of which the notopodia and neuropodia begin.

Lanassa Malmgren, 1866

Type species: *Lanassa nordeskioeldi* Malmgren, 1866, by monotypy
9 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part nearly indistinct to shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, distinctly wider than long; button-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, with low midventral lobe marginal to mouth. Segments 2 to 4 with anterior margins as protruding crests ventrally and pairs of low and thick lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular shields. Branchiae absent. Cylindrical to rectangular notopodia beginning on segment 4, extending for 15 segments, until segment 18; anterior notopodia with medially winged, distally serrated notochaetae in both rows, wings distinctly narrow; posterior notopodia with alimbate, distally serrated notochaetae in anterior row, those of posterior row as anterior segments. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest and back curved backward, in completely separated double rows, beak-to-beak alignment, from segment 11 until termination of notopodia, on segment 18, or a few segments after that. Nephridial and genital papillae sometimes present, nephridial papillae on segment 3, genital papillae on segments 6 to 8. Pygidium smooth.
Main references: Holthe 1986b, Hutchings and Glasby 1988, Nogueira et al. 2013.
Remarks: The genus counts on nine species, but two of those were considered as undeterminable by Hutchings and Glasby (1988) and another was considered as belonging to another genus. Although WoRMS spells the type species as *nordenskioldi*, the correct spelling is *nordenskioeldi* is after the Swedish-Finnish geologist and explorer Adolf Nordenskiöld, following Holthe (1986b) and Torkild Bakken (personal communication).

Lanice Malmgren, 1866

Type species: *Nereis conchilega* Pallas, 1766, by monotypy
15 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as wide as long; short, button-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, with pair of dorsolateral to lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip; segment 3 with large lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth to strongly corrugated, rectangular to trapezoidal shields. Three pairs of progressively shorter arborescent branchiae, on segments 2 to 4, with short main stalks. Cylindrical to rectangular notopodia beginning on segment 4; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled uncini, in partially intercalated to completely separated double rows, back-to-back arrangement, from segment 11 until termination of notopodia, on segment 20. Nephridial and genital papillae usually poorly developed, almost inconspicuous, of variable position and distribution. Pygidium smooth to papillate.
Main references: Hutchings and Glasby 1988, Nogueira et al. 2015d.

Lanicides Hessle, 1917

Type species: *Terebella (Phyzelia) bilobata* Grube, 1877, by original designation (Hessle 1917)
10 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; small, swollen and midventral lower lip. Segment 1 reduced dorsally, with pair of lobes of variable size and position; lobes of variable size and position also present on segments 2 and 3. Anterior segments highly glandular ventrally, with

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discrete, smooth to highly corrugated, rectangular to trapezoidal midventral shields. Two or three pairs of arborescent branchiae, on segments 2 and 3 or 2 to 4, with short main stalks. Cylindrical to rectangular notopodia beginning on segment 4; narrowly winged and/or narrowly winged medially and distally serrated notochaetae. Neuropodia beginning on segment 5, as low ridges throughout or only in conjunction with notopodia and short pinnules posteriorly; neurochaetae as avicular uncini with long handles of variable thickness on few anterior segments, short-handled thereafter; uncini in partially, prows or dorsal buttons aligned, to completely intercalated double rows, from segment 11 until termination of notopodia. Nephridial and genital papillae usually poorly developed, almost inconspicuous, of variable position and distribution. Pygidium smooth to slightly crenulated.

Main references: Hutchings and Glasby 1988, Nogueira et al. 2015d.

Remarks: Hessle (1917) did not designate a type species for *Lanicides*, but following the description of his new genus, the author included a redescription of *Lanicides vayssierei* Gravier, 1911, which he said was a possible synonym of *Terebella (P.) bilobata* Grube, 1877. Perhaps, for this reason, the latter taxon, *T. (P.) bilobata*, was considered to be the type species of the genus (Hartman 1966, Hutchings and Glasby 1988).

However, we have examined the holotype of *T. (P.) bilobata*, and that species is considerably different from the description of *L. vayssierei* provided by Hessle (1917). Comparing the description provided by Hessle (1917) for *L. vayssierei* to our own observations of the holotype of *T. (P.) bilobata*, we noticed that they are not only separate species but also belong to separate genera. Thus, as Hessle's material is no longer available, depending on which is determined to be the type species of the genus, *T. (P.) bilobata* or *L. vayssierei*, the diagnosis of this genus may change considerably.

Lanicides presents intrageneric variation in characters that usually do not vary in other genera of terebellids, such as the type of notochaetae present, the morphology of posterior neuropodia, and the type of long-handled uncini present, thin- or thick-handled. This is probably due to the taxonomic confusion on the identity of this genus described above, but, as currently defined, there is a considerable overlapping between the definitions of *Lanicides* and *Pista*.

Lanicola Hartmann-Schröder, 1986

Type species: *Lanicola lobata* Hartmann-Schröder, 1986, by monotypy

7 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; small, swollen, and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; segment 3 with pair of large lateral lobes, originating dorsolaterally from segment 3 and fused to body wall ventrally at anterior corners of midventral shield of segment 2, with conspicuous scar until segment 3. Anterior segments highly glandular ventrally, with discrete, smooth to highly corrugated, rectangular to trapezoidal midventral shields. Two pairs of arborescent branchiae on segments 2 and 3. Cylindrical to rectangular notopodia beginning on segment 4; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges throughout or only in conjunction with notopodia, and as short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in partially to completely intercalated double rows, from segment 11 until termination of notopodia. Nephridial papillae on segments 3 and 4, genital papillae on segments 6 and 7, posterior to notopodia and dorsal. Pygidium smooth to slightly crenulated.

Main references: Hutchings and Glasby 1988, Nogueira et al. 2015d.

Laphania Malmgren, 1866

Type species: *Laphania boecki* Malmgren, 1866, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; segment 2 with lobe as a low collar originating from anterior margin and completely encircling body; lobes absent on other segments. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Branchiae absent. Almost rectangular notopodia beginning on segment 3, extending for 17 segments, until segment 19; narrowly winged notochaetae in posterior row throughout, anterior row with broadly winged notochaetae on anterior segments, and alimbate and distally serrated, on posterior segments with notopodia. Neuropodia beginning on segment 9, as low ridges in conjunction with notopodia and short

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pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest, in completely intercalated double rows, from segment 11 until segment 19. Nephridial and genital papillae on segments 5 to 8, ventral to notopodia, in position equivalent to between parapodial lobes, if neuropodia were present. Pygidium unknown.

Main references: Holthe 1986b, Nogueira et al. 2013.

Leaena Malmgrem, 1866

Type species: *Leaena ebranchiata* (Sars, 1865), by monotypy

13 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, distinctly wider than long, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with cushion-like lobe across ventrum, posterior to mouth; segment 2 with pair of ventrolateral lobes on anterior margin, connected to each other by raised crest across ventrum; segment 3 with low, four-lobed collar originating from anterior margin and completely encircling body, one lobe at each lateral, and also dorsally and ventrally; segments 4 and 5 with low and progressively shorter pairs of lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal midventral shields. Branchiae absent. Almost rectangular notopodia beginning on segment 4, extending for 10 to 17 segments, until segments 13 to 20; notochaetae all broadly winged, those from anterior row with broad wings on both margins, notochaetae from posterior row with broad wings on one margin only. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia, and short, fleshy pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest, in almost completely intercalated double rows, from segment 11 until termination of neuropodia. Nephridial papillae on segment 3, genital papillae on segments 6 to 8, between parapodial lobes. Pygidium papillated.

Main references: Holthe 1986b, Nogueira et al. 2013.

Loimia Malmgren, 1866

Type species: *Loimia medusa* Savigny, 1818, by monotypy

29 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like; short, button-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, with pair of dorsolateral to lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip. Large lateral lobes present on segment 3; segment 4 sometimes also with pair of short lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth to strongly corrugated, rectangular to trapezoidal shields. Three pairs of progressively shorter arborescent branchiae, on segments 2 to 4, with short main stalks. Conical to rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled uncini throughout, with high, pectinate crest, in partially intercalated to completely separated double rows, back-to-back arrangement, from segment 11 until termination of notopodia. Nephridial papillae on segment 3, genital papillae on segments 6 to 8, posterior to notopodia and dorsal. Pygidium smooth to papillate.

Main references: Carrerette and Nogueira 2015b, Nogueira et al. 2015d.

Longicarpus Hutchings & Murray, 1984

Type species: *Terebella modesta* Quatrefages, 1865, by original designation, as the senior synonym of *Longicarpus glandulus* Hutchings & Murray, 1984

2 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; rectangular, swollen and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; segments 2 to 4 with pairs of low dorsolateral lobes, segments 2 and 3 also with pairs of ventrolateral lobes connected to each other by raised crests across ventrum. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular midventral shields. Three pairs of arborescent branchiae, on segments 2 to 4, with short main stalks. Conical to rectangular notopodia beginning on segment 4, extending for 16 to 25 segments, until segments 19 to 28; notochaetae all medially narrowly winged and distally serrated, wings basally bulbous. Neuropodia beginning on segment 5, as low ridges throughout; neurochaetae as avicular uncini with long handles originating only from heel until segments 9

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and 10, short-handled thereafter; uncini in partially, prows aligned, to completely intercalated double rows, from segments 10 and 11 until posterior body. Nephridial and genital papillae on segments 3 to 8, between parapodial lobes or equivalent position in case of segments 3 and 4. Pygidium smooth to slightly crenulated.
Main references: Hutchings and Murray 1984, Hutchings and Glasby 1988, Nogueira et al. 2013.

Morgana Nogueira & Amaral, 2001

Type species: *Morgana bisetosa* Nogueira & Amaral, 2001, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Branchiae absent. Almost rectangular notopodia beginning on segment 4, extending for 18 to 25 segments, until segments 21 to 28; notochaetae throughout alimbate and distally serrated in anterior row and narrowly winged in posterior row. Neuropodia beginning on segment 6, as low ridges throughout; neurochaetae as short-handled avicular uncini with high crest, in completely separated double rows, beak-to-beak arrangement, from segment 11 until posterior body. Nephridial and genital papillae inconspicuous or absent. Pygidium smooth.
Main references: Nogueira and Amaral 2001, Nogueira et al. 2013.

Naneva Chamberlin, 1919

Type species: *Naneva hespera* Chamberlin, 1919, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; narrow, button-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, crenulated, rectangular midventral shields. Two pairs of arborescent branchiae, on segments 2 and 3, nearly as long as body width, with short main stalks. Almost rectangular notopodia beginning on segment 3, extending for 26 segments, until segment 28; anterior notopodia with medially limbate and distally serrated notochaetae in both rows, wings with bulbous bases, posterior notopodia with alimbate and serrated chaetae in both rows. Neuropodia beginning on segment 5, as low ridges throughout; neurochaetae as short-handled avicular uncini, in completely separated double rows, beak-to-beak arrangement, from around segment 11 until posterior body. Nephridial papillae present on segment 3, genital papillae on segments 7 to 18, between parapodial lobes. Pygidium smooth.
Main references: Hartman 1969, Nogueira et al. 2013.
Remarks: There are considerable differences between the descriptions given by Chamberlin (1919) and Hartman (1969). The above definition is based on examination of the type by Nogueira et al. (2013).

Neoleprea Hessle, 1917

Type species: *Leprea streptochaeta* Ehlers, 1897, by original designation
10 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Two pairs of arborescent branchiae, on segments 2 and 3, usually much shorter than body width, with short main stalks. Almost rectangular notopodia beginning on segment 3, extending for 17 to 40 segments, until segments 19 to 42; notochaetae all medially limbate and distally serrated. Neuropodia beginning on segment 5, as low ridges throughout; neurochaetae as short-handled avicular uncini with high crest, in completely separated double rows, beak-to-beak arrangement, from around segment 11 until posterior body. Nephridial and genital papillae present from segment 3, extending for variable and relatively large number of segments. Pygidium smooth.
Main references: Hutchings and Glasby 1988, Carrerette and Nogueira 2015a.

Nicolea Malmgren, 1866

Type species: *Terebella zostericola* Örsted, 1844, by original designation
29 species.

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Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like, and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Two pairs of arborescent branchiae, on segments 2 and 3, usually with short main stalks. Conical to rectangular notopodia beginning on segment 4, extending for 15 to 40 segments, until segments 18 to 43; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low, sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in partially to completely intercalated double rows from around segment 11 until termination of notopodia. Nephridial papillae present on segment 3, genital papillae on segments 6 and 7, in line and posterior to notopodia; genital papillae with sexual dimorphism in several species, females with rounded papillae, males with elongate, digitiform papillae. Pygidium smooth to crenulate.
Main references: Nogueira 2008, Nogueira et al. 2015d.

Opisthopista Caullery, 1944

Type species: *Opisthopista sibogae* Caullery, 1944, by monotypy
Monotypic.
Definition: Two pairs of branched branchiae; lateral lappets present on at least segments 2 and 4. First notochaetae from segment 5 and uncini from segment 6. Anterior uncini long-handled.
Main reference: Fauchald 1977.
Remarks: The examination of the type reveals material in very poor condition (Nogueira personal observations), and with the brief original description, this genus could not be included in Nogueira et al. (2013). We suggest that this is a *nomen dubium* unless more material from the type locality becomes available.

Paralanice Caullery, 1944

Type species: *Paralanice timorensis* Caullery, 1944, by monotypy
Monotypic.
Definition: Three pairs of branched branchiae; large lateral buccal lappets connected across dorsum with a crest, lateral lappets also on segments 2 and 3. Seventeen thoracic chaetigers, smooth-tipped capillaries from segment 4.
Main reference: Fauchald 1977.
Remarks: The examination of the type reveals material in very poor condition (Nogueira personal observations), and with the brief original description, this genus could not be included in Nogueira et al. (2013). We suggest that this is a *nomen dubium* unless more material from the type locality becomes available.

Paramphitrite Holthe, 1976

Type species: *Paramphitrite tetrabranchia* Holthe, 1976, by monotypy
3 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; segments 2 to 4 with pairs of low lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Two pairs of arborescent branchiae, on segments 2 and 3, much shorter than body width, with short main stalks. Rectangular to conical notopodia beginning on segment 4, extending for 13 segments, until segment 16; notochaetae all medially limbate and distally serrated. Neuropodia beginning on segment 5, as low ridges until segment 20, shortly after termination of notopodia, and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest, in completely separated double rows, beak-to-beak arrangement, on segments 11 to 20. Nephridial papillae present on segment 3, genital papillae on segments 6 to 8, between parapodial lobes. Pygidium smooth.
Main references: Holthe 1976, Nogueira et al. 2013.
Remarks: The above description is largely based on the examination of type material of the type species (Nogueira et al. 2013).

Paraxionice Fauchald, 1972

Type species: *Paraxionice artifex* Fauchald, 1972, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present laterally; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; segments 2 to 4 partially fused ventrally, forming

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pair of low midventral lobes. Anterior segments highly glandular ventrally, with discrete, rectangular to trapezoidal midventral shields, deeply corrugated on segments 2 to 4, as part of midventral pair of lobes, then smooth. Single pair of arborescent branchiae, on segment 2, much longer than body width, with short main stalks. Conical to rectangular notopodia beginning on segment 4, extending for 16 segments, until segment 19; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with rounded heel and prow, in irregular, partially intercalated double rows on segments 11 to 19. Nephridial papillae present on segment 3, genital papillae on segments 6 to 9, between parapodial lobes and slightly posterior. Pygidium papillate.

Main references: Fauchald 1972, Nogueira et al. 2013.

Remarks: The above description is largely based on the examination of type material of the type species (Nogueira et al. 2013).

Phisidia Saint-Joseph, 1894

Type species: *Leaena ocullata* Langerhans, 1880, by monotypy

8 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots usually present laterally; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Branchiae absent. Conical to rectangular notopodia beginning on segment 4, extending for 13 to 16 segments, most species with 14 pairs, extending until segment 17; alimbate and serrated notochaetae in anterior row throughout, posterior row with narrowly winged chaetae on anterior notopodia and medially winged and finely serrated distally on posterior notopodia. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini throughout, in partially intercalated double rows, with prows aligned, from segment 11 until a few segments after termination of notopodia, usually around segment 20. Nephridial and genital papillae present on segments 3 to 8, between parapodial lobes. Pygidium smooth to crenulate.

Main references: Hutchings and Glasby 1986a, b, c, Nogueira and Alves 2006, Nogueira et al. 2013.

Pista Malmgren, 1866

Type species: *Amphitrite cristata* Müller, 1776, by original designation

76 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, with pair of lobes of variable size and position; segments 2 to 4 also with pairs of lobes of variable size and position, sometimes extending for a few more segments. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal midventral shields. Paired arborescent, pectinate or plumous branchiae present from segment 2, typically two pairs, on segments 2 and 3, rarely a single pair or three pairs. Conical to rectangular notopodia beginning on segment 4, typically extending for 17 segments, until segment 20; notochaetae all distally winged, frequently broadly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as long-handled avicular uncini, at least on anterior neuropodia, frequently until segment 10 or termination of notopodia, then short-handled; uncini in partially to completely intercalated double rows on segments 11 to 20. Nephridial papillae present on segment 3, genital papillae on a variable number of segments, usually on segments 6 and 7, posterior and dorsal to notopodia. Pygidium smooth to slightly crenulated.

Main references: Nogueira et al. 2011, 2015d.

Pistella Hartmann-Schröder, 1996

Type species: *Scionella lornensis* Pearson, 1969, by monotypy

4 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, usually with pair of ventrolateral lobes connected to each other across ventrum by low lobe marginal to mouth; segment 2 with pair of ventrolateral lobes connected to each other by raised crest across ventrum; segment 3 or segments 3 and 4, with pair(s) of short lateral lobes; lobes absent on following segments. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal midventral shields;

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shields typically divided in two parts, anterior part white and posterior part bright red to brown after preservation. Single pair of plumous branchiae, on segment 2, as long as body width or longer, with long main stalks. Conical to rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all distally winged, frequently broadly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini throughout, in partially to completely intercalated double rows on segments 11 to 20. Nephridial papillae present on segment 3, genital papillae usually on segments 6 and 7, posterior and dorsal to notopodia. Pygidium crenulated or with small rounded papillae.

Main references: Hartmann-Schröder 1996, Nogueira et al. 2015d, Mikac and Hutchings 2017.

Polymniella Verrill, 1900

Type species: *Eupolymnia (Polymniella) aurantiaca* Verrill, 1900, by monotypy

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin straight; large, cushion-like, and midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular midventral shields. Three pairs of branching branchiae, on segments 2, 4, and 7; branchiae shorter than body width, with short main stalks. Conical to rectangular notopodia beginning on segment 4, extending at least until segment 17; notochaetae all medially winged and distally serrate. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in partially intercalated double rows from segment 11 until posterior body. Nephridial papillae on segment 3, genital papillae, if present, on segments 7 to 12, dorsal and posterior to notopodia. Pygidium unknown.

Main references: Nogueira 2008, Londoño-Mesa 2009.

Remarks: Nogueira (2008) redescribed this species based on the syntypes, and Londoño-Mesa (2009) also redescribed it based on the syntypes and fresh material. However, it is doubtful that the additional specimens Londoño-Mesa examined belong to the same taxon, as they have 97 pairs of notopodia. Nogueira (2008) could not count the number of pairs of notopodia of the syntypes, as they were both incomplete and dissected and damaged posteriorly, but Hartman (1942) said that this species has 22 pairs of notopodia but from a damaged fragment.

Proclea Saint-Joseph, 1894

Type species: *Proclea graffi* Langerhans, 1884, by monotypy

5 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, wider than long, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 expanded ventrally, with pair of low ventrolateral lobes connected to each by ventral lobe marginal to mouth; segments 2 to 4 with pairs of short and thick lateral lobes; lobes absent from segment 5. Anterior segments highly glandular ventrally, with discrete, smooth to crenulated, rectangular midventral shields. Branchiae absent. Almost rectangular notopodia beginning on segment 4, extending for 16 to 23 segments, until segments 19 to 26; narrowly winged notochaetae in both rows on anterior notopodia, posterior notopodia with alimbate and serrated chaetae in anterior row and hirsute broadly winged chaetae in posterior row. Neuropodia beginning on segment 6, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest bent backward, in completely separated double rows, beak-to-beak arrangement, from segment 11 until termination of notopodia. Nephridial and genital papillae on segments 3 and 5–8, posterior and dorsal to notopodia. Pygidium smooth to crenulate.

Main references: Holthe 1986b, Nogueira et al. 2013.

Pseudopista Hutchings & Smith, 1997

Type species: *Pseudopista rostrata* Hutchings & Smith, 1997, by monotypy

Monotypic.

Definition: Compact tentacular lobe with numerous buccal tentacles. Lateral lobes on segments 2 and 3, poorly developed. Branchiae, three pairs on segments 2 to 4, dichotomously branched. Notopodia from segment 4, continuing for 21 segments; notochaetae narrow-winged capillaries, with serrations along one margin, some appearing flail-tipped. Neuropodia beginning on segment 5 and continuing to pygidium; uncini of anterior thoracic segments typically with posteriorly elongated bases, following uncini lacking elongated bases. Uncini arranged in single rows initially, in double rows from segment 11 to

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midabdominal segments, posterior abdominal neuropodia with uncini arranged in single rows.
Main reference: Hutchings and Smith 1997.
Remarks: The type species of this genus is a possible synonym of *Longicarpus modestus*.

Pseudoproclea Hutchings & Glasby, 1990

Type species: *Pseudoproclea australis* Hutchings & Glasby, 1990, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, wider than long, hood-like; swollen, button-like, midventral lower lip. Segment 1 expanded ventrally, with low ventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, and rectangular midventral shields. Branchiae absent. Almost rectangular notopodia beginning on segment 4, extending for 16 segments, until segment 19; notochaetae in anterior row alimbate and distally serrated throughout, posterior row with narrowly winged chaetae on anterior notopodia and medially winged, distally serrated chaetae on posterior notopodia. Neuropodia beginning on segment 5, as low ridges throughout; neurochaetae as short-handled avicular uncini, in completely separated double rows, beak-to-beak arrangement, from segment 11 until posterior body. Nephridial and genital papillae inconspicuous or absent. Pygidium unknown.
Main references: Hutchings and Glasby 1990, Nogueira et al. 2013.

Ramex Hartman, 1944

Type species: *Ramex californiensis* Hartman, 1944, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, longer than wide, hood-like; swollen, button-like, midventral lower lip. Segment 1 expanded ventrally, with low ventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Single pair of arborescent branchiae with short main stalks, on segment 2. Conical notopodia beginning on segment 4, extending for 13 segments, until segment 16; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in completely intercalated double rows from segment 10 until termination of notopodia. Nephridial papillae on segment 3, genital papillae on segments 6 and 7, dorsal to notopodia. Pygidium smooth to slightly crenulated.
Main references: Hartman 1944, Nogueira et al. 2013.

Reteterebella Hartman, 1963

Type species: *Reteterebella queenslandia* Hartman, 1963, by monotypy
3 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, usually as wide as long, hood-like; swollen, button-like, midventral lower lip. Segment 1 only conspicuous dorsally, ventrally fused to lower lip; short and flaring ventrolateral lobes usually present on segments 2 to 5, originating progressively more laterally. Anterior segments highly glandular ventrally, with discrete, smooth to highly corrugated, rectangular to trapezoidal midventral shields. Three pairs of arborescent branchiae with short main stalks on segments 2 to 4, branchiae shorter than body width. Rectangular notopodia beginning on segment 5, extending for 16 to 17 segments, until segments 20 and 21; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini, with sharp corners, in partially intercalated double rows, dorsal buttons aligned, from segment 10 until termination of notopodia. Nephridial and genital papillae on segments 3 to 8, dorsal to line of notopodia on segments 3 and 4, between parapodial lobes and minute on segments 5 to 8. Pygidium smooth to slightly crenulated.
Main references: Hutchings and Glasby 1988, Nogueira et al. 2015d.

Scionella Moore, 1903

Type species: *Scionella japonica* Moore, 1903, by monotypy
2 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, wider than long, hood-like; swollen,

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button-like, midventral lower lip. Segment 1 conspicuous all around; segments 1 to 4 with pairs of large ventrolateral to lateral lobes originating progressively more laterally; lobes of segment 1 fused to each other midventrally, and connected by raised crest across dorsum; lobes of segments 2 and 3 connected to each other within pairs by raised crests dorsally and ventrally; lobes of segment 4 connected to each other by low collar across dorsum. Anterior segments highly glandular ventrally, with discrete, crenulated, rectangular to trapezoidal midventral shields. Single pair of branchiae on segment 4, with unbranching filaments originating all together from distinctly short main stalks or in a spiraled arrangement. Rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest bent backward; uncini in partially intercalated double rows, dorsal buttons aligned, from segment 11 until termination of notopodia. Nephridial and genital papillae on segments 3, dorsal to bases of lobes, and segments 6 to 8, between parapodial lobes. Pygidium unknown.

Main references: Nogueira et al. 2010, 2013.

Scionides Chamberlin, 1919

Type species: *Terebella reticulata* Ehlers, 1887, by original designation

Monotypic.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, wider than long, hood-like; narrow and midventral lower lip. Segment 1 conspicuous all around, with ventral lobe marginal to mouth; segments 2 to 4 with pairs of short and thick ventrolateral to lateral lobes originating progressively more laterally; lobes of segments 2 to 4 connected to each other within pairs by raised crests across ventrum. Anterior segments highly glandular ventrally, with discrete, smooth to slightly crenulated, trapezoidal midventral shields. Three pairs of arborescent branchiae, on segments 2 to 4, much shorter than body width. Rectangular notopodia beginning on segment 4, extending for 13 to 14 segments, until segments 16 and 17; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest, in almost completely intercalated double rows from segment 11 until termination of notopodia. Nephridial papillae on segment 3, genital papillae on segments 6 to 8, between parapodial lobes. Pygidium smooth.

Main reference: Nogueira et al. 2013.

Remarks: The redescriptions of the material referred to this species by Hartman (1938) and Banse (1980) stated that the notochaetae are distally serrated; however, this may be an artifact depending on the angle of view, as the holotype, examined by J.M.M.N., has narrowly winged notochaetae. Other specimens examined also have narrowly winged notochaetae and the holotype is very poorly preserved, with most chaetae shaved off.

Spinosphaera Hessle, 1917

Type species: *Spinosphaera pacifica* Hessle, 1917, by monotypy

6 species.

Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present laterally; distal part at base of upper lip, nearly indistinct. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like; short and narrow, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal shields. Branchiae absent. Cylindrical notopodia beginning on segment 4, extending for a variable number of segments, segments 15 to 41, most species with 20 to 23 pairs, until segments 23 to 26; anterior notopodia with broadly winged notochaetae in both rows, posterior notopodia with distally serrated notochaetae, alimbate or medially winged, some species with chaetae of posterior row broadly winged medially, then with coarsely spinulated process originated from the shaft, followed by finely serrated tip (*Spinosphaera*-chaetae). Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini with high crest, in partially intercalated double rows, prows aligned, from segment 11 until near termination of notopodia, some species with double rows extending to posterior body. Nephridial papillae, if present, on segment 3, genital papillae frequently present, from segments 6 and 7, extending for a variable number of segments. Pygidium papillate.

Main references: Londoño-Mesa 2003, Nogueira and Hutchings 2007.

Remarks: Londoño-Mesa (2003) considered the presence of *Spinosphaera*-chaetae as the main diagnostic character for this species; however, several of the species he

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allocated to *Spinosphaera* do not have that type of chaetae but rather medially limbate and distally serrated chaetae, lacking the coarse spinulated process that characterizes the *Spinosphaera*-like chaetae.

Spiroverma Uchida, 1968

Type species: *Spiroverma ononokomachii* Uchida, 1968, by monotypy
Monotypic.
Definition: One pair of sessile branchiae on segment 2, each branchia with maximally eight filaments. Sixteen thoracic chaetigers, notochaetae distally serrated. Body strongly spiraled.
Main reference: Fauchald 1977.
Remarks: This is the only genus of Terebellidae *sensu stricto* that Nogueira et al. (2010, 2013) did not examine. The types could not be located, and additional material has never been found. The original description (Uchida 1968) is very brief, not mentioning several important diagnostic characters; therefore, we consider *Spiroverma ononokomachii* as a *nomen dubium*.

Stschapovella Levenstein, 1957

Type species: *Stschapovella tatjanae* Levenstein, 1957, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, wider than long, hood-like; swollen, button-like and midventral lower lip. Segment 1 conspicuous dorsally, with pair of dorsolateral to lateral lobes extending anteriorly to level of distal part of prostomium, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip; segment 2 swollen, protruding all around, with thick midventral lobe; lobes absent on following segments. Anterior segments highly glandular ventrally, with discrete, anteriorly corrugated then smooth, rectangular to trapezoidal midventral shields. Branchiae absent. Conical to rectangular notopodia beginning on segment 4, extending for 16 segments, until segment 19; notochaetae all narrowly winged. Neuropodia beginning on segment 5, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with rounded prow, in completely intercalated double rows from segment 11 until termination of notopodia. Nephridial and genital papillae on segments 3 and 5 to 8, between parapodial lobes. Pygidium papillated.
Main references: Levenstein 1957, Nogueira et al. 2013.

Terebella Linnaeus, 1767

Type species: *Terebella lapidaria* Linnaeus, 1767, by monotypy
37 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots frequently present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as long as wide; large, button-like to cushion-like, midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, expanded ventrally, frequently with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth to slightly crenulated, rectangular to trapezoidal midventral shields. Three pairs of branching branchiae with short main stalks, usually on segments 2 to 4, but sometimes on discontinuous segments. Conical notopodia beginning on segment 4, extending for a variable number of segments, frequently to posterior body; notochaetae medially winged and distally serrated, and alimbate and serrated, frequently with blade at an angle, usually with transition on types of chaetae from anterior to midbody notopodia. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in completely intercalated to partially back-to-back double rows from segment 11 until posterior body. Nephridial papillae on segment 3, genital papillae usually present from segment 6, extending for a variable number of segments, between parapodial lobes. Pygidium smooth to slightly crenulated.
Main references: Hutchings and Glasby 1988, Nogueira et al. 2015d.

Terebellobranchia Day, 1951

Type species: *Terebellobranchia natalensis* Day, 1951, by monotypy
4 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like; large, cushion-like, and midventral lower lip. Segment 1 conspicuous all around, dorsally narrow, indented by expanded lower lip ventrally; lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, crenulate, rectangular midventral shields. Three pairs of branching branchiae, on discontinuous segments (segments 3, 7, and 12 in the type species); branchiae about as long as body width, with short main stalks. Conical to

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rectangular notopodia beginning on segment 4, extending at least until segment 19 (last segment of the holotype of the type species, only known specimen); notochaetae all medially winged and finely serrated distally, or alimbate and serrated in one species. Neuropodia beginning on segment 5, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in partially intercalating double rows from around segment 11 until posterior body. Nephridial papillae on segment 3, genital papillae, if present, from segments 5 and 6 for a variable number of segments, between parapodial lobes. Pygidium papillate.
Main references: Day 1951, Londoño-Mesa 2009.
Remarks: This genus was not included in Nogueira et al. (2013), as the type specimen is incomplete and in poor condition. Londoño-Mesa (2009) redefined this genus, but we suggest that this is a synonym of *Polymniella*; perhaps both genera, *Polymniella* and *Terebellobranchia*, are synonyms of *Terebella*, considering that the latter genus may have branchiae on discontinuous segments.

Thelepides Gravier, 1911

Type species: *Thelepides koehleri* Gravier, 1911, by monotypy
3 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, wider than long, distal margin straight; small, button-like and midventral lower lip. Segments 1 to 4 with pairs of large ventrolateral lobes; lobes inserted progressively more laterally, those of segment 1 connected to each other by low midventral lobe marginal to mouth, those of segment 4 reaching bases of branchiae. Anterior segments highly glandular ventrally, with discrete, smooth to crenulated, rectangular midventral shields. Three pairs of branchiae, as independent, unbranching filaments originating all together from short main stalks on either side of pairs. Conical to rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; broadly winged notochaetae in both rows on anterior notopodia, posterior notopodia with alimbate and finely serrated chaetae in anterior row and broadly winged on one margin chaetae in posterior row. Neuropodia beginning on segment 5, as low sessile ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crests, in partially intercalated double rows, prows aligned, from segment 11 until termination of notopodia. Nephridial and genital papillae on segments 3 to 9, between parapodial lobes. Pygidium unknown.
Main reference: Nogueira et al. 2013.

Tyira Hutchings, 1997a

Type species: *Tyira owensi* Hutchings, 1997a, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like, wider than long; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with low midventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal midventral shields. Two pairs of arborescent branchiae, on segments 2 and 3, much shorter than body width, with short main stalks. Almost rectangular notopodia beginning on segment 2, extending for 19 segments, until segment 20; notochaetae all medially limbate and distally serrated. Neuropodia beginning on segment 5, as low ridges throughout; neurochaetae as short-handled avicular uncini, in completely separated double rows, beak-to-beak arrangement, from around segment 11 until posterior body. Nephridial papillae present on segment 3, genital papillae on segments 6 to 13, between parapodial lobes. Pygidium smooth to slightly crenulated.
Main references: Hutchings 1997a, Nogueira et al. 2013.

Varanusia Nogueira, Hutchings & Carrerette, 2015c

Type species: *Lizardia quasimodo* Nogueira, Hutchings & Carrerette, 2015d, by monotypy
Monotypic.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part shelf-like. Buccal tentacles unknown. Peristomium restricted to lips; relatively short upper lip, about as wide as long, hood-like; swollen, cushion-like and midventral lower lip. Segment 1 reduced dorsally, expanded ventrally, with cushion-like lobe across ventrum, posterior to mouth; segments 2 to 4 with pairs of thick and low lateral lobes, those of segments 2 and 3 connected to each other by protruding crests across ventrum, running from one side of the body to another. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular midventral shields. Branchiae absent. Notopodia beginning on segment 4, extending for nine segments, until segment 12; conical to rectangular notopodia, notochaetae originating from central core on top; narrowly winged notochaetae in both rows on anterior segments, alimbate and distally serrated chaetae on posterior notopodia. Neuropodia beginning on segment 6, as low ridges throughout; neurochaetae as short-handled avicular uncini with

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high crest, in completely separated double rows, beak-to-beak arrangement, from segment 11 to posterior body. Nephridial and genital papillae inconspicuous or absent. Pygidium smooth.
Main references: Nogueira et al. 2015c, d.

Family Trichobranchidae Malmgren, 1866

Trichobranchids are a small group of Terebelliformia, characterized by having acicular thoracic uncini and collar-like lobes on anterior segments, encircling partially or completely the posterior part of preceding segment. The branchiae are either as a single filament on each side of pairs, of variable morphology and 2–4 pairs may be present, beginning from segment 2, or two pairs, or two pairs fused in a single middorsal lamellate structure, inserted by a thick stalk between segments 2 and 3 or segments 2 to 4. Thoracic neurochaetae are acicular uncini, except for the first one to two pairs of neuropodia of *Terebellides*, which have acicular, distally bent spines (Hutchings et al. 2015).

The group was first recognized by Hessle (1917), who grouped Canephoridea Malmgren, 1866 and Trichobranchidea Malmgren, 1866 together with *Octobranchus* Marion & Bobretzky, 1875, which was described after Malmgren's paper. Since that time, trichobranchids have been considered either as a separate family (Colgan et al. 2001, Rousset et al. 2003, Glasby et al. 2004) or as a subfamily of Terebellidae (Rouse and Pleijel 2001, Garraffoni and Lana 2004, 2008) until in the recent phylogenetic analysis by Nogueira et al. (2013), who found trichobranchids nested among the groups traditionally viewed as Terebellidae; however, that paper suggested that each of these groups should be considered as a separate family, keeping the familial status of Trichobranchidae.

Trichobranchidae includes only three genera, *Octobranchus* Marion & Bobretzky, 1875, *Terebellides* Sars, 1835, and *Trichobranchus* Malmgren, 1866, separated from each other by the morphology of prostomium, lips, and branchiae, number of pairs of branchiae, and presence/absence of an eversible ventral process on segment 1. Some other genera have been described in this family, but they have all been synonymized, mostly with *Trichobranchus* or *Terebellides*.

Trichobranchidae Hessle, 1917

Type genus: *Trichobranchus* Malmgren, 1866, by original designation
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part at base of upper lip or extending along lip. Buccal tentacles of two types, uniformly cylindrical and expanded at tips, spatulate. Peristomium forming lips, sometimes also a ventral lobe, as an extension of the lower lip; lips expanded, circular upper lip, distal margin folded or convoluted; lower lip button-like, usually continuing by ventral lobe, or expanded, forming large scoop-shaped process. Segment 1 usually short, frequently only visible ventrally; anterior margin of anterior segments with lobes as low, even-length collars covering posterior margins of preceding segments, at least ventrally; ventrolateral or lateral lobes on anterior segments sometimes present. Anterior segments poorly glandular ventrally, smooth, discrete shields absent; midventral groove extending from posterior segments with notopodia. The branchiae are either as a single filament on each side of pairs, of variable morphology and 2–4 pairs may be present, beginning from segment 2, or two pairs, or two pairs fused in a single four-lobed structure originating middorsally between segments 2 and 3 or segments 2 to 4. Notopodia beginning from segments 3 to 6, typically terminating at segment 20; short, conical notopodia, chaetae emerging from central core on top, distal lobes absent; narrowly winged notochaetae in both rows throughout. Neuropodia beginning on same segment as notopodia or slightly posteriorly, rarely beginning before notopodia; sessile neuropodia until termination of notopodia, neurochaetae emerging directly from body wall, as rectangular to foliaceous pinnules after termination of notopodia; thoracic neurochaetae as acicular uncini, sometimes with small hood or beard below main fang; avicular abdominal uncini, with secondary teeth in rows on top and laterally to main fang. Nephridial papillae on segment 3 usually present, other papillae sometimes present on segments 6 and 7 but reduced to inconspicuous in most taxa. Pygidium smooth to slightly crenulate, sometimes bilobed.
Main references: Garraffoni and Lana 2004, Muir 2011, Nogueira et al. 2013, Hutchings et al. 2015, Lavesque et al. 2019.

Octobranchus Marion & Bobretzky, 1875

Type species: *Terebella lingulata* Grube, 1863, by monotypy
10 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part of prostomium as thick crest, eye spots present; distal part at base of upper lip. Buccal tentacles of two types, uniformly cylindrical and expanded at tips, spatulate. Peristomium forming lips; lips expanded, circular upper lip, distal margin folded or convoluted; button-like lower lip, midventral. Segment 1 with midventral lobe; anterior segments with transverse lobes as low collars extending across ventrum; lobes usually protruding laterally for short extension on segments 2 to 4. Four pairs of branchiae, on segments 2 to 5, with single thick filament on either side of pair, filaments cirriform, foliaceous, or in rosette. Notopodia beginning on segment 4, extending for 16 segments, until segment 19; narrowly winged notochaetae in both

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rows throughout. Neuropodia beginning from segment 7; thoracic uncini acicular, usually with small hood as a beard below man fang, and crest with several transverse rows of secondary teeth; abdominal uncini avicular, with rows of secondary teeth on top and laterally to main fang. Nephridial and genital papillae present or not. Pygidium smooth to slightly crenulate.
Main references: Garraffoni and Lana 2000, Hutchings and Peart 2000.

Terebellides Sars, 1835

Type species: *Terebellides stroemii* Sars, 1835, by monotypy
66 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots absent; distal part extending along upper lip until near anterior border of lip. Buccal tentacles of two types, uniformly cylindrical and expanded at tips, spatulate. Peristomium forming lips and complete annulation; lips expanded, circular upper lip, distal margin convoluted; expanded lower lip, scoop-shaped, with large marginal lobe. Segment 1 short, conspicuous all around or only visible ventrally; following anterior segments with lobes as low ventral collars, frequently protruding laterally for short extension on segments 2 to 4, at least. Branchiae as single, stalked, four-lobed structure, inserted middorsally on segments 2 and 3 or segments 2 to 4, lobes in two pairs, each with multiple lamellae with ciliary tracts and rows of ciliated papillae. Notopodia beginning on segments 3 or 4, usually segment 3, extending for 17 to 18 segments, until segment 20; narrowly winged notochaetae in both rows throughout. Neuropodia beginning from segments 7 or 8, usually segment 8; sessile thoracic neuropodia, uncini emerging directly from body wall; first pair of neuropodia or first two pairs, when beginning from segment 7, with subdistally bent, distally tapered spines, from segment 9 thoracic neurochaetae as avicular uncini, hood below main fang absent, crest with relatively few transverse rows of secondary teeth; abdominal neuropodia as foliaceous pinnules, bearing avicular uncini, with rows of secondary teeth on top and laterally to main fang. Nephridial papillae only on segment 3, genital papillae, if present, on segments 6 and 7, at bases of notopodia, posterior and dorsal. Pygidium smooth to slightly crenulate.
Main references: Garraffoni et al. 2005, Muir 2011, Parapar and Hutchings 2014, Hutchings et al. 2015, Nygren et al. 2018, Zhang and Hutchings 2018, Lavesque et al. 2019.

Trichobranchus Malmgren, 1866

Type species: *Trichobranchus glacialis* Malmgren, 1866, by monotypy
12 species.
Definition: Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots present or not, distal part at base of upper lip. Buccal tentacles of two types, uniformly cylindrical and expanded at tips, spatulate. Peristomium forming lips; lips expanded, circular, relatively short upper lip, distal margin folded or convoluted; button-like lower lip, midventral, continuing as pair of flaring ventrolateral lobes, terminating at each lateral. Segment 1 forming large midventral structure, folded between segments 1 and 2 when retracted; lateral lobes may be present on segment 1, usually part of the eversible process and inconspicuous when it is fully extended; following anterior segments with lobes as low collars at least ventrally, slightly protruding laterally on segments 2 to 4. Two to three pairs of branchiae, on segments 2 and 3 or segments 2 to 4, each with single, thick, cirriform filament on either side of pair. Notopodia beginning on segments 5 and 6, extending until segment 20; narrowly winged notochaetae in both rows throughout. Neuropodia beginning from segments 5 or 6, sessile thoracic neuropodia, uncini emerging directly from body wall; thoracic neurochaetae as acicular uncini with many transverse rows of secondary teeth, frequently with subrostral beard; abdominal neuropodia as foliaceous pinnules, bearing avicular uncini with rows of secondary teeth on top and laterally to main fang. Nephridial and genital papillae usually inconspicuous. Pygidium smooth to slightly crenulate, sometimes bilobed.
Main references: Hutchings and Peart 2000, Hutchings et al. 2015.

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Although all the plates included in the present paper are original, mounted especially for this paper, many of the photos included were also used for plates in our previous papers (Nogueira and Alves 2006, Nogueira and Hutchings 2007, Nogueira 2008, Nogueira et al. 2010, 2013, 2015a, b, d, Fitzhugh et al. 2015, Hutchings et al. 2015). J.M.M.N. received a productivity grant from CNPq-Conselho Nacional de Desenvolvimento Científico e Tecnológico.

References

Anderson, D.J. & Kendziorek, M. (1982): Spacing patterns in terebellid polychaetes. *Journal of Experimental Marine Biology and Ecology* 58: 193–205.

Annenkova-Chlopina, N.P. (1924): Neues über die Verbreitung einiger Arten der Polychaeten. *Comptes Rendus de l'Académie des Sciences de SSSR*, Leningrad, 1924: 125–128.

Audouin, J.V. & Milne Edwards, H. (1834): *Recherches pour servir a l'histoire naturelle du littoral de la France, ou Recueil de*

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

mémoires sur l'anatomie, la physiologie, la classification et les moeurs des animaux de nos côtes; ouvrage accompagné de planches faites d'après nature. Crochard, Paris.

Augener, H. (1918): Polychaeta. *Beiträge zur Kenntnis der Meeresfauna Westafrikas* 2: 67–625.

Augener, H. (1922): Über littorale Polychaeten von Westindien. *Sitzungsberichte der Gesellshaft naturforschender Freunde zu Berlin*: 38–63.

Banse, K. (1980): Terebellidae (Polychaeta) from the northeast Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 20–40.

Barrios, D., D'Antonio, J., McCombs, N.L., Zhao, J., Franzen, S., Schmidt, A., Sombers, L. & Ghiladi, R.A. (2014): Peroxygenase and oxidase activities of dehaloperoxidase-hemoglobin from *Amphitrite ornata*. *Journal of American Chemical Society* 136: 7914–7925.

Benham, W.B. (1894): Suggestions for a new classification of the Polychaeta. *Report of the British Association for the Advancement of Science*: 696–697.

Benham, W.B. (1896): Archiannelida, Polychaeta, Myzostomidaria. In: Farmer, S.F. & Shipley, A.E. (eds.), *The Cambridge Natural History*. Macmillan, London: 241–334.

Bhaud, M. (1988): Change in setal pattern during early development of *Eupolymnia nebulosa* (Polychaeta: Terebellidae) grown in simulated natural conditions. *Journal of the Marine Biological Association of the United Kingdom* 68: 677–687.

Bhaud, M.R. (1991): Larval release from the egg mass and settlement of *Eupolymnia nebulosa* (Polychaeta, Terebellidae). *Bulletin of Marine Science* 48: 420–431.

Bhaud, M. & Grémare, A. (1988): Larval development of the terebellid polychaete *Eupolymnia nebulosa* (Montagu) in the Mediterranean Sea. *Zoologica Scripta* 17: 347–356.

Bielakoff, J., Damas, D. & Vovelle, J. (1975): Histologie et histochimie des formations glandulaires impliquées dans l'élaboration du tube chez *Lanice conchilega* (Annélide Polychète). *Archives de Zoologie Expérimentale et Générale* 11: 499–520.

Blainville, H. de (1825): *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'apres l'élat actuel de nos connaisance, soit relativement à l'utilité qu'en peuvent retirer la médicine, l'agriculture, le commerce et les arts. Suivi d'une biographie des plus célèbres naturalistes*. Vol. 34. F.G. Levrault: Strasbourg.

Blake, J.A. (1991): Larval development of Polychaeta from the northern California coast. V. *Ramex californiensis* Hartman (Polychaeta: Terebellidae). *Bulletin of Marine Science* 48: 448–460.

Capa, M. & Hutchings, P. (2006): Terebellidae (Polychaeta) from the Pacific coast of Panama (Coiba National Park) including descriptions of four new species and synonymy of the genus *Paraeupolymnia* with *Lanicola*. *Zootaxa* 1375: 1–29.

Carrerette, O. & Nogueira, J.M.M. (2015a): New species and new records of Terebellidae (Annelida: Terebelliformia) from off the Brazilian coast. *Zootaxa* 4020: 313–334.

Carrerette, O. & Nogueira, J.M.M. (2015b): The genus *Loimia* Malmgren, 1866 (Annelida: Terebellidae) off the Brazilian coast, with description of three new species and notes on some morphological characters of the genus. *Zootaxa* 3999: 001–031.

Carus, J.V. & Gerstäcker, E.A. (1863): *Handbuch der Zoologie*. Wilhelm Engelmann, Leipzig: 1–642.

Caullery, M. (1915): Sur les térébelliens de la tribu des Thelepinae. Examen des genres. *Bulletin de la Société Zoologique de France* 40: 44–53.

Caullery, M. (1944): Polychètes Sédentaires de l'Expédition du 'Siboga'. Ariciidae, Spionidae, Chaetopteridae, Chlorhaemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. Siboga-Expedition 24: 1–200.

Chamberlin, R.V. (1919): The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology of Harvard* 48: 1–514.

Colgan, D.J., Hutchings, P.A. & Brown, S. (2001): Phylogenetic relationships within the Terebellomorpha. *Journal of the Marine Biological Association of the United Kingdom* 81: 765–773.

Colgan, D.J., Hutchings, P.A. & Braune, M. (2006): A multigene framework for polychaete phylogenetic studies. *Organisms, Diversity and Evolution* 6: 220–235.

Cribb, T.H., Adlard, R.D., Hayward, C.J., Bott, N.J., Ellis, D., Evans, D. & Nowak, B.F. (2011): The life cycle of *Cardicola forsteri* (Trematoda: Aporocotylidae), a pathogen of ranched southern bluefin tuna, *Thunnus maccoy*. *International Journal of Parasitology* 41: 861–870.

Dales, R.P. (1955): Feeding and digestion in terebellid polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 34: 55–79.

Dales, R.P. (1957): Preliminary observations on the role of the coelomic cells in food storage and transport in certain polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 36: 91–110.

Dales, R.P. (1961): The coelomic and peritoneal cell systems of some sabellid polychaetes. *Quarterly Journal of Microscopical Science* 102: 327–346.

Dales, R.P. (1962): The polychaete stomodeum and the interrelationships of the families of the Polychaeta. *Proceedings of the Zoological Society of London* 139: 289–328.

Dales, R.P. (1963): *Annelids*. Hutchinson University Library, London.

Dales, R.P. (1964): The coelomocytes of the terebellid polychaete *Amphitrite johnstoni*. *Quarterly Journal of Microscopical Science London* 105: 263–279.

Dales, R.P. (1977): The polychaete stomatodeum and phylogeny. In: Reish, D.J. & Fauchald, K. (eds.), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 525–546.

Day, J.H. (1951): The polychaete fauna of South Africa. Part 1. The intertidal and estuarine Polychaeta of Natal and Mosambique. *Annals of the Natal Museum* 12: 1–67.

Day, J.H. (1955): The Polychaeta of South Africa. Part 3. Sedentary species from Cape shores and estuaries. *Journal of the Linnean Society of London, Zoology* 42: 407–452.

Day, J.H. (1967): *A Monograph on the Polychaeta of Southern Africa*. British Museum (Natural History), London: 1–878.

Delle Chiaje, S. (1828): *Memorie sulla storia e notomia degli Animali senza vertebre del regno di Napoli*. Vol. III. Napoli: 1–232 pp. + 109 pls.

Desbruyères, D. & Laubier, L. (1986): Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines: systématique, biologie et écologie. *Canadian Journal of Zoology* 64: 2227–2245.

Duchêne, J.C. (1980): Variations saisonnières de la densité du macrobenthos dans l'étage circalittoral. Exemple de l'annélide polychète *Terebellides stroemii* pour la région de Banyuls, Méditerranée occidentale. *Vie et Milieu* 30: 113–119.

Ebbe, B. & Purschke, G. (2020): 7.7.2 Ampharetidae Malmgren, 1866. In: Purschke, G. Böggemann, M.& Westheide, W. (eds.) *Handbook of Zoology. Annelida. Vol 3: Sedentaria III and Errantia I*. Degruyter, Berlin: 49–66.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Eckelbarger, K.J. (1975): A light and electron microscope investigation of gametogenesis in *Nicolea zostericola* (Polychaeta: Terebellidae). *Marine Biology* 30: 353–370.

Eckelbarger, K.L. (1976): Origin and development of the amoebocytes of *Nicolea zostericola* with a discussion of their possible role in oogenesis. *Marine Biology* 36: 169–182.

Ehlers, E. (1887): Florida-Anneliden (Report on the annelids of the dredging expedition of the U.S. coast survey steamer Blake). *Memoirs of the Museum of Comparative Zoology of Harvard* 15: 1–335, 1–60.

Ehlers, E. (1897): Polychaeten. *Ergebnisse der Hamburger Magalhaensischen Sammelreise 1892/93* 3: 1–148, 9 plates.

Fabricius, O. (1780): *Fauna Groenlandica, systematice sistents, Animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli prout detegendi occasio fuit, maximaque parte secondum proprias observationes*. Hafniae et Lipsiae, Copenhagen: 452.

Fauchald, K. (1972): Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology* 7: 1–575.

Fauchald, K. (1977): *The Polychaete Worms. Definitions and Keys to the Orders, Families and Genera*. Natural History Museum of Los Angeles County: 188 pp.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review* 17: 193–284.

Faulwetter, S., Vasileiadou, A., Kouratoras, M., Dailianis, T. & Arvanitidis, C. (2013): Micro-computed tomography: Introducing new dimensions to taxonomy. *ZooKeys* 263: 1–45.

Fauvel, P. (1923): *Polychètes errantes*. Faune de France 16. Lechevalier, Paris: 448.

Fauvel, P. (1927): *Polychètes Sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires*. Faune de France 16. Lechevalier, Paris: 494 pp.

Fauvel, P. (1953): *The Fauna of India Including Pakistan, Ceylon, Burma and Malaya. Annelida Polychaeta*. The Indian Press, Allahabad: 507 pp.

Fitzhugh, K. (1991): Uncini and the anchor-function hypothesis: empirical tests and causal explanations. In: Reish, D.J. (ed.), *Third International Polychaete Conference held at California State University*, Long Beach, California, August 6–11, 1989. *Bulletin of Marine Science* 48: 574–583.

Fitzhugh, K., Nogueira, J.M., Carrerette, O. & Hutchings, P. (2015): An assessment of the status of Polycirridae genera (Annelida: Terebelliformia) with the evolutionary transformation series of characters within the family. *Zoology Journal of Linnean Society* 2015: 1–36.

Fournier, J.A. & Barrie, J. (1984): *Baffinia hesslei* (Annenkova), n. comb. (Polychaeta: Terebellidae) from eastern Canada. *Canadian Journal of Zoology* 62: 1397–1401.

Franzen, S., Ghiladi, R.A., Lebioda, L. & Dawson, J. (2015): Chapter 10 Multi-functional hemoglobin haloperoxidases. In: Raven, E., Dunford, B. (eds.), *Heme Peroxidases*, RSC Metallobiology Series No. 4. The Royal Society of Chemistry, Cambridge: 218–246.

Friedman, M.M. & Weiss, L. (1980): An electron microscopic study of hemoglobin synthesis in the marine annelid, *Amphitrite ornata* (Polychaeta: Terebellidae). *Journal of Morphology* 164: 121–138.

Garraffoni, A.R.S. & Amaral, A.C.Z. (2009): Postlarval development of *Nicolea uspiana* (Polychaeta: Terebellidae). *Zoologia* 26: 61–66.

Garraffoni, A.R.S. & Lana, P.C. (2000): Análise cladística do gênero *Octobranchus* Marion and Bobretzky, 1875 (Trichobranchidae: Polychaeta). *Notas Técnicas da Facimar* 4: 43–48.

Garraffoni, A.R.S. & Lana, P.C. (2003): Species of *Terebellides* (Polychaeta, Terebellidae, Trichobranchinae) from the Brazilian coast. *Iheringia Zoologia* 93: 355–363.

Garraffoni, A.R.S. & Lana, P.C. (2004): Cladistic analysis of the subfamily Trichobranchinae (Polychaeta, Terebellidae). *Journal of the Marine Biological Association of the United Kingdom* 84: 973–982.

Garraffoni, A.R.S. & Lana, P.C. (2008): Phylogenetic relationships within the Terebellidae (Polychaeta: Terebellida) based on morphological characters. *Invertebrate Systematics* 22: 605–626.

Garraffoni, A.R.S. & Lana, P.C. (2009): A critical review of ontogenetic development in Terebellidae (Polychaeta). *Acta Zoologica (Stockholm)* 91: 390–401.

Garraffoni, A.R.S., Lana, P.C. & Hutchings, P. (2005): A catalogue of the Trichobranchinae (Polychaeta: Terebellidae) of the world. *Zootaxa* 1065: 1–27.

Glasby, C.J. (1991): Phylogenetic relationships in the Nereididae (Annelida, Polychaeta), chiefly in the subfamily Gymnonereidinae, and the monophyly of the Namanereidinae. *Bulletin of Marine Science* 48: 559–573.

Glasby, C.J. (1993): Family revision and cladistic analysis of the Nereidoidea (Polychaeta: Phyllodocida). *Invertebrate Taxonomy* 7: 1551–1573.

Glasby, C.J. (1999): The Namanereidinae (Polychaeta: Nereididae). Part 1, taxonomy and phylogeny. *Records of the Australian Museum* 25: 1–129.

Glasby, C.J. & Glasby, T.M. (2006): Two types of uncini in *Polycirrus* (Polychaeta: Terebellidae: Polycirrinae) revealed using geometric morphometrics. *Journal of Natural History* 40: 237–253.

Glasby, C.J. & Hutchings, P.A. (2014): Revision of the taxonomy of *Polycirrus* Grube, 1850 (Annelida: Terebellida: Polycirridae). *Zootaxa* 3877: 1–117.

Glasby, C.J., Hutchings, P.A. & Hall, K. (2004): Phylogeny of the polychaete order Terebellomorpha (Polychaeta: Terebellidae) based on morphology. *Journal of the Marine Biological Association of the United Kingdom* 84: 961–971.

Goodrich, E.S. (1945): The study of nephridia and genital ducts since 1895. *Quarterly Journal of Microscopical Science London* 86: 113–392.

Gravier, C. (1911): Expédition antarctique française du 'Pourquoi-Pas', dirigiée par M. le Dr. J.B. Charcot (1908–1910). Espèces nouvelles d'Annélides polychètes. *Bulletin de la Musée Nationale d'Histoire Naturelle* 17: 310–316.

Grube, A.E. (1850): Die Familie der Anneliden. *Archiv für Naturgeschichte (Berlin)* 16: 249–364.

Grube, A.E. (1860): Beschreibung neuer oder wenig bekannter Anneliden. *Archiv für Naturgeschichte (Berlin)* 26: 71–118, pl. III–V.

Grube, A.E. (1863): Beschreibung neuer oder wenig bekannter Anneliden. Sechster Beitrag. *Archiv für Naturgeschichte (Berlin)* 29: 37–69.

Grube, A.E. (1877): Anneliden - Ausbeute S.M.S. Gazelle. *Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1877*: 509–554.

Grube, A.E. (1878): Annulata Semperiana. Beiträge zur Kenntniss der Anneliden Fauna der Philippinen nach den von Herrn Prof. Semper mitgebrachten Sammlungen. *Memoires l'Académie Imperiale des Sciences de St. Petersbourg*, série, 7, 25: 1–300.

Guido, A., Mastandrea, A., Rosso, A., Sanfillipo, R., Tosti, F., Riding, F. & Russo, F. (2014): Commensal symbiosis between

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

agglutinated polychaetes and sulfate-reducing bacteria. *Geobiology* 3: 265–275.

Hall, K.A., Hutchings, P.A. & Colgan, D.J. (2004): Further phylogenetic studies of the Polychaeta using 18S rDNA sequence data. *Journal of the Marine Biological Association of the United Kingdom* 84: 949–960.

Harant, H. & Grassé, P.-P. (1959): Classe des Annélides Achètes ou Hirudinées ou Sangues. In: Grassé, P.-P. (ed.), *Traité de Zoologie. Anatomie, Systématique, Biologie* 5. Paris: 470–593.

Hartman, O. (1938): Annotated list of the types of polychaetous annelids in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology* 85: 1–31, 3 pls.

Hartman, O. (1942): A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collection* 8: 1–98.

Hartman, O. (1944): Polychaetous annelids from California, including the description of two new genera and nine new species. *Allan Hancock Pacific Expeditions* 10: 239–307.

Hartman, O. (1955): Quantitative survey of the benthos of San Pedro Basin, southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pacific Expeditions* 27: 1–86.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Part II. *Occasional Papers of the Allan Hancock Foundation* 23: 355–628.

Hartman, O. (1963): *Reteterebella queenslandia*, a new genus and species of polychaetous annelid from Queensland, Australia. *Records of the Australian Museum* 25: 355–357.

Hartman, O. (1966): Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarctic Research Series* 7: 158 pp.

Hartman, O. (1967): Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. *Allan Hancock Monographs in Marine Biology* 2: 1–387.

Hartman, O. (1968): *Atlas of Errantiate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California: 828 pp.

Hartman, O. (1969): *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California: Los Angeles 812 pp.

Hartman, O. & Fauchald, K. (1971): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. *Allan Hancock Monographs in Marine Biology* 6: 1–327.

Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. In: Dahl, C.F.T. (ed.), *Die Tierwelt Deutschlands*. Vol. 58. Gustav Fischer, Jena: 594 pp.

Hartmann-Schröder, G. (1986): Zur Kenntnis des Eulittorals der australischen Küsten unter besonderer Berucksichtigung der Polychaeten und Ostracoden (Teil 12). Die Polychaeten der antiborealen Südküste Australiens (zwischen Wallgwoyarrma im Westen und Port MacDonnell im Osten). In: Hartmann-Schröder, G. & Hartmann, G. (eds.), *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut Hamburg* 83: 31–70.

Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. In: Dahl, C.F.T. (ed.), *Die Tierwelt Deutschlands* Vol. 58. Gustav Fischer, Jena: 1–648.

Hatschek, B. (1893): System der Anneliden, ein vorlaufiger Bericht. *Lotos* 13: 123–126.

Heimler, W. (1981): Untersuchung zur Larvalentwicklung von *Lanice conchilega* (Pallas) 1766 (Polychaeta, Terebellomorpha). Teil II: Bau und Ultrastruktur der Trochophora-Larve. *Zoologische Jahrbücher (Abteilung für Anatomie und Ontogenie der Tiere)* 106: 236–277.

Heimler, W. (1983): Untersuchungen zur Larvalentwicklung von *Lanice conchilega* (Pallas 1766) (Polychaeta, Terebellomorpha). Teil III: Bau und Struktur der Aulophora-Larve. *Zoologische Jahrbücher (Anatomie und Ontogenie der Tiere)* 110: 411–478.

Hessle, C. (1917): Zur Kenntnis der terebellomorphen Polychaeten. *Zoologiska Bidrag från Uppsala* 5: 39–258.

Hilbig, B. (2000): Family Terebellidae Grube, 1851. In: Blake, J., Hilbig, B. & Scott, P.V. (eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Barbara Basin and the Western Santa Barbara Channel*. Vol. 7 – The Annelida Part 4: Polychaeta (Flabelligeridae to Sternaspidae). Santa Barbara Museum of Natural History, Santa Barbara, California: 230–293.

Holthe, T. (1976): *Paramphitrite tetrabranchia* gen. et sp. nov. A new terebellid polychaete from western Norway. *Sarsia* 61: 59–62.

Holthe, T. (1977): The systematic position of *Artacamella* Hartman, 1955 (Polychaeta, Terebellomorpha). *Sarsia* 63: 35–37.

Holthe, T. (1986a): Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. *Gunneria* 55: 1–236.

Holthe, T. (1986b): Polychaeta Terebellomorpha. *Marine Invertebrates of Scandinavia*, No. 7. Norwegian University Press, Oslo: 1–194.

Howell, B.F. (1953): A new terebellid worm from the carboniferous of Texas. *Wagner Free Institute of Science of Philadelphia Bulletin* 28: 1–4.

Hutchings, P.A. (1974): Polychaeta of Wallis Lake, New South Wales. *Proceedings of the Linnean Society of New South Wales* 98: 175–195.

Hutchings, P.A. (1977): The terebelliform polychaeta from Australia, chiefly from Moreton Bay, Queensland. *Records of the Australian Museum* 31: 1–39.

Hutchings, P.A. (1990): Terebellidae (Polychaeta) from the Hong Kong region. In: Moreton, B. (ed.), *Proceedings of the Second International Workshop on the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986*. University of Hong Kong: 377–412.

Hutchings, P.A. (1997b): New species of the family Terebellidae (Polychaeta) from Darwin Harbour Australia. In: Hanley, R. (ed.), *Proceedings of the 6th International Marine Biological Workshop. The Marine Flora and Fauna of Darwin Harbour, Northern Territory. Beagle*: 133–161.

Hutchings, P.A. (2000): Family Terebellidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes & Allies: The Southern Synthesis*. Fauna of Australia. Vol. 4A, Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, xii: 226–232.

Hutchings, P.A. & Glasby, C.J. (1986a): The Polycirrinae (Polychaeta: Terebellidae) from Australia. *Records of the Australian Museum* 38: 319–350.

Hutchings, P.A. & Glasby, C.J. (1986b): A new genus of Thelepinae (F. Terebellidae) *Glossothelepus* from Mexico. *Proceedings of the Biological Society of Washington* 99: 84–87.

Hutchings, P.A. & Glasby, C.J. (1986c): The genus *Euthelepus* (Terebellidae: Thelepinae) together with a description of a new species. *Records of the Australian Museum* 38: 105–117.

Hutchings, P.A. & Glasby, C.J. (1987): The Thelepinae (F. Terebellidae) from Australia together with a discussion of the generic and specific characters of the family. *Bulletin of the Biological Society of Washington* 7: 217–250.

Hutchings, P.A. & Glasby, C.J. (1988): The Amphitritinae (Polychaeta: Terebellidae) from Australia. *Records of the Australian Museum* 40: 1–60.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Hutchings, P.A. & Glasby, C.J. (1990): Additional new species of the family Terebellidae (Polychaeta) from Western Australia, with a key to all described species of the region. In: Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge R. (eds.), *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany,* Western Australia: Perth, Western Australian Museum: 251–289.

Hutchings, P.A. & Glasby, C.J. (1991): Phylogenetic implications of the biogeography of Australian Terebellidae. *Ophelia Supplement* 5: 565–572.

Hutchings, P.A. & Glasby, C.J. (1995): Description of the widely reported terebellid polychaetes *Loimia medusa* (Savigny) and *Amphitrite rubra* (Risso). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut Hamburg* 92: 149–154.

Hutchings, P.A. & Glasby, C.J. (2000): Class Polychaeta. History of discovery. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes & Allies: The Southern Synthesis*. Fauna of Australia. Vol. 4A, Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, xii: 3–9.

Hutchings, P.A. & Murray, A. (1984): Taxonomy of polychaetes from the Hawkesbury River and the southern estuaries of New South Wales, Australia. *Records of the Australian Museum Supplement* 3: 1–119.

Hutchings, P.A. & Peart, R. (2000): A revision of the Australian Trichobranchidae (Polychaeta). *Invertebrate Taxonomy* 14: 225–272.

Hutchings, P.A. & Smith, R.I. (1997): New species of the family Terebellidae (Polychaeta) from New Zealand and Australia. In: Reish, D.J. & Qian, P.Y. (eds.), Fifth International Polychaete Conference held at Qingdao, Peoples' Republic of China, July 1–6, 1995. *Bulletin of Marine Science* 60: 324–349.

Hutchings, P., Nogueira, J.M.M. & Carrerette, O. (2015): Telothelepodidae, Thelepodidae and Trichobranchidae (Annelida, Terebelliformia) from Lizard Island, Great Barrier Reef, Australia. *Zootaxa* 4019: 240–274.

Hutchings, P., Carrerette, O. & Nogueira, J.M.N. (2020): Pectinariidae de Quatrefages, 1866. In: Purschke, G. Böggemann, M.& Westheide, W. (eds.) *Handbook of Zoology. Annelida. Vol 3: Sedentaria III and Errantia I*. Degruyter, Berlin: 33–48.

International Code of Zoological Nomenclature (1985): 4th ed. Accessed at: http://www.vliz.be/imisdocs/publications/271138.pdf.

Johnson, H.P. (1901): The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History* 29: 381–437.

Johnston, G. (1846): An index to the British Annelides. *Annals and Magazine of Natural History* 1: 433–462.

Johnston, G. (1865): *A Catalogue of the British Non-parasitical Worms in the Collection of the British Museum*. British Museum, London: 1–365.

Jollivet, D. & Hourdez, S. (2020): 7.7.4 Alvinellidae Desbruyeres & Laubier, 1986. In: Purschke, G. Böggemann, M.& Westheide, W. (eds.) *Handbook of Zoology. Annelida. Vol 3: Sedentaria III and Errantia I*. Degruyter, Berlin: 144–160.

Jouin-Toulmond, J. & Hourdez, S. (2006): Morphology, ultrastructure and functional anatomy of the branchial organ of *Terebellides stroemii* (Polychaeta: Trichobranchidae) and remarks on the systematic position of the genus *Terebellides*. *Cahiers de Biologie* 47: 287–299.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Kennedy, G.Y. & Dales, R.P. (1958): The function of the heart-body in polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 37: 15–31.

Koie, M. & Petersen, M.E. (1988): A new annelid intermediate host (*Lanassa nordenskioeldi* Malgren, 1866) (Polychaetes: Terebellidae) for *Aporocotyle sp.* and a new final host family (Pisces: Bothidae) for *Aporocotyle simplex* Odhner, 1900 (Digenea: Sanguinicolidae). *American Journal of Parasitologists* 74: 499–502.

Langerhans, P. (1880): Die Wurmfauna von Madeira. III. *Zeitschrift für wissenschaftliche Zoologie* 34: 87–143.

Langerhans, P. (1884): Die Wurmfauna von Madeira. IV. *Zeitschrift für wissenschaftliche Zoologie* 40: 247–285.

Lavesque, N., Hutchings, P., Daffe, G., Nygren, A. & Londoño-Mesa. M.H. (2019): A revision of the French Trichobranchidae (Polychaeta), with descriptions of nine new species. *Zootaxa* 4664: 151–190.

Leidy, J. (1855): Contributions towards a knowledge of the marine Invertebrate fauna of the coasts of Rhode Island and New Jersey. *Journal of the Academy of Natural Sciences of Philadelphia* 3: 135–152, pls. 10–11. (xii-1855).

Leuckart, R. (1849): Zur Kenntnis der Fauna von Island. *Archiv für Naturgeschichte (Berlin)* 15: 149–208.

Levenstein, R.Y. (1957): Novye i redkie v fgaunae Beringova Moria glubokovodnye vidy Mnogoshtinkovyhkh chervei (Polychaeta). [A new and rare deep-water species of polychaetous worms in the bottom fauna of the Bering Sea.]. *Trudy Instituta Okeanologia, Akademia nauk SSSR* 23: 286–290.

Levin, L.A. & Greenblatt, P.R. (1981): Bottoms up: Juvenile terebellid polychaetes feeding in the water column. *Bulletin of the Southern California Academy of Sciences* 80: 131–133.

Levinsen, G.M.R. (1893): Annulata, Hydroidae, Anthozoa, Porifera. Videnskabelige Udbytte ad Kanonbaaden Hauchs, *Togter*: 321–464.

Lezzi, M. & Giangrande, A. (2019): New species of *Streblosoma* (Thelepodidae, Annelida) from the Mediterranean Sea: *S. pseudocomatus* sp. nov., *S. nogueirai* sp. nov. and *S. hutchingsae* sp. nov. *Journal of Natural History* 52: 2857–2873.

Linnaeus, C. (1767): *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 12th ed. Vol. 1. L. Salvius, Holmiae: 533–1327.

Llansó, R.J. & Diaz, R.J. (1994): Tolerance to low dissolved oxygen by the tubicolous polychaete *Loimia medusa*. *Journal of the Marine Biological Association of the United Kingdom* 74: 143–148.

Londoño-Mesa, M.H. (2003): Revision of *Spinosphaera* and establishment of the new genus *Hutchingsiella* (Polychaeta: Terebellidae: Terebellinae). *Journal of the Marine Biological Association of the United Kingdom* 83: 747–759.

Londoño-Mesa, M.H. (2006): Revision of *Paraeupolymnia*, and redescription of *Nicolea uspiana* comb. nov. (Terebellidae: Polychaeta). *Zootaxa* 1117: 21–35.

Londoño-Mesa, M.H. (2009): Terebellidae (Polychaeta: Terebellida) from the Grand Caribbean Region. *Zootaxa* 2320: 1–93.

Londoño-Mesa, M.H. & Carrera-Parra, L.F. (2005): Terebellidae (Polychaeta) from the Mexican Caribbean with description of four new species. *Zootaxa* 1057: 1–44.

Malmgren, A.J. (1866): Nordiska Hafs-Annulater. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm* 22: 355–410.

Mangum, C.P., Woodin, B.R., Bonaventura, C., Sullivan, B. & Bonaventura, J. (1975): The role of coelomic and vascular hemoglobin in the annelid family Terebellidae. *Comparative Biochemistry Physiology* 51: 281–294.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Marion, A.F. & Bobretzky, N.V. (1875): Étude des Annélides du Golfe de Marseille. *Annales des Sciences Naturelles (sixième série)* 2: 1–106.

McCombs, N.L., D'Antonio, J., Barrios, D.A., Carey, L.M & Ghiladi, R.A. (2016): Non-microbial nitrophenol degradation via peroxygenase activity of dehaloperoxidase-hemoglobin from *Amphitrite ornata*. *Biochemistry* 55: 2465–2478.

McHugh, D. (1993): A comparative study of reproduction and development in the polychaete family Terebellidae. *Biological Bulletin* 185: 153–167.

McHugh, D. (1995): Phylogenetic analysis of the Amphitritinae (Polychaeta: Terebellidae). *Zoological Journal of the Linnean Society* 114: 405–429.

McIntosh, W.C. (1869): On the structure of the British nemerteans, and some new British annelids. *Transactions Royal Society of Edinburgh* 25: 249–252.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. 'Challenger' during the years 1873–76. *Report of the Scientific Results of the Exploring Voyage of H.M.S. Challenger 1873–76* 12: 1–554.

Meyer, E. (1887): Studien über den Körperbau der Anneliden. *Mitteilungen aus der zoologischen Station zu Neapel* 7: 592–741.

Mikac, B. & Hutchings, P. (2017): One new species of *Pista* Malmgren, 1866 (Annelida: Terebellidae) and one new species of *Pistella* Hartmann-Schröder, 1996 (Annelida: Terebellidae) from the Adriatic Sea (Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* 97: 943–953.

Mohammad, M.B.M. (1980): Polychaete annelids from Kuwaitian islands, Arabian Gulf, with descriptions of four new species. *Zoological Journal of the Linnean Society* 69: 31–42.

Montagu, G. (1819): Descriptions of five British species of the genus *Terebella*. *Transactions of the Linnean Society of London* 12: 340–344, pl. 11–13.

Moore, J.P. (1903): Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 55: 401–490.

Muir, A.I. (2011): A redescription of *Unobranchus* (Annelida: Terebellidae: Trichobranchidae), with notes on the systematics of Trichobranchidae. *Italian Journal of Zoology* 78: 140–147.

Müller, F. (1858): Einiges über die Annelidenfauna der Insel Santa Catharina an der brasilianischen Küste. *Archiv für Naturgeschichte (Berlin)* 24: 211–220.

Müller, O.F. (1771): *Von Würmern des süssen und salzigen Wassers*. H. Mumme and Faber, Copenhagen.

Müller, O.F. (1776): *Zoologica Danica. Prodromus seu animalium Daniae et Norvegiae indegenarum characteris, nomine et synonyma imprimis popularium*. Copenhagen.

Nogueira, J.M.M. (2003): A new species of *Paraeupolymnia* Young & Kritzler, 1986 (Polychaeta: Terebellidae: Terebellinae) from Brazil. *Scientia Marina* 67: 403–411.

Nogueira, J.M.M. (2008): Review of some terebelliform polychaetes (Polychaeta: Terebelliformia) at the Yale Peabody Museum. *Bulletin of the Peabody Museum of Natural History* 49: 209–234.

Nogueira, J.M.M. (2019): Redescriptions of *Streblosoma bairdi* (Malmgren, 1866) and *Thelepus cincinnatus* (Fabricius, 1780), based on types and material from the type localities. *Zootaxa* 4544: 419–428.

Nogueira, J.M.M. & Alves, T.M. (2006): Two new terebellid polychaetes (Polychaeta: Terebellidae) from the State of São Paulo, southeastern Brazil. *Zootaxa* 1205: 31–54.

Nogueira, J.M.M. & Amaral, A.C.Z. (2001): New terebellids (Polychaeta: Terebellidae) living in colonies of a stony coral in the State of São Paulo, Brazil. *Proceedings of the Biological Society of Washington* 114: 285–296.

Nogueira, J.M.M. & Hutchings, P.A. (2007): New species of terebellid polychaetes (Polychaeta: Terebellidae) from Australia. *Zootaxa* 1473: 1–24.

Nogueira, J.M.M., Hutchings, P.A. & Amaral, A.C.Z. (2003): *Articulatia*, a new genus of Terebellinae (Polychaeta: Terebellidae) living in Brazilian corals. *Journal of the Marine Biological Association of the United Kingdom* 83: 761–770.

Nogueira, J.M.M., Garraffoni, A.R.S. & Alves, T.M. (2004): A new species of *Streblosoma* Sars, 1872 (Polychaeta, Terebellidae, Thelepodinae) from Brazil, with comments on *Streblosoma oligobranchiatum*. *Beaufortia* 54: 93–103.

Nogueira, J.M.M., Hutchings, P.A. & Fukuda, M.V. (2010): Morphology of terebelliform polychaetes (Annelida: Polychaeta: Terebelliformia), with a focus on Terebellidae. *Zootaxa* 2460: 1–185.

Nogueira, J.M., Harris, L., Hutchings, P.A. & Fukuda, M.V. (2011): Four terebellines (Polychaeta, Terebellidae) with problematic taxonomic histories. *Zootaxa* 2995: 1–26.

Nogueira, J.M.M., Fitzhugh, K. & Hutchings, P. (2013): The continuing challenge of phylogenetic relationships in Terebelliformia (Annelida: Polychaeta). *Invertebrate Systematics* 27: 186–238.

Nogueira, J.M.M., Carrerette, O. & Hutchings, P. (2015a): Review of *Amaeana* Hartman, 1959 (Annelida, Terebelliformia, Polycirridae) with descriptions of seven new species. *Zootaxa* 3994: 1–52.

Nogueira, J.M.M., Hutchings, P. & Carrerette, O. (2015b): Polycirridae (Annelida, Terebelliformia) from Lizard Island Group, Great Barrier Reef, Australia. *Zootaxa* 4019: 437–483.

Nogueira, J.M.M., Hutchings, P.A. & Carrerette, O. (2015c): *Varanusia* nom. nov., a replacement name for *Lizardia* Nogueira, Hutchings & Carrerette, 2015 (Annelida: Terebellidae), preoccupied by *Lizardia* Pleijel & Rouse, 2005. *Zootaxa* 4058: 141.

Nogueira, J.M.M., Hutchings, P. & Carrerette, O. (2015d): Terebellidae (Annelida, Terebelliformia) from the Lizard Island Group, Great Barrier Reef, Australia. *Zootaxa* 4019: 484–576.

Nogueira, J.M.M., Fitzhugh, K. Hutchings, P. & Carrerette, O. (2017): Phylogenetic analysis of the family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 (Annelida: Terebelliformia). *Marine Biology Research* 2017.

Nogueira, J.M.M., Carrerette, O., Hutchings, P. & Fitzhugh, K. (2018): Systematic review of the species of the family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 (Annelida, Terebelliformia), with descriptions of three new species. *Marine Biology Research* 14: 217–257.

Nygren, A., Parapar, J., Pons, J., Meißner, K., Bakken, T., Kongsrud, J.A., Oug, E., Gaeva, D., Sikorski, A., Johansen, R.A., Hutchings, P., Lavesque, N. & Capa, M. (2018): A megacryptic species complex hidden among one of the most common annelids in the North East Atlantic. *PLoS ONE* 13: e0198356.

Orrhage, L. (2001): On the anatomy of the central nervous system and the morphological value of the anterior end appendages of Ampharetidae, Pectinariidae and Terebellidae (Polychaeta). *Acta Zoologica (Stockholm)* 82: 57–71.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.

Örsted, A.S. (1844): Zur Classification der Annulaten mit Beschreibung einiger neuer oder unzulänglich bekannter Gattungen und Arten. *Archiv für Naturgeschichte (Berlin)* 10: 99–112.

Pallas, P.S. (1766): *Miscellanea Zoologica, quibus novæ imprimis atque obscuræ animalium species describuntur et*

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

observationibus iconibusque illustrantur. Hagæ Comitum, apud Petrum van Cleef, Netherlands: 224 + XIV pl.

Parapar, J. & Hutchings, P. (2014): Redescription of *Terebellides stroemii* (Polychaeta, Trichobranchidae) and designation of a neotype. *Journal of the Marine Biological Association of the United Kingdom*.

Parapar, J. & Moreira, J. (2008a): Redescription of *Terebellides kerguelensis* stat. nov. (Polychaeta: Trichobranchidae) from Antarctic and subantarctic waters. *Helgoland Marine Research* 62: 143–152.

Parapar, J. & Moreira, J. (2008b): Revision of three species of *Terebellides* (Polychaeta: Trichobranchidae) described by C. Hessle in 1917 from the Southern Ocean. *Journal of Natural History* 42: 1261–1275.

Parapar, J., Moreira, J., Gil, J. & Martin, D. (2016): A new species of the genus *Terebellides* (Polychaeta, Trichobranchidae) from the Iranian coast. *Zootaxa* 4117: 321–340.

Paterson, G.L.J., Sykes, D., Faulwetter, S., Merk, R., Ahmed, F., Hawkins, L.E., Dinley, J., Ball, A.D. & Arvanitidis, C. (2014): The pros and cons of using micro-computed tomography in gross and micro-anatomical assessments of polychaetous annelids. *Memoirs of Museum Victoria* 71: 237–246.

Pearson, T.H. (1969): *Scionella lornensis* sp. nov., a new terebellid (Polychaeta: Annelida) from the west coast of Scotland, with notes on the genus *Scionella* Moore, and a key to the genera of the Terebellidae recorded from European waters. *Journal of Natural History* 3: 509–516.

Pickett, J.W. (1972): The ecology of worm populations in the Erins Vale Formation (Late Permian) Southern Sydney Basin. *Journal of the Geological Society of Australia* 19: 313–320.

Picton, L.J. (1899): On the heartbody and coelomic fluid of certain Polychaeta. *Quarterly Journal of Microscopical Science, New Series* 41: 263–302. [issued in 1898]

Polloni, P.T., Rowe, G.T. & Teal, J.M. (1973): *Biremis blandi* (Polychaeta: Terebellidae), new genus, new species, caught by D.S.R.V. 'Alvin' in the Tongue of the Ocean, New Providence, Bahamas. *Marine Biology* 20: 170–175.

Quatrefages, A. de (1865): *Histoire naturelle des Annéles marins et d'eau douce. Annélides et géphyriens*. Librairie Encyclopédique de Roret, Paris: 588 pp. (Vol. I): 794 pp. (Vol. II), Tome 2.

Quatrefages, A. de (1866): *Histoire naturelle des Annéles marins et d'eau douce. Annélides et géphyriens*. Librarie Encyclopédique de Roret, Paris: 794 pp., Tome 3, atlas: 38 pp., 29 pls.

Read, G.B. (2019): A history of Annelida research. In: *Handbook of Zoology. Annelida*. Vol. 1. De Gruyter, Berlin: 3–36.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Fitzhugh, K. (1994): Broadcasting fables: Is external fertilization really primitive? Sex, size and larvae in sabellid polychaetes. *Zoological Scripta* 23: 271–312.

Rouse, G.W. & McHugh, D. (1994): Ultrastructure of spermatids and spermatozoa in *Ramex californiensis* and *Nicolea zostericola* (Terebellidae; Polychaeta). *Ophelia* 39: 225–238.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford, UK.

Rousset, V., Rouse, G.W., Féral, J.P., Desbruyères, D. & Pleijel, F. (2003): Molecular and morphological evidence of Alvinellidae relationships (Terebelliformia, Polychaeta, Annelida). *Zoologica Scripta* 32: 185–197.

Rullier, F. (1951): Étude morphologique, histologique et physiologique de t'organe nucal chez les annélides polychètes sédentaires. *Annales de l'Institut océanographique* 25: 207–341.

Saint-Joseph, A. (1894): Les Annelides polychaetes des cotes de Dinard. *Annales des sciences nature lie*, Paris, Pt. 3 Serie (7) 17: 1–395.

Sars, G.O. (1872): Diagnoser af nye Annelider fra Christianiafjorden, efter Professor M. Sar's efterladte Manuskripter. *Forhandlinger fra Videnskabs-Selskabet i Christiania* 1871: 406–417.

Sars, M. (1835): *Beskrivelser og Iagttagelser over nogle maerkelige eller nye i Havet ved den Bergenske Kyst Levende Dyr af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort Oversigt over de hidtil af Forfatteren sammesteds fundne Arter og deres Forekommen*. T. Hallager, Bergen: 81.

Sars, M. (1863): Geologiske og zoologiske Iagttabelse, anstillede paa en Reise i en Deelaf Trondhjems Stift i Sommerren 1862. *Nyt Magasin for Naturvidenskaberne, Christiania* 12: 253–340.

Sars, M. (1865): Fortsatte Bidrag til Kundskaben om Norges Annelider. *Forhandlinger fra Videnskabs-Selskabet i Christiania* 1865: 5–20.

Savigny, J.S. (1818): Section on Annelida. In: Lamarck, J.B. (ed.), *Histoire naturelle des animaux sans vertèbres*. Vol. 5. Déterville & Verdière, Paris: 618.

Schüller, M. & Hutchings, P.A. (2012): New species of *Terebellides* (Polychaeta: Trichobranchidae) indicate long-distance dispersal between western South Atlantic deep-sea basins. *Zootaxa* 3254: 1–31.

Schulte, E. & Riehl, R. (1976): Elektronenmikroskopische Untersuchungen an den Tentakeln von *Lanice conchilega* (Polychaeta, Sedentaria). *Helgoländer wissenschaftliche Meeresuntersuchungen* 28: 191–205.

Scott, J.W. (1911): Further experiments on the methods of egg-laying in *Amphitrite*. Biological Bulletin, *Marine Biological Laboratory Woods Hole* 20: 252–265.

Seitz, R.D. & Schaffner, L.C. (1995): Population ecology and secondary production of the polychaete *Loimia medusa* (Terebellidae). *Marine Biology* 121: 701–711.

Self, R.F.L. & Jumars, P.A. (1978): New resource axes for deposit feeders? *Journal of Marine Research* 36: 627–641.

Self, R.F.L. & Jumars, P.A. (1988): Cross-phyletic patterns of particle selection by deposit feeders. *Journal of Marine Research* 46: 119–43.

Serrano, V., D'Antonio, J., Franzen, S. & Ghiladi, R.A. (2010): Structure of dehaloperoxidase B at 1.58 °A resolution and structural characterization of the AB dimer from *Amphitrite ornata*. *Acta Crystallographica* 66: 529–538.

Shirakashi, S., Tani, K., Ishimaru, K., Shin Sang, P., Honryo, T., Uchida, H. & Shirakashi, K.O.S. (2016): Discovery of intermediate hosts for two species of blood flukes *Cardicola orientalis* and *Cardicola forsteri* (Trematoda: Aporocotylidae) infecting Pacific bluefin tuna in Japan. *Parasitology International* 65: 128–136.

Smith, R.I. (1988): Mixonephridia or nephromixia in terebellid polychaetes? A clarification. *Comparative Biochemistry and Physiology*, *Series C, Comparative Pharmacology and Toxicology*, 91: 265–272.

Smith, R.I. (1989a): Notes on gamete production in *Lanice conchilega* (Annelida, Polychaeta, Terebellidae). *Invertebrate Reproduction and Development* 1: 7–12.

Smith, R.I. (1989b): Observations on spawning behavior of *Eupolymnia nebulosa*, and comparisons with *Lanice conchilega* (Annelida, Polychaeta, Terebellidae). *Bulletin of Marine Science* 45: 406–414.

Smith, R.I. (1992): Three nephromixial patterns in polychaete species currently assigned to the genus *Pista* (Annelida, Terebellidae). *Journal of Morphology* 213: 365–393.

Smith, R.I. (1994): A systematic problem of inter- and intrageneric variation in nephromixia of Terebellidae. In: Dauvin, J.C., Laubier, L. & Reish, D. (eds.), *Actes de la 4ème Confèrence*

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

International des Polychètes. Mémoires du Muséum National d'Histoire Naturelle 162: 287–289.
Southern, R. (1914): Clare Island survey. Archiannelida and Polychaeta. *Proceedings of the Royal Irish Academy* 31: 1–160.
Storch, V. (1968): Zur vergleichenden Anatomie der segmentalen Muskelsysteme und zur Verwandtschaft der Polychaeten-Familien. *Zeitschrift für Morphologie und Ökologie der Tiere* 63: 251–342.
Storch, V. (1988): Integument. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of Polychaeta. Microfauna Marina* 4: 13–36.
Storch, V. & Schlötzer-Schrehardt, U. (1988): Sensory structures. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of Polychaeta. Microfauna Marina* 4: 121–133.
Struck, T.H. (2012): *Phylogeny of Annelida. Zoology Online*. Berlin: De Gruyter.
Struck, T. (2019): Phylogeny of Annelida. In: *Handbook of Zoology. Annelida*. Vol. 1. De Gruyter, Berlin: 37–68.
Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.
Sugihara, Y., Yamada, T., Tamaki, A., Yamanishi, R. & Kanai, K. (2013): Larval stages of the bluefin tuna blood fluke *Cardicola* Opisthorchis 2 (Trematoda: Aporocotylidae) found from *Terebella* sp. 3 (Polychaeta: Terebellidae). *Parasitology International* 63: 295–299.
Sutton, M.F. (1957): The feeding mechanism, functional morphology and histology of the alimentary canal of *Terebella lapidaria* (Polychaeta). *Journal of Zoology* 129: 487–523.
The Terebellidae (F. Polychaeta) from the Wallabi Group, Houtman Abrohlos Islands, Western Australia. Wells, F.E. (ed.), *Proceedings of the 7th International Marine Biological Workshop. The Marine Flora and Fauna of Abrohlos Island, Western Australia*. Western Australian Museum, 2: 459–502.
Thomas, A.T. & Smith, M.P. (1998): Terebellid polychaete burrows from the Lower Palaeozoic. *Palaeontology* 41: 317–333.
Thorson, G. (1946): Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser, Serie Plankton* 4: 1–523.
Tiberi, J. & Vovelle, J. (1975): Données histochimiques sur la nature et la formation du tube larvaire chez *Lanice conchilega* Pallas, Polychaete Terebellidae. *Archives de Zoologie Expérimentale et Générale* 116: 303–318.
Trueblood, D.D. (1991): Spatial and temporal effects of terebellid polychaete tubes on soft-bottom community structure in Phosphorescent Bay, Puerto Rico. *Journal of Experimental Marine Biology and Ecology* 149: 139–159.
Tzetlin, A.B. & Filippova, A. (2005): Muscular system in polychaetes (Annelida). In: Bartolomaeus, T. & Purschke, G. (eds.), *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa*, Hydrobiologia 535/536, Springer: 113–126.
Uchida, H. (1968): Polychaetous annelids from Shakotan (Hokkaido). I. The collection in 1967. *Journal of the Faculty of Science*, Hokkaido University, Ser. 6, Zoology 16: 595–612.
Ushakov, P.V. (1955) *Polychaeta of the Far Eastern Seas of the U.S.S.R.* Academy of Sciences of the U.S.S.R.: 419 pp. [in Russian]
Vandergon, T.L., Noblet, G.P. & Colacino, J.M. (1988): Identification and origin of hemoglobin in a gymnophallid metacercaria (Trematoda: Digenea), a symbiote in the marine polychaete *Amphitrite ornata* (Annelida: Terebellidae). *Biological Bulletin* 174: 172–180.
Verrill, A.E. (1873): Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. In: *Report on the Condition of the Sea Fisheries of the South Coast of New England, 1871–1872, Article 18*. Government Printing Office, Washington, DC: 295–778.
Verrill, A.E. (1879): Preliminary check-list of the marine Invertebrata of the Atlantic coast, from Cape Cod to the Gulf of St. Lawrence. [Prepared for the United States Commission of Fish and Fisheries.]. *Tuttle, Morehouse & Taylor, printers; Author's edition*. 32 pp., available online at https://books.google.com/books/about/Preliminary_check_list_of_the_marine_inv.html?id=EoEuAAAAYAAJ
Verrill, A.E. (1900): Additions to the Turbellaria, Nemertina, and Annelida of the Bermudas, with a revision of the New England genera and species. *Transactions of the Connecticut Academy of Arts and Sciences* 10: 595–671.
Vinn, O. & Toom, U. (2014): First record of the trace fossil Oikobesalon from the Ordovician (Darriwilian) of Baltica. *Estonian Journal of Earth Sciences* 63: 118–121.
Wesenberg-Lund, E. (1950): Polychaeta. *Danish-Ingolf Expedition* 4: 1–92.
Westheide, W. (2003): A temporarily planktonic terebellid polychaete. *Journal of the Marine Biological Association of the United Kingdom* 83: 771–774.
Williams, S.J. (1984): The status of *Terebellides stroemii* (Polychaeta; Trichobranchidae) as a cosmopolitan species, based on a worldwide morphological survey, including description of new species. In: Hutchings, P.A. (ed.), *Proceedings of the First International Polychaete Conference, Sydney, Australia, 1984*. Linnean Society New South Wales, Sydney: 118–142.
Wilson, D.P. (1928): Post-larval development of *Loimia medusa* Sav. *Journal of the Marine Biological Association of the United Kingdom* 15: 129–149.
Wilson, W.H. (1991): Sexual reproductive modes in polychaetes: classification and diversity. I*n*: Reish, D.J. (ed.), Third International Polychaete Conference held at California State University, Long Beach California August 6–11, 1989. *Bulletin of Marine Science* 48: 500–516.
Wirén, A. (1885): Om Cirkulation- och digestions-organen hos Annelider af familjerna Ampharetidae Terebellidae och Amphictenidae. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1–58.
Wolf, P.S. (1983): A revision of the Bogueidae Hartman and Fauchald 1971, and its reduction to Bogueinae, a subfamily of Maldanidae (Polychaeta). *Proceedings of the Biological Society of Washington* 96: 238–249.
Woodin, S.A. & Merz, R.A. (1987): Holding on by their hooks: Anchors for worms. *Evolution* 41: 427–432.
Zhadan, A.E. & Tzetlin, A.B. (2002): Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta). *Cahiers de Biologie Marine* 43: 149–164.
Zhadan, A.E. & Tzetlin, A.B. (2003): Comparative study of the diaphragm (gular membrane) in Terebelliformia (Polychaeta, Annelida). *Hydrobiologia* 496: 269–278.
Zhang, J. & Hutchings, P. (2018): Taxonomy and distribution of *Terebellides* (Polychaeta: Trichobranchidae) in the northern South China Sea, with description of three new species. *Zootaxa* 4377: 387–411.
Zrzavý, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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Didier Jollivet and Stéphane Hourdez

7.7.4 Alvinellidae Desbruyères & Laubier, 1986

Introduction

The family Alvinellidae Desbruyères & Laubier, 1986 comprises only 12 currently described species and is only found at deep-sea hydrothermal vents in the Pacific Ocean. The Pompeii worm *Alvinella pompejana* Desbruyères & Laubier, 1980 was the first species described, only 3 years after the discovery of diffuse vent emissions and associated communities on the Galápagos Rift (Lonsdale 1977, Corliss et al. 1979) and only 1 year after the species was first collected on the 21°N of the East Pacific Rise (EPR) chimneys called "black smokers" in 1979 (Rise Project Group 1980). The genus was named after the manned submersible Alvin, which was the first submersible to collect the species. The species name refers to its environment, on chimney walls, where it is permanently exposed to a rain of polymetallic particles associated with the abrupt cooling of the very hot (300–350°C) and sulfidic hydrothermal vent fluid. In their initial description, Desbruyères and Laubier (1980) indicated that the species represents an "aberrant" Ampharetidae, with a very well developed reddish branchial crown. Two years later, the first species in the genus *Paralvinella* Desbruyères & Laubier, 1982 was described (Desbruyères and Laubier 1982) in what was then considered a subfamily of Ampharetidae (Alvinellinae). With the description of additional new species, Desbruyères and Laubier (1986) eventually erected the family Alvinellidae that comprises two genera, *Alvinella* and *Paralvinella*. Species from this family correspond to Terebellomorpha with a relatively high number (55–180) of short chaetigerous segments and a body that is not subdivided into distinct regions.

The extreme environment in which these species are found prompted a series of studies on their taxonomy, biology, reproduction, physiology, and evolution. This chapter provides an overview of what is known on the species belonging to this family. An extensive review was published by Desbruyères et al. (1998) on the very emblematic species *Alvinella pompejana*, but much progress has been made since, not only on this species but also on other species of the family.

Morphology

According to Desbruyères and Laubier (1986), the diagnosis of the family Alvinellidae relies on several specific morphological features, which are (1) a reduced prostomium with a retractable buccal apparatus positioned ventrally that comprises grooved ciliated tentacles and a dorsal organ, (2) four pairs of hypertrophied gills made of lamellae (*Alvinella*) or simple unbranched filaments (*Paralvinella*) with the first pair of branchiae inserted on the first achaetigerous segment and the others on the fused second and third segments, (3) biramous parapodia with capillary chaetae on the notopodia and a single row of breviavicular uncini on the neuropodia, and (4) fourth and fifth (*Alvinella*) or seventh (*Paralvinella*) anterior chaetigers highly modified with capillary chaetae replaced by two pairs (*Alvinella*) or one pair (*Paralvinella*) of hooks.

The family Alvinellidae belongs to the order Terebellida, sharing several morphological traits, such as retractable buccal tentacles with a ciliated groove directly inserted on the ventral lobe of the pharyngeal cavity similar to ampharetid worms; avicular shape of uncini and long-shafted neuropodia similar to Trichobranchid worms; and a plesiomorphic distribution of notopodia over the whole body like some other subfamilies of terebellid worms.

However, alvinellids differ from other species belonging to Terebellida by the lack of a clear separation between the thorax and the abdomen of the worm, and this trait may be considered as plesiomorphic. The dorsal organ of alvinellid worms, which is a glandular and ciliated evagination of the pharyngeal cavity situated dorsally, is also specific and not shared with other families of Terebellida. The genital pore located at the base of the branchial crown is also a characteristic typifying alvinellid worms and, together with the sexual tentacles, plays a crucial role in their reproduction. They can be used to discriminate males and females as, unlike other terebellomorph species, all alvinellid species display a clear sexual dimorphism that might represent a secondary adaptation of the worm to secure egg fertilization in the highly fragmented and instable hydrothermal vent environment (Faure et al. 2007).

History of species discovery

The epibiotic Pompeii worm *A. pompejana* and its sister species *Alvinella caudata* Desbruyères & Laubier, 1986 were first described as two successive ontogenetic forms of the same species by Desbruyères and Laubier (1980) from the top of vent chimneys at the site 21°N of the EPR. Because of the presence of an elongated and flattened tail supporting filamentous Proteobacteria, *A. caudata*

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was indeed first considered as a possible juvenile form of the worm able to swim for dispersal. The genetic analysis of the two forms by Autem et al. (1985) using allozymes demonstrated without any doubt that they represent "old" and distinct morphological species with no allele sharing. Recent comparative analyses of the transcriptomes of the two worms confirmed this latter hypothesis with reciprocal monophylies at nearly all loci and an average gene divergence of about 0.3 fixed substitutions per site (Fontanillas et al. 2017, Thomas-Bulle et al. 2020, submitted).

Paralvinella grasslei Desbruyères & Laubier, 1982 was then described from washings of the chitinous tubes of the siboglinid worm *Riftia pachyptila* Jones, 1981 from samples collected at 13°N of the EPR. Since then, nine additional *Paralvinella* species have been described from a series of expeditions at deep-sea vent hydrothermal sites all over the globe, indicating that the family Alvinellidae is endemic only to the Pacific Ocean. Additional alvinellid populations have been, however, newly discovered on the wall of small vent edifices of the Solitaire and Edmond fields along the central Indian Ridge on the Rodriguez segment (Nakamura et al. 2012, Watanabe and Beedessee 2015). Alvinellid worms have been found in close association with the peltospirid "scaly foot" gastropods, and species are currently under description.

Among *Paralvinella* species, several are associated with the tubes of siboglinid worms, such as *R. pachyptila*, *Tevnia jerichonana* Jones, 1985 or *Ridgeia piscesae* Jones, 1985, or cracks in the basaltic crust where diffuse hydrothermal venting occurs. Some species, however, directly live on the walls of vent chimneys and could represent ecological homologs to the *Alvinella* spp. on either the northeastern Pacific ridges (Tunnicliffe et al. 1993) or the vent sites of the western back-arc basins (Desbruyères et al. 1994, Ohta and Kim 2001). The description of additional materials sampled from the EPR and the northeastern Pacific Juan de Fuca Ridge led to the concept that deep-sea hydrothermal organisms may form sibling species according to the geography and the plate movement history (also see Tunnicliffe 1988). To this extent, two pairs of sibling species have been described by Desbruyères and Laubier (1986). In the first pair, *Paralvinella palmiformis* Desbruyères & Laubier, 1986, usually found on the Juan de Fuca, Explorer, and Gorda ridges of the northeastern Pacific, is morphologically similar to *P. grasslei*, with only a few minor differences, which only occurs along the northern EPR. In the second pair, *Paralvinella pandorae pandorae* Desbruyères & Laubier, 1986 sampled at the same localities along the northeastern Pacific is almost identical to *Paralvinella pandorae irlandei* Desbruyères & Laubier, 1986, which is also collected from the EPR. Genetic analyses of these pairs of species also showed that they have similar levels of divergence (~7.5% of divergence), which allowed Chevaldonné et al. (2002) to calculate a new substitution rate for the *cytochrome oxidase 1* (*Cox1*) gene of the vent annelids.

In 1988, Detinova described a new *Paralvinella* species found in association with *P. pandorae pandorae* in the deep-sea vent communities of Axial Seamount. This species previously called "megaplume worm" was named *Paralvinella dela* Detinova, 1988 in honor of D. Desbruyères (de) and L. Laubier (la). This new species also represents a sibling species to *Paralvinella bactericola* Desbruyères & Laubier, 1991 described 1 year later from specimens collected in hydrothermal vent sediments of the Guaymas Basin (Desbruyères and Laubier 1989). Finally, three additional species were also described from the western Pacific back-arc basins following the first American expedition on the Marianas back-arc spreading center (Hessler and Lonsdale 1991) and other basins (Desbruyères et al. 1994, Auzende et al. 1997) in this part of the globe. These species are *Paralvinella hessleri* Desbruyères & Laubier, 1989 from Marianas back-arc spreading center and the Okinawa Trough (Desbruyères and Laubier 1989, Miura and Ohta 1991) but also found in great numbers in the Manus Basin (Hashimoto et al. 1999) and, to lesser extent, in the North Fiji Basin (Reuscher et al. 2012), *Paralvinella fijiensis* Desbruyères & Laubier, 1993 and *Paralvinella unidentata* Desbruyères & Laubier, 1993 from both Lau and North Fiji basins (Desbruyères and Laubier 1989, 1993). A fourth species from the North Pacific ridge was also secondarily identified thanks to diagnostic alleles of several enzyme loci when compared to *P. palmiformis* (Tunnicliffe et al. 1993). *Paralvinella sulfincola* Desbruyères & Laubier, 1993, although shorter and thicker than *P. grasslei* and *P. palmiformis*, is morphologically and genetically more similar to *P. fijiensis* and indicates the possibility of a geographic expansion of several distinct ancestral lineages at the scale of the Pacific Ocean (Jollivet et al. 1995b). This latter hypothesis is strengthened by the finding of *P. dela*-like specimens at station 35 TVG of the North Fiji Basin (Reuscher et al. 2012). Additional species, including new tube-building *Paralvinella* worms, are likely to co-occur under the names of *P. hessleri* and *P. unidentata* on the walls of vent chimneys from different places from the Manus Basin to the Kermadec Arc, some of which are currently under description (Hourdez personal observations).

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Biology and ecology

Ecology

Most species of Alvinellidae build tubes or cocoons on the wall of vent chimneys, in basaltic cracks with venting, or at the base of vestimentiferan (Siboglinidae) tubes (Figs. 7.7.4.1–7.7.4.3). The habitat preference of *Alvinella* spp. Paralvinella spp. is so far restricted to active basalt-hosted sulfide mounds but not to the sediment-hosted carbonate edifices, where only a few specimens of an undescribed *Paralvinella* species have been sampled, as recently shown by Goffredi et al. (2017) when describing

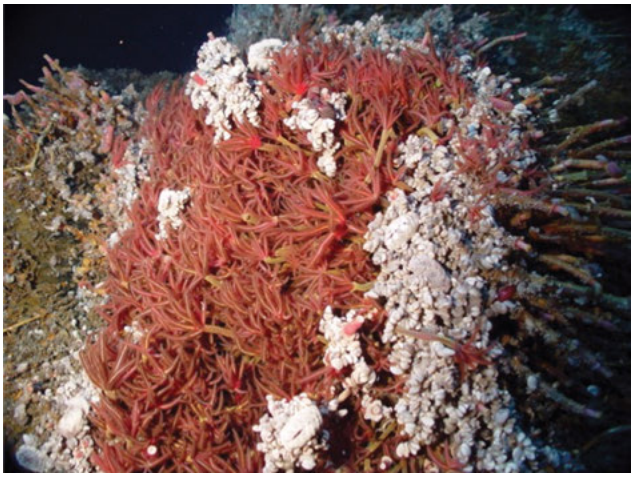


Fig. 7.7.4.1: Population of *Paralvinella palmiformis* Desbruyères & Laubier, 1986 associated with limpets and *Ridgeia* tubeworms on a sulfide mound of Juan de Fuca Ridge. Courtesy of V. Tunnicliffe.



Fig. 7.7.4.2: Population of the tubicolous *Paralvinella sulfincola* Desbruyères & Laubier, 1993 on the wall of a vent chimney on Juan de Fuca Ridge. Courtesy of V. Tunnicliffe.



Fig. 7.7.4.3: Close-up of *Alvinella pompejana* Desbruyères & Laubier, 1980 outside its tube on the wall of a vent chimney on the southern EPR (photograph taken by Nautile during the Biospeedo cruise. Copyright IFREMER, chief scientist D. Jollivet).

communities of the southern Gulf of California hydrothermal vent edifices. The inner part of the tube and/or the mucous threads of cocoons are covered by either filamentous epsilon proteobacteria or rod bacteria (Desbruyères and Laubier 1986, Tunnicliffe et al. 1993, Le Bris et al. 2005, Le Bris and Gaill 2010). The mucus secreted by the worm is made of polysaccharides and glycoproteins often used to trap metallic compounds possibly to detoxify their immediate surroundings (Taghon et al. 1988).

Habitat and geographic range. In the East Pacific, both *Alvinella pompejana* and *Alvinella caudata* live sympatrically on the walls of hydrothermal vent chimneys along the EPR and the Pacific-Antarctic Ridge from 21°N to 38°S (Hurtado et al. 2004). *A. pompejana* is also present on active chimneys of the Guaymas Basin. The two species have also been recently sampled from newly formed chimneys on the Galápagos Rift near the Rose Garden vent field. *P. grasslei* is typically found at the base of the Siboglinidae *Riftia pachyptila* and has a geographic range very similar to that of the two *Alvinella* species but seems to be quite rare on the southern EPR and is absent further south. Finally, *Paralvinella pandorae irlandei* has been found in association with the Siboglinidae *Tevnia jerichonana* on most of the sites of the EPR and the Pacific-Antarctic Ridge but is not present at sites of the Guaymas Basin and the Galápagos Rift. In the northeast Pacific, the three species *Paralvinella palmiformis*, *Paralvinella sulfincola*, and *P. pandorae pandorae* are present over all the vent fields of the North Pacific ridge

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segments from the Gorda Ridge to the Explorer Ridge but inhabit different niches. *P. sulfincola* inhabits chimney walls, whereas *P. pandorae pandorae* and *P. palmiformis* are found with the Siboglinidae *Ridgeia piscesae* (Tunnicliffe et al. 1993). *P. dela* is mostly restricted to Axial Seamount but can also be observed although rare at Middle Valley, Cleft, and Endeavour with *Ridgeia* tubeworms (Detinova 1988). Its sister species *Paralvinella bactericola* is endemic to diffuse venting of the Guaymas Basin with a more specific habitat preference to hydrothermal sediments covered by bacterial mats. Other species are only present along the fragmented ridges of the western Pacific back-arc basins. *Paralvinella hessleri*, originally described from the Marianas back-arc spreading center, is mostly found on the chimney walls of the northwestern Pacific from the Okinawa Trough to the Manus Basin (Miura and Ohta 1991, Hashimoto et al. 1999), with a few specimens collected at vents of the North Fiji Basin (Reuscher et al. 2012). *Paralvinella unidentata* and *Paralvinella fijiensis* are more likely present in the eastern part of the western Pacific on the base and top of vent chimneys of the Lau and North Fiji basins (Desbruyères et al. 1994) but have also been observed on hydrothermal vents from active seamounts of the Vanuatu subduction arc, at least for *P. unidentata* (V. Tunnicliffe personal communication). Some of the main alvinellid species are pictured in Fig. 7.7.4.4.

Thermal adaptation. One of the main adaptations investigated in Alvinellidae is their ability to cope with high temperature and rapid temperature variations. Tubes represent a very efficient means to insulate the worm from high temperatures (Gaill and Bouligand 1987) and from the chaotic variations of temperature over short time intervals (<1 min). Alvinellidae are also well adapted to live under severe hypoxic conditions (see Respiration

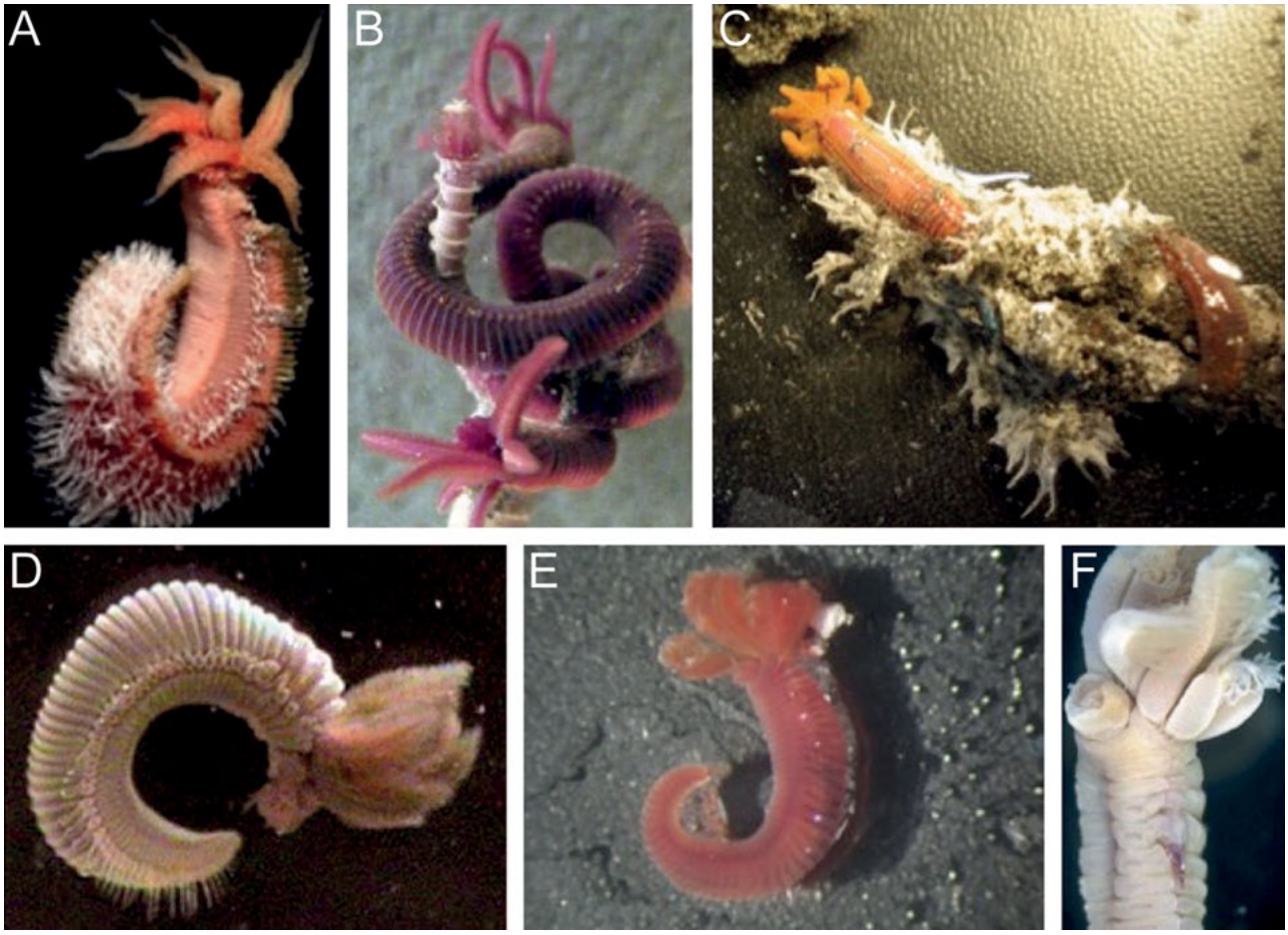


Fig. 7.7.4.4: Diversity of Alvinellidae. A, *Alvinella pompejana* Desbruyères & Laubier, 1980; B, *Paralvinella palmiformis* Desbruyères & Laubier, 1986; C, *Paralvinella hessleri* Desbruyères & Laubier, 1989; D, *Paralvinella sulfincola* Desbruyères & Laubier, 1993; E, *Paralvinella fijiensis* Desbruyères & Laubier, 1993; F, *Paralvinella pandorae irlandei* Desbruyères & Laubier, 1986. Micrographs: A, D. Desbruyères; B–D, V. Tunnicliffe; E, M. Matabos; P. Briant.

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and oxygen transport section) and have high activities of anaerobic and oxidative stress enzymes (Dilly et al. 2012, Genard et al. 2013). These activities are even more pronounced for species that live in colder but diffuse venting conditions, where H_2S concentrations can be higher than on the chimney walls (Rinke and Lee 2009). Temperature tolerance and preference have been investigated in a few alvinellid species to date. The chimney-dwelling *Alvinella pompejana* was observed near a temperature probe that indicated 105°C (Chevaldonné et al. 1992), and temperature values consistently close to 80°C were reported within its tube while inhabited (Cary et al. 1998). However, Chevaldonné et al. (2000) questioned this consistently high temperature regime from the available biochemical and physiological data gathered on the species. Based on this information, these authors concluded that the worm probably cannot withstand temperatures above 50°C over long periods of time. This was confirmed by controlled laboratory experiments that indicated that an exposure to temperature of 50°C to 55°C for 2 h was lethal (Ravaux et al. 2013). Temperature preference investigations revealed that another chimney-dwelling species, *Paralvinella sulfincola*, preferred temperatures between 40°C and 50°C (some individuals remaining at the upper temperatures for 7 h, the duration of the experiment), and some specimens spend at least 15 min at 55°C (Girguis and Lee 2006). The same experiments carried out on the species *Paralvinella palmiformis*, usually found with the tubeworm *Ridgeia piscesae* (Siboglinidae), preferred temperatures ranging from 25°C to 35°C, consistently avoiding higher temperatures.

To cope with high temperatures, a series of specific adaptations at the molecular level has been reported for *Alvinella pompejana* and *Paralvinella sulfincola*, including a protective tube/cocoon made of positively and negatively twisted polymers layers of unusually stable glycoprotein matrix and elemental sulfur (Gaill and Hunt 1986, Juniper 1988, Taghon 1988), a very efficient arsenal of heat shock proteins and stress oxidative enzymes (Dilly et al. 2012), enzymes able to remain stable and still active at temperatures above 50°C (Jollivet et al. 1995a, Rinke and Lee 2009), and the production of a thermally stable collagen (Sicot et al. 2000). In *A. pompejana*, exposure to 55°C, although lethal, induced a heat shock response, whereas exposure to 42°C did not (Ravaux et al. 2013). A similar response was observed in *Paralvinella palmiformis* when transferred from 12°C to 38°C, but no response was observed in the chimney-dwelling *P. sulfincola* when transferred from 10°C to 45°C, suggesting that this species constantly expressed heat shock proteins (i.e., constitutively expressed rather than inducible) (Dilly et al. 2012). Overall, the proteome of alvinellid worms comprises proteins with specific enrichments in charged aromatic and alanine residues in a way similar to the protein composition of thermophilic/ultrathermophilic prokaryotes (Jollivet et al. 2012, Fontanillas et al. 2017). This state could represent an ancestral trait for the family, and adaptation to lower temperature could be a secondarily acquired character (Fontanillas et al. 2017).

Biology

Symbiosis/epibiosis. Among Alvinellidae, only the two *Alvinella* species have developed a complex epibiotic relationship with filamentous epsilon Proteobacteria, located either on the dorsal part of the animal (*A. pompejana*) (Haddad et al. 1995, Cary et al. 1997) or the modified parapodia of the worms' tail (*A. caudata*). *Paralvinella* species that live on the wall of vent chimneys, such as *P. hessleri*, *P. fijiensis*, and *P. sulfincola*, also inhabit tubes covered by rod and filamentous bacteria on their inner surface but are not epibiotic, although they host rod bacteria attached to the uncini. Nearly all studies on the trophic relationship between the worm and its epibiotic bacteria have been performed on *A. pompejana* (Gaill et al. 1988, Gulik and Gaill 1988, Desbruyères et al. 1998, Campbell et al. 2001, Lee et al. 2008). The acquisition of epibiotic bacteria led to specific adaptations of the worm, such as dorsal or tail expansions with modified geniculate chaetae (Desbruyères et al. 1998) and the evolution of its antibacterial peptide arsenal by duplication and positive selection (Tasiemski et al. 2014, Papot et al. 2017), some of which appear to be used for the control of the epibiosis. The epibiotic bacteria consortium is made of a few dominant filamentous bacteria that are eurythermal and involved in a unilateral nonobligatory symbiotic relationship possibly leading to nutritional (but see below) and detoxifying processes that can be beneficial for the worm.

Feeding. The digestive system is linear and subdivided into an esophagus followed by a stomach and an intestine that ends in a terminal anus (Fig. 7.7.4.5) (Saulnier-Michel et al. 1990). As in all Terebellomorpha, Alvinellidae have grooved and ciliated buccal tentacles and, as in most Ampharetidae, are attached to a dorsal organ on the roof of the mouth (Desbruyères and Laubier 1986, Zhadan and Tzetlin 2002). They are shorter and less numerous than those of Terebellidae (Rouse and Pleijel 2001). The authors have suggested that some *Paralvinella* species could supplement their deposit feeding diet by collecting particles suspended in the water (Desbruyères and Laubier 1991), essentially filtering water with their gills. This feeding

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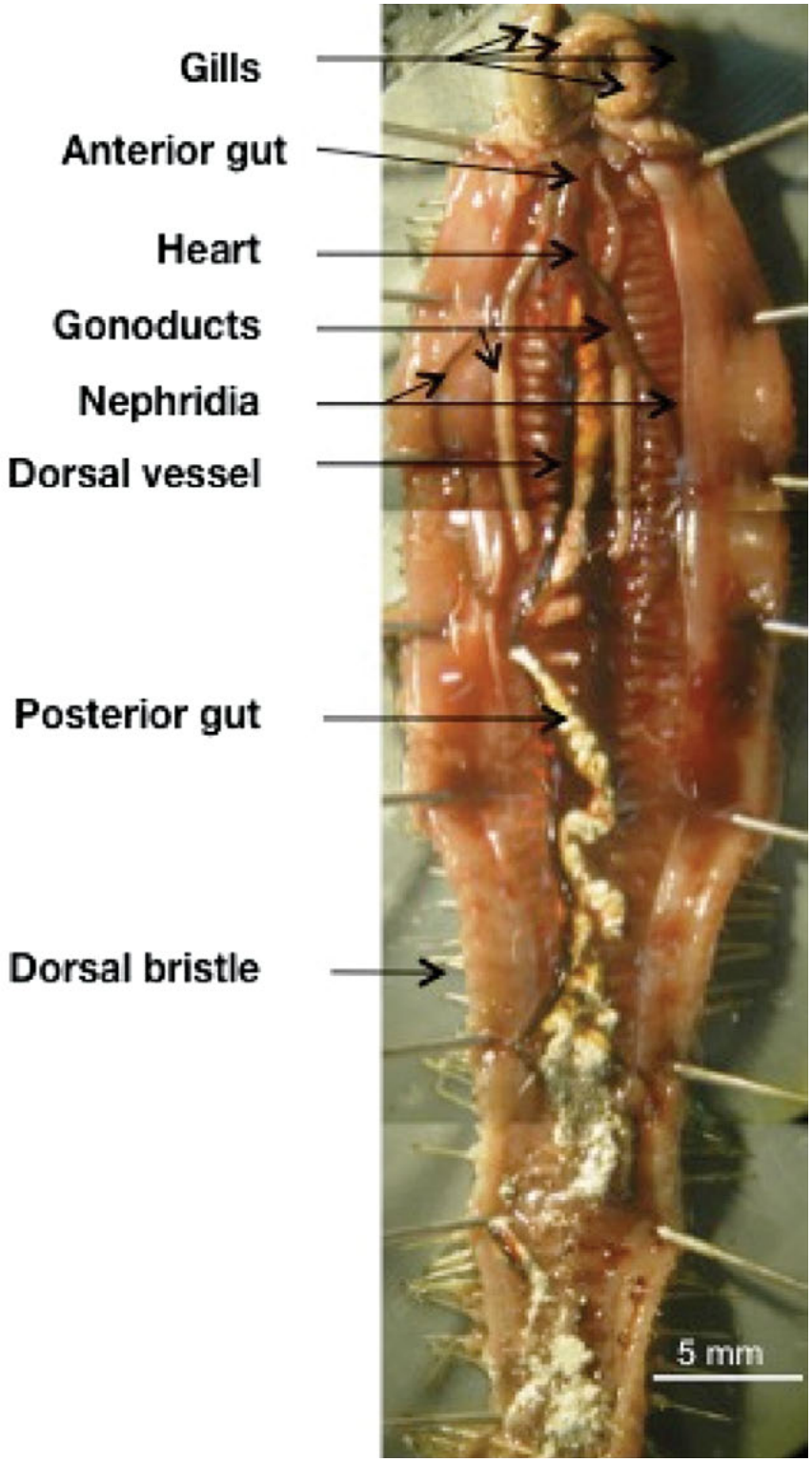


Fig. 7.7.4.5: Internal anatomy of *Alvinella pompejana* Desbruyères & Laubier, 1980, dorsal view of a dissected specimen. The presence of gonoducts and a well-developed vascular system in the anterior part is characteristic for the family Alvinellidae. A main part of the gut is highly colonized by symbionts that form clearly visible white aggregates (micrograph from MESCAL 2 scientific cruise, dissection under binocular done by A. Tasiemski).

strategy has been observed in *Flabelliderma commensalis* Moore, 1909 (Flabelligeridae) (see Jumars et al. 2015 and references therein). Desbruyères and Laubier (1991) also suggested that the two large tentacles in *Paralvinella bactericola* could be used to feed on larger suspended particles, whereas the smaller tentacles are used in deposit feeding. Buccal tentacles are easy to see on *in situ* videos of live specimens such as *Paralvinella palmiformis*, which extend them as suspension feeders. *Paralvinella sulfincola* also seems to use its buccal tentacles to fight

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with nearby congeners to defend its territory (Grelon et al. 2006). The tentacles are, however, most likely used for deposit feeding, including on the bacterial residents of the worm tubes (Desbruyères and Laubier 1982). Attached, filamentous bacteria on the posterior dorsal surface of *Alvinella*, however, do not appear to be directly involved in their nutrition (Alayse-Danet et al. 1986). In addition, male Alvinellidae also have a pair of larger tentacles attached to the ventral surface of the buccal cavity that are used in sperm transfer (Desbruyères and Laubier 1986). The ventral pharynx is muscular and thought to be eversible (Fig. 7.7.4.5) (Saulnier-Michel et al. 1990). Unusual structures in this part of the worm resemble racks of teeth that could be used for sorting or shredding particles that have been collected by the tentacles (Saulnier-Michel et al. 1990). In *Alvinella pompejana*, the esophageal gland seems to be the origin of the proteolytic activity detected in the lumen. The stomach lining is the location of intracellular enzymatic activities and contains numerous iron concretions and polyphagosomes (Saulnier-Michel et al. 1990). Finally, the intestinal wall is composed of cells consistent with an absorbing function (enterocytes, myocytes, and cells that contain zymogenic granules). In the hindgut, the feces are mostly composed of elemental sulfur (Saulnier-Michel et al. 1990).

Stable isotope analyses show a consistent reliance on chemoautotrophic bacteria (Desbruyères et al. 1998, Levesque et al. 2003, Bergquist et al. 2007, Lelièvre et al. 2018). Interestingly, sympatric species of *Paralvinella* often exhibit significant differences in stable isotope values, suggesting putative differences in the diet between species (Levesque et al. 2003, Bergquist et al. 2007, Lelièvre et al. 2018). Local conditions of venting are also likely to modify the stable isotope values of species and could affect the diet of vent species over their life cycle as shown previously in *P. palmiformis* (Levesque et al. 2003).

Nervous system. The nervous system of Alvinellidae was recently studied in *Paralvinella hessleri* (see Shigeno et al. 2014). The authors described different peridermal ciliated sensory cell types that resemble those of other annelids and are rich in mitochondria and electron-dense granules. In the head sensory system, there are specialized glial cells and serial myelin-like repeats. The head sensory inputs and structure of the neural cell bodies of the brain, however, show some specificity that could have an adaptive value (Shigeno et al. 2014). In particular, the latter are surrounded by several membranes that could provide enhanced protection for the production and transmission of electrical signals. However, this is limited to the head region, interestingly the part of the worm that is most directly exposed to the environment.

Vascular system. All Alvinellidae possess a closed vascular system (Fig. 7.7.4.5). As in other Terebellida, the dorsal vessel separates from the gut anteriorly at the stomach-esophagus junction. In *Alvinella pompejana*, a supraesophageal vessel separates from the main dorsal branch, adheres to esophagus, and runs forward (Fig. 7.7.4.6) (Jouin-Toulmond et al. 1996, Hourdez and Lallier 2007). As in other Terebellida, the main dorsal branch corresponds to a contractile heart and contains a heart body that is responsible for vascular hemoglobin synthesis (Figs. 7.7.4.5, 7.7.4.6). In *A. pompejana*, both the supraesophageal vessel and the heart penetrate the wall of the dissepiment separating the coelomic cavity between segments 1 and 2 and extending far back on the esophagus (Fig. 7.7.4.6). In other Terebellida, this dissepiment exists but does not extend far back around

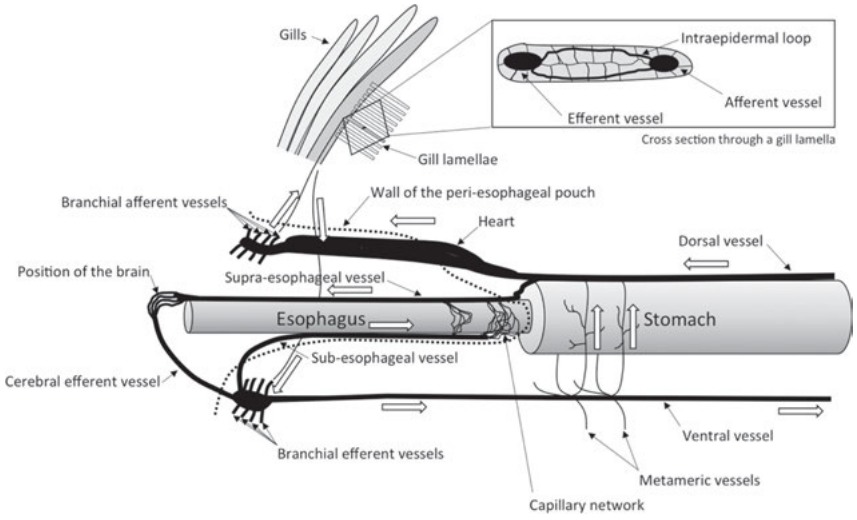


Fig. 7.7.4.6: Schematic representation of the blood vascular system and direction of circulation (hollow arrows) in the anterior part of *Alvinella pompejana* Desbruyères & Laubier, 1980 (modified after Hourdez and Lallier 2007).

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the esophagus. In *A. pompejana* and other Alvinellidae, the periesophageal pouch is formed, which holds large numbers of coelomocytes containing intracellular hemoglobin (Hourdez et al. 2000, S. Hourdez personal observation). Anteriorly, the heart splits up into four pairs of branchial afferent vessels (Fig. 7.7.4.6). The branchial efferent vessels merge ventrally with the ventral vessel that runs posteriorly to the end of the body. From the region where the four pairs of efferent branchial vessels merge, the subesophageal vessel originates and carries oxygenated blood to the back of the pouch. In the pouch, the supraesophageal vessel is further connected to the subesophageal vessel through a dense capillary network that allows gas exchange with the densely packed coelomocytes. Metameric blood vessels encircle the stomach and intestine, connecting the dorsal and the ventral vessels.

Respiration and oxygen transport. Alvinellidae are endemic to deep-sea hydrothermal vents and therefore exposed to chronic hypoxia (Hourdez and Lallier 2007). They all possess four pairs of well-developed gills anteriorly (on segments 2–5) (see Jouin-Toulmond and Hourdez 2006). These gills represent a very large specific surface area, reaching 12 cm^2/g wet weight in *Alvinella pompejana* and 47 cm^2/g wet weight for *Paralvinella grasslei* (Jouin and Gaill 1990). In comparison, the surface area only reaches 6 cm^2/g in the Trichobranchidae *Terebellides stroemii* Sars, 1835 (Jouin-Toulmond and Hourdez 2006). This enlarged gill surface area favors gas exchange across the gills, a key feature in a chronically hypoxic habitat (Hourdez and Lallier 2007). Gas exchange is further facilitated by a reduced diffusion distance in *A. pompejana* and *P. grasslei* (1–4 µm) compared to that measured in *T. stroemii* (7–10 µm) (Jouin-Toulmond and Hourdez 2006). This reduced diffusion distance is made possible by the presence of intraepidermal loops forming a shallower blood network (Jouin and Gaill 1990).

All Alvinellidae studied to date possess an extracellular hexagonal-bilayer hemoglobin (HBL-Hb) in their well-developed closed vascular system and, at least for *Alvinella pompejana*, *Alvinella caudata*, and *Paralvinella grasslei*, a globin contained in erythrocytes in the coelomic fluid (Toulmond et al. 1990, Hourdez et al. 2000, S. Hourdez unpublished personal observations). The presence of an HBL-Hb in the vascular system and intracellular hemoglobin in the coelomic fluid is typical among Terebellomorpha. In Alvinellidae, however, these hemoglobins exhibit very high affinities for oxygen, another characteristic that bears an adaptive value in a chronically hypoxic habitat (Hourdez and Lallier 2007). This high affinity is counterbalanced by a more pronounced Bohr effect. This effect allows an enhanced release of oxygen when pH decreases (e.g., near metabolically active tissues) (Terwilliger and Terwilliger 1984, Toulmond et al. 1990, Hourdez et al. 2000, Hourdez and Weber 2005).

In the periesophageal pouch, the very close proximity of the dense capillary network and the numerous erythrocytes allows gas exchange between the vascular and coelomic compartments. This gas transfer system has been described in other Terebellomorpha as well, although the periesophageal pouch is specific for Alvinellidae. Compared to other Terebellomorpha, the exchange can be bidirectional in *A. pompejana*, whereas it is unidirectional in Terebellidae (Hourdez et al. 2000). This likely buffers the changes in environmental oxygen concentrations, especially for the cerebral area that is directly perfused by the supraesophageal vessel after the capillary network in the periesophageal pouch (Hourdez and Lallier 2007). Exposure to variable oxygen concentrations also led to a cascade of protein overexpression in A. pompejana, including specific unknown haemic proteins and heat shock proteins (Mary et al. 2010).

Reproduction and larval development

Alvinellidae are all gonochoristic with a marked sexual differentiation on the dorsal organ with a well-developed genital pore in females and a pair of modified buccal tentacles in males on the first chaetigerous segment (Zal et al. 1994, Zhadan et al. 2000, Pradillon and Gaill 2003). Females possess a wide genital pore located dorsally at the base of the branchial crown on the first achaetigerous segment. Depending on the species, females also have one or two pairs of gonoducts that connect to the pore passing through a spermatheca. Males have a less developed genital pore that is connected to a pair of spermioducts and seminal vesicles (Zal et al. 1994, Zhadan et al. 2000). The sperm is transferred as bundles (spermatozeugmata) to the female genital opening by the modified sexual tentacles (Zal et al. 1994, Desbruyères et al. 1998). *Paralvinella pandorae pandorae* and *P. pandorae irlandei* may be exceptions to this reproductive strategy. In both *Alvinella* species and *Paralvinella grasslei*, a specific sexual behavior has been observed from close-up videos of individuals located on the wall of vent chimneys showing neighboring individuals entering the tube of other congeners and/or mating head to head (Chevaldonné and Jollivet 1993, Faure et al. 2007). Such behavior has also been described in several intertidal Terebellidae such as *Ramex californiensis* Hartman, 1944 and *Nicolea zostericola* Örsted, 1844 (see Herpin 1925, Eckelbarger

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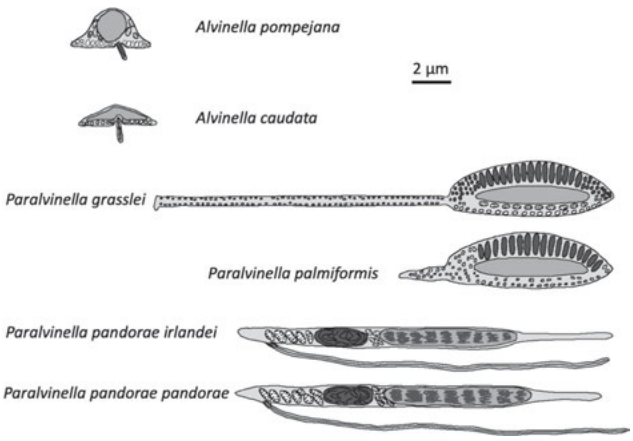


Fig. 7.7.4.7: Schematic drawings of spermatozoa for six species of Alvinellidae illustrating the ultrastructural diversity (modified after Jouin-Toulmond et al. 2002).

1975, Rouse and McHugh 1994). In *P. pandorae irlandei*, large cocoons of white mucus have also been found containing males and females and small juveniles, suggesting that mating could still occur but in a slightly different way (D. Jollivet personal observations). Because the two subspecies of *P. pandorae* are lacking sexual appendages, cocoons may be a way to maximize internal reproduction without sperm transfer.

Spermatozoa are greatly modified in *Alvinella pompejana*, *Alvinella caudata* (see Jouin-Toulmond et al. 2002), *Paralvinella grasslei*, and *Paralvinella palmiformis*, with a strongly reduced flagellum in the first species and aflagellate in the last two species (Fig. 7.7.4.7) (Zal et al. 1994, Jouin-Toulmond et al. 2002). This contrasts with the spermatozoa ultrastructure of *Paralvinella pandorae pandorae* and *P. pandorae irlandei*, which are also modified but with a longer flagellum (McHugh 1995, Jouin-Toulmond et al. 2002). The small length of the flagella clearly indicates a lack of sperm motility in *Alvinella* and its absence in *P. grasslei* and *P. palmiformis*, which fits well with the occurrence of specific sexual assemblages and the head-to-head sperm transfer behavior (Fig. 7.7.4.7). In contrast, the presence of more elongated spermatozoa with longer flagella in the two *P. pandorae* subspecies may represent a more plesiomorphic reproductive strategy, closer to Ampharetidae (Giangrande 1997). Although quite diverse, all spermatozoa morphologies belong to the introsperm category because of their modified structure (see Jamieson and Rouse 1989): although they may have flagella, they have no acrosome and an atypical or absent midpiece.

The presence of spermathecae in all species is a characteristic not found in any other member of Terebellomorpha to date (Jouin-Toulmond et al. 2002). This morphological character could be a way of maximizing reproductive success with a slightly male-biased sex ratio (Faure et al. 2007). Female fecundities vary widely, from a maximum of 978,000 oocytes per female in *Alvinella pompejana* (see Faure et al. 2007) down to 3,900 oocytes per female in *P. grasslei* (see Zal et al. 1995). A ventral gonad in the anterior part of the worm releases immature oocytes in the coelomic cavity; in *A. pompejana*, from 0 to 5 oocyte size cohorts (ranging from 80 to 275 µm in diameter) can be found. As a result, reproductive females have high but unequal coelomic fecundities, ranging between 67,000 and 978,000 oocytes (all maturation stages combined), but the number of mature oocytes recruited into gonoducts was always small (hundreds of eggs) and very similar between individuals [with exception of females having spawned all their mature oocytes (empty gonoducts)]. The same observation was made for *Paralvinella pandorae* (see McHugh 1989), *Paralvinella grasslei* (see Zal et al. 1995), and *Paralvinella palmiformis* (see Copley et al. 2003), thus suggesting that Alvinellidae exhibit a continuous to semicontinuous gametogenesis with a great accumulation of oocytes in the coelom but are likely to produce discontinuous and synchronized spawning throughout the year. Alvinellidae seem to have a very rapid growth phase followed by an intensive reproductive effort during which size cohorts are mixing. Such dynamics in reproduction is probably advantageous in a highly variable and patchy environment with periodic cohorts of settlers in populations throughout the year for nearly all species (McHugh 1989, Zal et al. 1995, Copley et al. 2003, Pradillon et al. 2005, Faure et al. 2007).

Very little information has been reported on the larval development of Alvinellidae but a 7-chaetiger erpochaete larva of *Paralvinella grasslei* has been sampled and described by Desbruyères and Laubier (1986), suggesting that this species may have restricted capabilities of dispersal and/or a direct development (Fig. 7.7.4.8). The size of fertilized eggs is quite large (>250 µm) in *Paralvinella* spp. and a little bit less but negatively buoyant in *Alvinella* spp. (Faure et al. 2007). This suggests that Alvinellidae likely have lecithotrophic embryos and may represent poor dispersers. This is reminiscent of a great number of Ampharetidae, which usually settle a week after spawning at the 3- or 4-chaetiger stage (Grehan 1991, Giangrande 1997), or some Terebellidae, which brood their progeny in tubes or inside cocoons (Rouse and McHugh 1994). Brooding seems to likely occur in the two subspecies of *P. pandorae*, for which cocoons containing juveniles have been found among faunal samples. However, because of cold and oligotrophic conditions of the deep-sea waters outside areas of venting, larval development may be stopped or slowed down and the vitellus storage of the egg may be sufficient to delay

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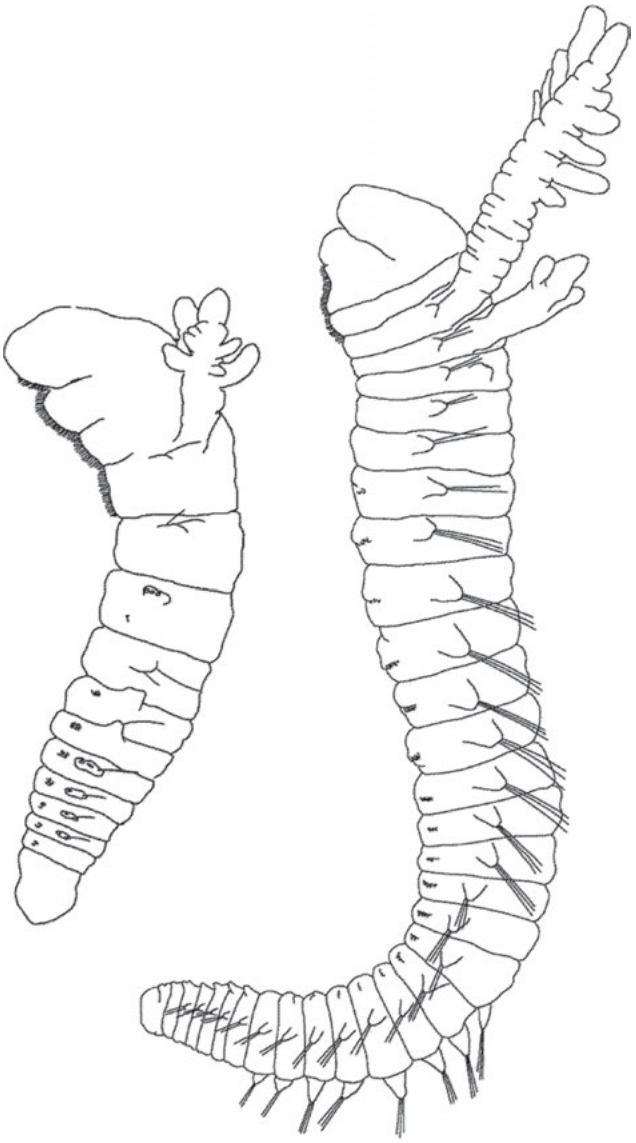


Fig. 7.7.4.8: Erpochaete larvae of *Paralvinella grasslei* Desbruyères & Laubier, 1982 (redrawn from Desbruyères and Laubier 1986).

settlement and metamorphosis for a long period of time until environmental conditions are appropriate (Pradillon et al. 2001). This latter hypothesis fits well with population genetics studies that indicated almost no barrier to gene flow between alvinellid populations over large portions of oceanic ridges, provided that the ridge segments are not offset by large transform faults or microplates (Jollivet et al. 1995b, Hurtado et al. 2004, Knowles et al. 2005, Plouviez et al. 2010, Jang et al. 2016). This therefore strengthens hypotheses that alvinellid larvae are entrained by bottom currents and channeled along the axial valley of the rift (Chevaldonné et al. 1997, Jollivet et al. 1999).

Predation

Alvinellidae are often preyed upon by Bythograeidae crabs as *Cyanagraea praedator* or Lithodidae crabs such as *Macroregonia macrochira* (see Desbruyères et al. 1982, Tunnicliffe and Jensen 1987). They do not seem to fall prey to zoarcid fishes (Sancho et al. 2005), which are also endemic to deep-sea hydrothermal vents. Fragments of body and cirri have been recovered in large numbers in the stomachs of the crabs *Bythograea thermydron* and *C. praedator* along with limpet shells on the EPR (D. Jollivet personal observations). Young recruits and juveniles could also be prey for other errant polychaetes such as *Nereis sandersi* or some Polynoidae such as *Lepinotopodium fimbriatum*.

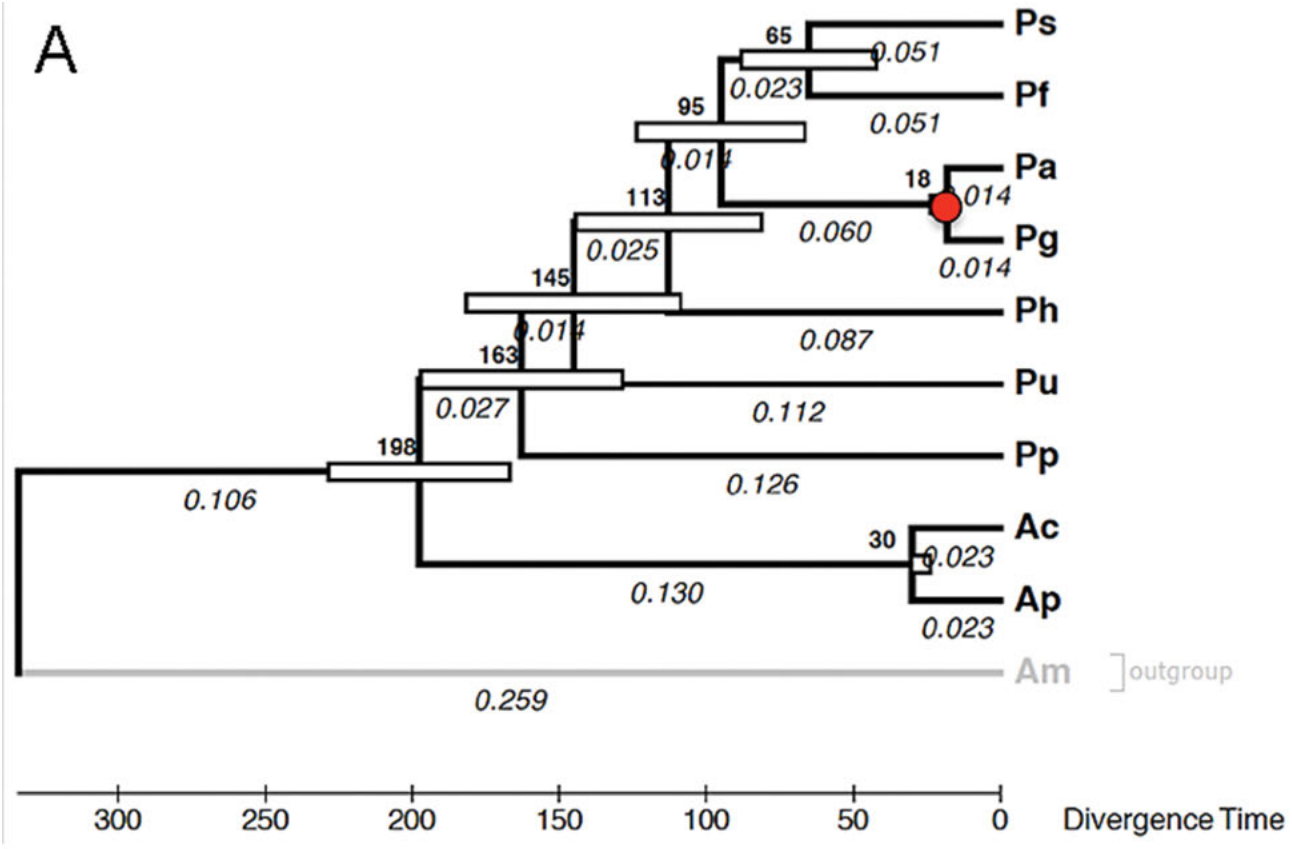
Phylogeny and taxonomy

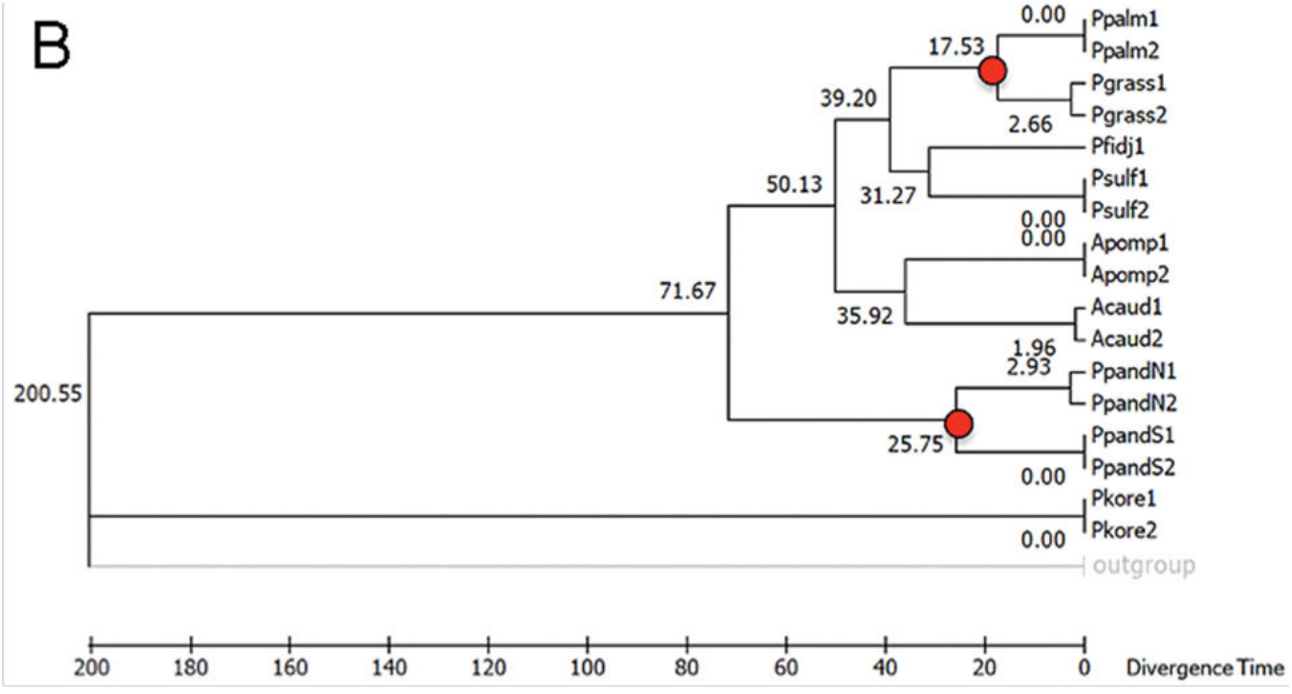
Phylogeny

Although the initial description qualified Alvinellidae as aberrant Ampharetidae, its position within Terebellomorpha remains unclear. Rousset et al. (2003), based on

▸ **Fig. 7.7.4.9:** A, Ultrametric phylogenomic tree of alvinellid worms obtained by TimeTree with Mega7. The initial tree based on 278 orthologous genes was performed using RaxML and the GTR substitution model implemented in the Galaxy pipeline AdaptSearch, which uses Trinity transcriptome assemblies as input files to produce an alignment of a concatenated set of coding sequences. Divergence times are derived from the calibration point associated with the subduction of the Farallon plate under the American plate, 25 Ma. Tree is rooted with the terebellid *Amphitritides* spp. (Antarctica, DDU). Ps, *Paralvinella sulfincola* Desbruyères & Laubier, 1993; Pf, *Paralvinella fijiensis* Desbruyères & Laubier, 1993; Pa, *Paralvinella palmiformis* Desbruyères & Laubier, 1986; Pg, *P. grasslei* Desbruyères & Laubier, 1982; Ph, *Paralvinella hessleri* Desbruyères & Laubier, 1989; Pu, *Paralvinella unidentata* Desbruyères & Laubier, 1993; Pp, *Paralvinella pandorae irlandei* Desbruyères & Laubier, 1986; Ap, *Alvinella pompejana* Desbruyères & Laubier, 1980; Ac, *Alvinella caudata* Desbruyères & Laubier, 1986. B, Ultrametric polyphyletic tree of alvinellid worms obtained by TimeTree with Mega7. The ML tree is based on partial sequences of the *Cox1* gene using pairwise deletions and the K2P substitution model implemented with the software PhyML. Divergence times are derived from the two calibration points associated with the subduction of the Farallon plate under the American plate, 25 Ma. Tree is rooted with the pectinariid polychaete *Pectinaria koreni* (Malmgren, 1866) (Pkore). Psulf, *P. sulfincola*; Pfidj, *P. fijiensis*; Ppalm, *P. palmiformis*; Pgras, *P. grasslei*; PpandN, *P. pandorae pandorae* Desbruyères & Laubier, 1986; PpandS, *P. pandorae irlandei*; Apomp, *A. pompejana*; Acaud, *A. caudata*.

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morphological and molecular (28S rRNA) characters, did not support the view that Ampharetidae is a sister taxon of Alvinellidae, although the obtained trees were poorly resolved. In agreement with Rouse and Fauchald (1997), the tree solely based on morphological data placed Alvinellidae close to Ampharetidae, but support for this relationship was weak. The combined data yielded four equally parsimonious trees that only differed by relationships among Ampharetidae. In this tree, Alvinellidae is a sister group of *Terebellides* (Trichobranchidae), the next sister group being *Pectinaria* (Pectinariidae). However, this view has been challenged by Zhong et al. (2011) and Nogueira et al. (2013), who now placed Alvinellidae close to Ampharetidae based on a multilocus molecular analysis on the one hand and a complete analysis of the morphological traits of Terebellomorpha on the other hand. The placement of Alvinellidae, Ampharetidae, Terebellidae, and Trichobranchidae families remains, however, uncertain in relation to Pectinariidae (*Pectinaria gouldii*).

Within the family, some studies have used molecular data for phylogenetic analyses. Using a fragment of mitochondrial marker COI, a phylogenetic tree of Alvinellidae (without the species of the subgenus *Miralvinella*) proposed that *Paralvinella* could be polyphyletic, as *P. pandorae pandorae* was basal to the clades grouping the two *Alvinella* species on the one hand and a clade comprising the remaining *Paralvinella* species on the other hand (Vrijenhoek 2013). New phylogenomic analyses using 423 orthologous genes obtained from the comparison of the transcriptome assemblies of nine Alvinellidae, including species of the three *Paralvinella* subgenera and the two *Alvinella* species, clearly indicate that the family Alvinellidae and the two genera *Paralvinella* and *Alvinella* are monophyletic (unpublished data) (see Fig. 7.7.4.9A, B). However, the phylogenetic signal does not totally agree with the taxonomic arrangement of Alvinellidae proposed by Desbruyères and Laubier (1993), suggesting that *P. unidentata* and *P. pandorae* are clearly basal to the *Paralvinella* lineage and not sister species. In a recent study addressing Terebellida phylogenetic relationships using transcriptomics Stiller et al. (2020) undoubtedly found Alvinellidae monophyletic and sister of Ampharetinae (Ampharetidae except Melinniae). Within Alvinellidae the genus *Paralvinella* is clearly paraphyletic with *Paralvinella pandorae irlandei (Nautalvinella)* being sister to *Alvinella* and the other species of *Paralvinella*. This confirms previous works done with the *Cox1* mitochondrial gene (Fig. 7.4.4.11B) but this positioning still remains uncertain when *Paralvinella unidentata (Nautalvinella)* is added (Fig 7.4.4.11A). The four other *Paralvinella* species (*P. grasslei, P. palmiformis, P. fijiensis*, and *P. sulfincola*) cluster together and clearly form pairs of sibling geographic species. *P. hessleri* has a basal position to this *Paralvinella* clade, which may validate its placement into another clade. To clarify this point, acquiring transcriptomes of *P. dela* and *P. bactericola* is still needed to validate this potential clade as corresponding to the subgenus *Miralvinella*.

Molecular dating using the Farallon plate subduction date around 28 Mya to calibrate the molecular clock indicates that both the speciation events leading to *A. pompejana* and *A. caudata* on the one hand and *P. fijiensis* and *P. sulfincola* on the other hand occurred before this geological event. It also suggests that radiation in Alvinellidae predates the series of anoxic episodes in the deep sea at the end of the Cretaceous about 60 Mya (Jacobs and Lindberg 1998) and that this family of worms may have inhabited shallower areas in the past. Increasing the number of calibration points is now needed, as using two splitting dates of sibling species clearly reduced the age of the alvinellid radiation (cf. alvinellid tree with *Cox1* sequences in Fig. 7.7.4.9B).

Taxonomy

The family Alvinellidae only comprises two genera: the genus *Alvinella* with 2 morphological species already described from the East Pacific and the genus *Paralvinella* with 10 described species. The genus *Paralvinella* was initially erected by Desbruyères and Laubier (1982) based on the discovery of a first species, *P. grasslei*, in the washing of the chitinous tubes of the siboglinid worm *R. pachyptila*.

All Alvinellidae have four pairs of gills located on segments 2 to 5 (Figs. 7.7.4.6, 7.7.4.10). In *Paralvinella*, the first chaetigerous segment is segment 3; in *Alvinella*, the first chaetigerous segment is segment 6. In *Alvinella*, the gills correspond to stacked lamellae attached to the stems, whereas in *Paralvinella* they are simple filaments attached to the stems. The two genera also differ by the presence of modified hooks on segment 9 only for *Paralvinella* (chaetiger 7) and on segments 9 and 10 for *Alvinella* (chaetigers 4 and 5). Other differences have been reported. The prostomium is also sometimes bilobate in *Paralvinella*. The capillary notochaetae are smooth for *Paralvinella* and geniculate with two rows of teeth for *Alvinella*. A conspicuous ventral shield is present in the anterior part of the worm involved in the mucous secretion in *Alvinella*. Epibiotic bacteria have only been reported in that latter genus on either the dorsal part (*A. pompejana*) or the tail (*A. caudata*) of the worm where the notopodia are modified.

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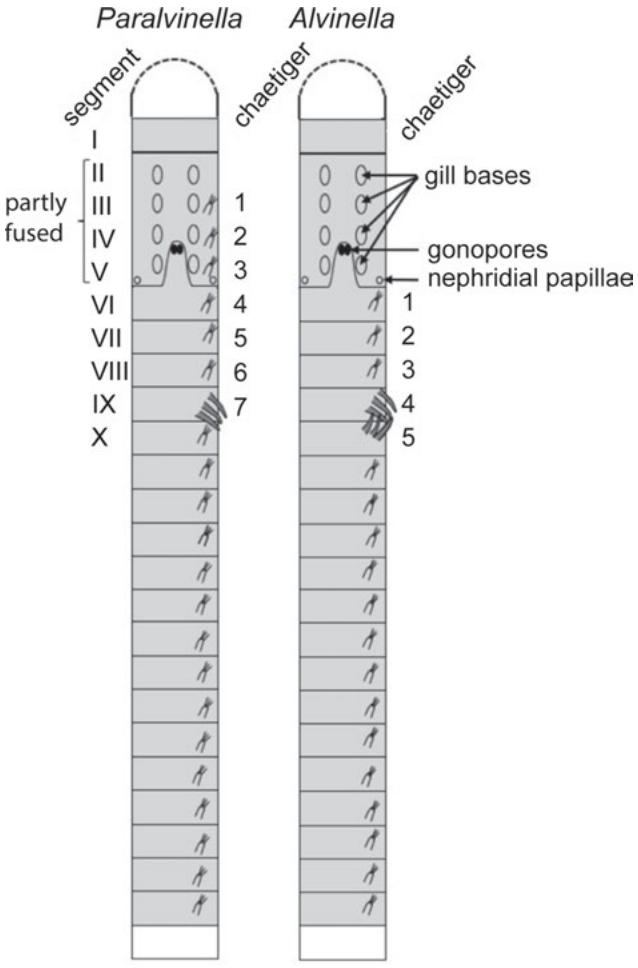


Fig. 7.7.4.10: Schematic representation of the typical anterior morphology of *Alvinella* and *Paralvinella*, highlighting the main differences between the two genera. The segment numbers are given in Roman numbers, and the chaetiger numbers in Arabic numbers. Modified after Jouin-Toulmond and Hourdez, 2006.

Important morphological characters

The essential morphological features in identifying the species of Alvinellidae are (Fig. 7.7.4.10):

- Structure of the gills (lamellae in *Alvinella* vs. filaments in *Paralvinella*),
- Presence of hooks on segment 9 (*Paralvinella*) or segments 9 and 10 (*Alvinella*),
- Position of the first chaetiger (segment 3 in *Paralvinella* and segment 6 in *Alvinella*),
- Whether the tip of each gill is a free filament or undistinguishable among the other filaments for species of *Paralvinella*,
- Number of rows of branchial filaments on each stem,
- Position of the first segment with ventral uncini,
- Shape and number of teeth on the uncini, and
- Presence of a digitiform lobe on the notopodia.

Desbruyères and Laubier (1993) proposed to subdivide the genus *Paralvinella* into three subgenera (*Paralvinella*, *Miralvinella*, and *Nautalvinella*). They used the shape and disposition of the gill filaments on the stem of the branchiae, the shape of the modified buccal paired tentacles associated with the dorsal organ, the presence of lobes on the notopodia of the worm, and the position of the uncinigerous tori (see Fig. 7.7.4.11 for the species diagnostic keys initially proposed by Desbruyères and Laubier 1991) for most but not all species.

A diagnosis of the family, the genera, and subgenera follows.

Alvinellidae Desbruyères & Laubier, 1986

Type genus: *Alvinella* Desbruyères & Laubier, 1980

Diagnosis: Large specimens with a large number of chaetigers (>100) with epibiotic bacteria covering either the dorsal part of the worm or the notopodia of the posterior part of the worm. Anterior part of the worm exhibits a ventral shield used to secrete a parchment-like tube. Numerous buccal grooved tentacles inserted on a semicircular buccal membrane, a pair of thick buccal tentacles in males. Stalked gills with lamellar filaments inserted along the stem. Two pairs of hooks inserted on segments 9 and 10 (i.e., chaetiger 4 and 5).

Paralvinella Desbruyères & Laubier, 1982

Subgenus *Paralvinella* Desbruyères & Laubier, 1993

Type species: *Paralvinella* (*Paralvinella*) *grasslei* Desbruyères & Laubier, 1982

Other species: *Paralvinella* (*Paralvinella*) *palmiformis* Desbruyères & Laubier, 1986, *Paralvinella* (*Paralvinella*) *fijiensis* Desbruyères & Laubier, 1993, *Paralvinella* (*Paralvinella*) *sulfincola* Desbruyères & Laubier, 1993 (in Tunnicliffe et al. 1993)

Diagnosis: Large specimens with a number of chaetigers varying from 55 to 180. Numerous buccal grooved tentacles inserted on a semicircular buccal membrane, large pair of trilobate appendages in males, with a globular eversible ventral organ. Stalked bipennate gills with two rows of cylindrical filaments inserted on opposite sides along the stem. Digitiform or rounded notopodial lobes mostly present on the anterior part of the worm. One pair of hooks inserted on chaetiger 7. First uncini appear inserted well after the seventh modified chaetiger (chaetigers 13–32).

Paralvinella Desbruyères & Laubier, 1982

Subgenus *Miralvinella* Desbruyères & Laubier, 1993

Type species: *Paralvinella* (*Miralvinella*) *dela* Detinova, 1988

Other species: *Paralvinella* (*Miralvinella*) *hessleri* Desbruyères & Laubier, 1989, *Paralvinella* (*Miralvinella*) *bactericola* Desbruyères & Laubier, 1991

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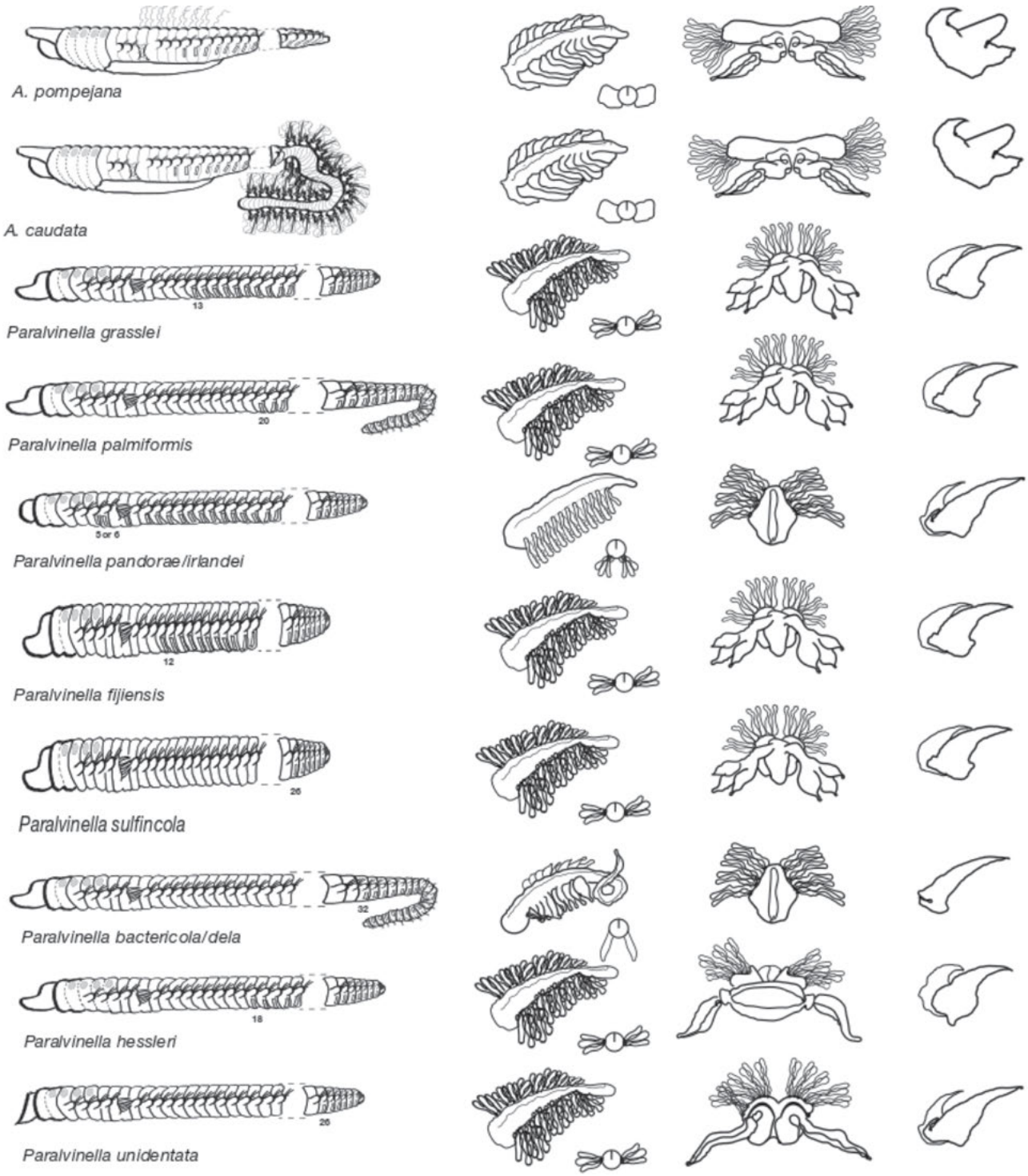


Fig. 7.7.4.11: Diagnostic features of the 12 alvinellid worms (adapted from Desbruyères & Laubier 1991) with (1) the body shape and position of the uncinigerous tori, (2) gill shape, (3) buccal apparatus with tentacles, and (4) the shape of uncini.

Diagnosis: Small specimens, number of chaetigers varying from 50 to 75. Complex buccal apparatus with grooved tentacles inserted on the buccal membrane dorsally above a pair of pointed and coiled tapering tentacles in males and the globular eversible ventral organ. Stalked bipennate gills with two rows of cylindrical filaments inserted on opposite directions along the stem. Digitiform notopodial lobes mostly present on the anterior part of the worm. One pair of hooks inserted on chaetiger 7. First uncini appear inserted well after the seventh modified chaetiger (chaetigers 18–20).

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***Paralvinella* Desbruyères & Laubier, 1982**
Subgenus *Nautalvinella* Desbruyères & Laubier, 1993
Type species: *Paralvinella* (*Nautalvinella*) *pandorae* Desbruyères & Laubier, 1986
Other species: *Paralvinella* (*Nautalvinella*) *pandorae irlandei* Desbruyères & Laubier, 1986, *Paralvinella* (*Nautalvinella*) *unidentata* Desbruyères & Laubier, 1993

Diagnosis: Small specimens with a number of chaetigers varying from 50 to 75. Unpaired pointed buccal apparatus with a longitudinal slit surrounded by numerous grooved tentacles with or without an eversible globular organ. No pair of large tentacles in males. Stalked bipinnate gills with leaf-shaped filaments inserted on two adjacent rows along the stem as a comb. Without gill filaments at the tip of the branchiae. No digitiform notopodial lobes. One pair of hooks inserted on chaetiger 7. First uncini appear inserted before the seventh modified chaetiger (chaetigers 5 and 6) for the two *pandorae* subspecies but not *unidentata* (first insertion on chaetigers 28 and 29).

References

Alayse-Danet, A.M., Gaill, F. & Desbruyères, D. (1986): In situ bicarbonate uptake by bacteria-*Alvinella* associations. *Marine Ecology* 7: 233–240.

Autem, M., Salvidio, S., Pasteur, N., Desbruyères D. & Laubier, L. (1985): Mise en évidence de l'isolement génétique des deux formes sympatriques d'*Alvinella pompejana* (Polychaeta: Ampharetidae), annélides inféodées aux sites hydrothermaux actifs de la dorsale du Pacifique oriental. *Comptes Rendus de l'Académie des Sciences, Paris, Série 3* 301: 301–131.

Auzende, J. M., Hashimoto, J., Fiala-Médioni, A. & Ohta, S. (1997): Etude géologique et biologique in situ de deux zones hydrothermales du bassin de Manus (Papouasie Nouvelle-Guinée). *Comptes Rendus de l'Académie des Sciences, Série IIA, Earth and Planetary Science* 325: 585–591.

Bergquist, D.C., Eckner, J.T., Urcuyo, I.A., Cordes, E.E., Hourdez, S., Macko, S.A. & Fisher, C.R. (2007): Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. *Marine Ecology Progress Series* 330: 49–65.

Campbell, B.J., Jeanthon, C., Kosta, J.E., Luther III, G.W. & Cary, S.C. (2001): Growth and phylogenetic properties of novel bacteria belonging to the epsilon subdivision of the Proteobacteria enriched from *Alvinella pompejana* and deep-sea hydrothermal vents. *Applied and Environmental Microbiology* 67: 4566–4572.

Cary, S.C., Cottrell, M.T., Stein, J.L., Camacho, F. & Desbruyères, D. (1997): Molecular identification and localization of filamentous symbiotic bacteria associated with the hydrothermal vent annelid *Alvinella pompejana*. *Applied and Environmental Microbiology* 63: 1124–1130.

Cary, S.C., Shank, T. & Stein, J. (1998): Worms bask in extreme temperatures. *Nature* 391: 545–546.

Chevaldonné, P. & Jollivet, D. (1993): Videoscopic study of deep-sea hydrothermal vent alvinellid polychaete populations: estimation of biomass and behaviour. *Marine Ecology Progress Series* 95: 251–262.

Chevaldonné, P., Desbruyéres, D. & Childress, J.J. (1992): ... and some even hotter. *Nature* 359: 593.

Chevaldonné, P., Jollivet, D., Vangriesheim, A. & Desbruyères, D. (1997): Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. I. Influence of vent-site distribution pattern, bottom currents and biological features. *Limnology and Oceanography* 42: 67–80.

Chevaldonné, P., Fisher, C.R., Childress, J.J., Desbruyères, D., Jollivet, D., Zal, F. & Toulmond, A. (2000): Thermotolerance and the "Pompeii worms". *Marine Ecology Progress Series* 208: 293–295.

Chevaldonné, P., Jollivet, D., Desbruyères, D., Lutz, R.A. & Vrijenhoek, R.C. (2002): Sister-species of eastern Pacific hydrothermal vent worms (Ampharetidae, Alvinellidae, Vestimentifera) provide new mitochondrial COI clock calibration. *Cahiers de Biologie Marine* 43: 367–370.

Copley, J.T.P., Tyler, P.A., Van Dover, C.L., & Philp, S.J. (2003): Spatial variation in the reproductive biology of *Paralvinella palmiformis* (Polychaeta: Alvinellidae) from a vent field on the Juan de Fuca Ridge. *Marine Ecology Progress Series* 255: 171–181.

Corliss, J.B., Dymond, J., Gordon, L.I., Edmond, J.M., Von Herzen, R.P., Ballard, R.D., Green, K., Williams, D., Bainbridge, A., Crane, K. & Van Andel, T.H. (1979): Submarine thermal springs on the Galapagos Rift. *Science* 203: 1073–1083.

Desbruyères, D. & Laubier, L. (1980): *Alvinella pompejana* gen. sp. nov., Ampharetidae aberrant des sources hydrothermales de la ride East-Pacifique. *Oceanologica Acta* 3: 267–274.

Desbruyères, D. & Laubier, L. (1982): *Paralvinella grasslei*, new species of Alvinellinae (Polychaeta: Ampharetidae) from the Galapagos Rift geothermal vents. *Proceedings of the Biological Society of Washington* 95: 484–494.

Desbruyères, D. & Laubier, L. (1986): Les Alvinellidae. Une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines: systématique, biologie et écologie. *Canadian Journal of Zoology* 64: 2227–2245.

Desbruyères, D. & Laubier, L. (1989): *Paralvinella hessleri,* new species of Alvinellidae (Polychaeta) from the Mariana back-arc basin hydrothermal vents. *Proceedings of the Biological Society of Washington* 102: 761–767.

Desbruyères, D. & Laubier, L. (1991): Systematics, phylogeny, ecology and distribution of the Alvinellidae (Polychaeta) from deep-sea hydrothermal vents. *Ophelia* 5: 31–45.

Desbruyères, D. & Laubier, L. (1993): New species of Alvinellidae (Polychaeta) from the North Fiji back-arc basin hydrothermal vents (southwestern Pacific). *Proceedings of the Biological Society of Washington* 106: 225–236.

Desbruyères, D., Crassous, P., Grassle, J., Khripounoff, A., Reyss, D., Rio, M. & Van Praet, M. (1982): Données écologiques sur un nouveau site d'hydrothermalisme actif de la ride du Pacifique oriental. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris* 295: 489–494.

Desbruyères, D., Alayse-Danet, A.-M., Ohta, S. & the Scientific Parties of Biolau and Starmer Cruises (1994): Deep-sea hydrothermal communities in southwestern Pacific back-arc basins (the North Fiji and Lau Basins): Composition, microdistribution and food web. *Marine Geology* 116: 227–242.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Desbruyères, D., Chevaldonné, P., Alayse, A.M., Jollivet, D., Lallier, F.H., Jouin-Toulmond, C., Zal., F., Sarradin, P.M., Cosson, R., Caprais, J.-C., Arndt, A., O'Brien, J., Guezennec, J., Hourdez, S., Riso, R., Gaill., F., Laubier, L. & Toulmond, A. (1998): Biology and ecology of the Pompeii worm (*Alvinella pompejana* Desbruyères & Laubier), a normal dweller of an extreme deep-sea environment: A synthesis of current knowledge and recent developments. *Deep Sea Research Part II* 45: 383–422.

Detinova, N.N. (1988): New species of polychaetous annelids from hydrothermal vents of the Juan de Fuca Ridge (Pacific Ocean). *Zoologichesky Zhurnal* 57: 858–864.

Dilly, G.F., Young, C.R., Lane, W.S., Pangilinan, J. & Girguis, P.R. (2012): Exploring the limit of metazoan thermal tolerance via comparative proteomics: Thermally induced changes in protein abundance by two hydrothermal vent polychaetes. *Proceedings of the Royal Society B: Biological Sciences* 279: 3347–3356.

Eckelbarger, K.J. (1975): A light and electron microscope investigation of gametogenesis in *Nicolea zostericola* (Polychaeta: Terebellidae). *Marine Biology* 30: 353–370.

Faure, B., Chevaldonné, P., Pradillon, F., Thiébaut, E. & Jollivet, D. (2007): Spatial and temporal dynamics of reproduction and settlement in the Pompeii worm (Polychaeta: Alvinellidae). *Marine Ecology Progress Series* 348: 197–211.

Fontanillas, E., Galzitskaya, O.V., Lecompte, O., Lobanov, M.Y., Tanguy, A., Mary, J., Girguis, P.R., Hourdez, S. & Jollivet, D. (2017): Proteome evolution of deep-sea hydrothermal vent alvinellid polychaetes supports the ancestry of thermophily and subsequent adaptation to the cold for some lineages. *Genome Biology and Evolution* 9: 279–296.

Gaill, F. & Bouligand, Y. (1987): Supercoil of collagen fibrils in the integument of *Alvinella*, an abyssal annelid. *Tissue & Cell* 19: 625–642.

Gaill, F. & Hunt, S. (1986): Tubes of deep-sea hydrothermal vent worms *Riftia pachyptila* (Vestimentifera) and *Alvinella pompejana* (Annelida). *Marine Ecology Progress Series* 34: 267–274.

Gaill, F., Desbruyères, D. & Laubier, L. (1988): Relationships between the Pompeii worms and their epibiotic bacteria. *Oceanologica Acta N°SP* 8: 147–154.

Genard, B., Marie, B., Loumaye, E., Knoops, B., Legendre, P., Zal, F. & Rees, J.F. (2013): Living in a hot redox soup: Antioxidant defences of the hydrothermal worm *Alvinella pompejana*. *Aquatic Biology* 18: 217–228.

Giangrande, A. (1997): Polychaete reproductive patterns, life cycles and life histories: An overview. *Oceanography and Marine Biology* 35: 323–386.

Girguis, P. & Lee, R.W. (2006): Thermal preference and tolerance of alvinellids. *Science* 312: 231.

Goffredi, S.K., Johnson, S., Tunnicliffe, V., Caress, D., Clague, D., Escobar, E., Lundsten, L., Paduan, J.B., Rouse, G., Salcedo, D.L., Soto, L.A., Spelz-Madero, R., Zierenberg, R. & Vrijenhoek, R.C. (2017): Hydrothermal vent fields discovered in the southern Gulf of California clarify role of habitat in augmenting regional diversity. *Proceedings of the Royal Society of London B* 284: 20170817.

Grehan, A.J. (1991): Demography and reproductive biology of *Melinna palmata* (Ampharetidae: Polychaeta) in Inner Galway Bay on the west coast of Ireland. *Marine Biology* 109: 459–467.

Grelon, D., Morineaux, M., Desrosiers, G. & Juniper, S.K. (2006): Feeding and territorial behavior of *Paralvinella sulfincola*, a polychaete worm at deep-sea hydrothermal vents of the northeast Pacific Ocean. *Journal of Experimental Marine Biology and Ecology* 329: 174–186.

Gulik, A. & Gaill, F. (1988): Ultrastructural characteristics of *Alvinella pompejana* associated bacteria. *Oceanologica Acta N°SP* 8: 161–165.

Haddad, A., Camacho, F., Durand, P. & Cary, S.C. (1995): Phylogenetic characterization of the epibiotic bacteria associated with the hydrothermal vent polychaete *Alvinella pompejana*. *Applied and Environmental Microbiology* 61: 1679–1687.

Hashimoto, Y., Ohta, S., Fiala-Médioni, A., Auzende J.-M., Kojima, S., Segonzac, M., Fujiwara, K., Hunt, J.-C., Gena, K., Miura, T., Kikuchi, T., Yamaguchi, T., Toda, T., Chiba, H., Tsuchida, S., Ishibashi, J., Henri, K., Zbinden, M., Pruski, A., Inoue, A., Kobayashi, H., Birrien, J.-L., Naka, J., Yamanaka, T., Laporte, C., Nishimura, K., Yeats, C., Malagun, S., Kia, P., Oyaizu, M. & Katayama, T. (1999): Hydrothermal vent communities in the Manus Basin, Papua New Guinea: Results of the BioAccess cruises 96 & 98. *InterRidge News* 8: 12–18.

Hessler, R.R. & Lonsdale, P. (1991): Biogeography of Mariana through hydrothermal vent communities. *Deep Sea Research* 38: 185–199.

Herpin, R. (1925): La ponte et la développement chez une Annélide polychète sédentaire *Nicolea zostericola*. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris* 180: 864–866.

Hourdez, S. & Lallier, F.H. (2007): Adaptations to hypoxia in hydrothermal vent and cold-seep invertebrates. *Reviews of Environmental Sciences and Biotechnology* 6: 143–159.

Hourdez, S. & Weber, R.E. (2005): Molecular and functional adaptations in deep-sea hemoglobins. *Journal of Inorganic Biochemistry* 99: 130–141.

Hourdez, S., Lallier, F.H., De Cian, M.-C., Green, B.N. & Weber, R.E. (2000): The gas transfer system *in Alvinella pompejana* (Annelida Polychaeta, Terebellida). Functional properties of intracellular and extracellular hemoglobins. *Physiological and Biochemical Zoology* 73: 365–373.

Hurtado, L.A., Lutz, R.A. & Vrijenhoek, R.C. (2004): Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Molecular Ecology* 13: 2603–2615.

Jacobs, D.K. & Lindberg, D.R. (1998): Oxygen and evolutionary patterns in the sea: Onshore/offshore trends and recent recruitment of deep-sea faunas. *Proceedings of the National Academy of Sciences of the United States of America* 95: 9396–9401.

Jamieson, B.G.M. & Rouse, G.W. (1989): The spermatozoa of the Polychaeta (Annelida): An ultrastructural review. *Biological Reviews* 64: 93–157.

Jang, S.-J., Park, E., Lee, W.-K., Johnson, S.B., Vrijenhoek, R.C. & Won, Y.-J. (2016): Population subdivision of hydrothermal vent polychaete *Alvinella pompejana* across equatorial and eastern microplate boundaries. *BMC Evolutionary Biology* 16: 235.

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Jollivet, D., Desbruyères, D., Ladrat, C. & Laubier, L. (1995a): Evidence for differences in allozyme thermostability in deep-sea hydrothermal vent polychaetes Alvinellidae: A possible selection by habitat. *Marine Ecology Progress Series* 123: 125–136.

Jollivet, D., Desbruyères, D., Moraga, D. & Bonhomme, F. (1995b): Genetic differentiation of deep-sea hydrothermal vent alvinellid populations (Annelida: Polychaeta) along the East Pacific Rise. *Heredity* 74: 376–391.

Jollivet, D., Chevaldonné, P. & Planque, B. (1999): Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 2. A metapopulation model based on habitat shifts. *Evolution* 53: 1128–1142.

Jollivet, D., Gagnière, N., Mary, J., Tanguy, A, Fontanillas, E., Boutet, I., Hourdez, S., Segurens, B., Weissenbach, J., Poch, O. & Lecompte, O. (2012): Proteome adaptation to high temperatures in the ectothermic hydrothermal vent Pompeii worm. *PLoS One* 7: e31150.

Jouin, C. & Gaill, F. (1990): Gills of hydrothermal vent annelids: Structure, ultrastructure and functional implications in two alvinellid species. *Progress in Oceanography* 24: 59–69.

Jouin-Toulmond C. & Hourdez, S. (2006): Morphology, ultrastructure and functional anatomy of the branchial organ of *Terebellides stroemii* (Polychaeta: Trichobranchidae), with remarks on the systematic position of the genus *Terebellides*. *Cahiers de Biologie Marine* 47: 287–299.

Jouin-Toulmond, C., Augustin, D., Desbruyères, D. & Toulmond, A. (1996): The gas transfer system in alvinellids (Annelida Polychaeta, Terebellida). Anatomy and ultrastructure of the anterior circulatory system and characterization of a coelomic, intracellular, haemoglobin. *Cahiers de Biologie Marine* 37: 135–152.

Jouin-Toulmond C., Mozzo, M. & Hourdez, S. (2002): Ultrastructure of spermatozoa in four species of Alvinellidae (Annelida: Polychaeta). *Cahiers de Biologie Marine* 43: 391–394.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Reviews of Marine Science* 7: 497–520.

Juniper, S.K. (1988): Géochimie et écologie d'un microenvironnement hydrothermal: les secretions de mucus de *Paralvinella palmiformis*. *Oceanologica Acta N°SP* 8: 167–172.

Knowles, J.D., Wenink, E., Schult, N., Tunnicliffe, V. & McHugh, D. (2005): Molecular analysis indicates gene flow among populations of *Paralvinella pandorae* Desbruyères and Laubier 1986 (Alvinellidae, Terebellida), a polychaete annelid endemic to hydrothermal vents of the northeast Pacific. *Marine Biology* 26: 216–222.

Le Bris, N. & Gaill, F. (2010): Microbial habitats associated with deep-sea hydrothermal vent invertebrates: Insights from microanalysis and geochemical modelling. In: Kiel, S. (ed.), *The Vent and Seep Biota*. Springer, Berlin/Heidelberg, 51–71.

Le Bris, N., Zbinden, M. & Gaill, F. (2005): Processes controlling the physico-chemical micro-environments associated with Pompeii worms. *Deep Sea Research* 52: 1071–1083.

Lee, C.K., Cary, S.C., Murray, A.E. & Daniel, R.M. (2008): Enzymic approach to eurythermalism of *Alvinella pompejana* and its episymbionts. *Applied and Environmental Microbiology* 74: 774–782.

Lelièvre, Y., Sarrazin, J., Marticorena, J., Schaal, G., Day, T., Legendre, P., Hourdez, S. & Matabos, M. (2018): Biodiversity and trophic ecology of hydrothermal vent fauna associated with tubeworm assemblages on the Juan de Fuca Ridge. *BioGeosciences* 15: 2629–2647.

Levesque, C., Juniper, S.K. & Marcus, J. (2003): Food resource partitioning and competition among alvinellid polychaetes of Juan de Fuca Ridge hydrothermal vents. *Marine Ecology Progress Series* 246: 173–182.

Lonsdale, P. (1977): Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep Sea Research* 24: 857–863.

Mary, J., Rogniaux, H., Rees, J. F., & Zal, F. (2010): Response of Alvinella pompejana to variable oxygen stress: a proteomic approach. *Proteomics,* 10(12): 2250–2258.

McHugh, D. (1989): Population structure and reproductive biology of two sympatric hydrothermal vent polychaetes, *Paralvinella pandorae* and *P. palmiformis*. *Marine Biology* 103: 95–106.

McHugh, D. (1995): Unusual sperm morphology in a deep-sea hydrothermal-vent polychaete, *Paralvinella pandorae* (Alvinellidae). *Invertebrate Biology* 114: 161–168.

Miura, T. & Ohta, S. (1991): Two polychaete species from the deep-sea hydrothermal vent in the middle Okinawa Trough. *Zoological Science* 8: 383–387.

Nakamura, K., Watanabe, H., Miyazaki, J., Takai, K., Kawagucci, S., Nogichi, T., Nemoto, S., Watsuji, T., Matsuzaki, T., Shibuya, T., Okamura, K., Mochizuki, M., Orihashi, Y., Ura, T., Asada, A., Marie, D., Koonjul, M., Singh, M., Beedessee, G., Bhikajee, M. & Tamaki, K. (2012): Discovery of new hydrothermal activity and chemosynthetic fauna on the central Indian Ridge at 18°-20°S. *PLoS One* 7: e32965.

Nogueira, J.M.d.M., Fitzhugh, K. & Hutchings, P. (2013): The continuity challenge of phylogenetic relationships in Terebelliformia (Annelida: Polychaeta). *Invertebrate Systematics* 27: 186–238.

Ohta, S. & Kim, D. (2001): Submersible observations of the hydrothermal vent communities on the Iheya Ridge, Mid Okinawa Trough, Japan. *Journal of Oceanography* 57: 663–677.

Papot, C., Massol, F., Jollivet, D. & Tasiemski, A. (2017): Antagonistic evolution of an antibiotic and its molecular chaperone: How to maintain a vital ectosymbiosis in a highly fluctuating habitat. *Scientific Reports* 7: 1454.

Plouviez, S., Le Guen, D., Lecompte, O., Lallier, F.H. & Jollivet, D. (2010): Determining gene flow and the influence of selection across the equatorial barrier of the East Pacific Rise in the tube-dwelling polychaete *Alvinella pompejana*. *BMC Evolutionary Biology* 10: 220.

Pradillon, F. & Gaill, F. (2003): Oogenesis characteristics in the hydrothermal vent polychaete *Alvinella pompejana*. *Invertebrate Reproduction and Development* 43: 223–235.

Pradillon, F., Shillito, B., Young, C.M. & Gaill, F. (2001): Deep-sea ecology: Developmental arrest in vent worm embryos. *Nature* 413: 698.

Pradillon, F., Le Bris, N., Shillito, B., Young, C.M. & Gaill, F. (2005): Influence of environmental conditions on early development of the hydrothermal vent polychaete *Alvinella pompejana*. *Journal of Experimental Biology* 208: 1551–1561.

Ravaux, J., Hamel, G., Zbinden, M., Tasiemski, A.A., Boutet, I., Léger, N., Tanguy, A., Jollivet, D. & Shillito, B. (2013): Thermal limit for metazoan life in question: *In vivo* heat tolerance of the Pompeii worm. *PLoS One* 8: e64074.

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Reuscher, M., Fiege, D. & Wehe, T. (2012): Terebellomorph polychaetes from hydrothermal vents and cold seeps with the description of two new species of Terebellidae (Annelida: Polychaeta) representing the first records of the family from deep-sea vents. *Journal of the Marine Biological Association of the United Kingdom* 92: 997–1012.

Rinke, C. & Lee, R.W. (2009): Pathways, activities and thermal stability of anaerobic and aerobic enzymes in thermophilic vent paralvinellid worms. *Marine Ecology Progress Series* 382: 99–112.

Rise Project Group (1980): East Pacific Rise: Hot springs and geophysical experiments. *Science* 207: 1421–1433.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & McHugh, D. (1994): Ultrastructure of spermatids and spermatozoa in *Ramex californiensis* and *Nicolea zostericola* (Terebellidae; Polychaeta). *Ophelia* 39: 225–238.

Rouse, G.W. & Pleijel, F. (2001): Terebellidae Grube, 1850. In: Rouse, G.W. & Pleijel, F. (eds.), *Polychaetes*. Oxford University Press, Oxford, New York: 246–250.

Rousset, V., Rouse, G.W., Féral, J.P., Desbruyères, D. & Pleijel, F. (2003): Molecular and morphological evidence of Alvinellidae relationships (Terebelliformia, Polychaeta, Annelida). *Zoologica Scripta* 32: 185–197.

Sancho, G., Fisher, C.R., Mills, S., Micheli, F., Johnson, G.A., Lenihan, H.S. & Mullineaux, L.S. (2005): Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents. *Deep Sea Research Part I Oceanographic Research Papers* 52: 837–844.

Saulnier-Michel, C., Gaill, F., Hily, A., Alberic, P. & Cosson-Mannevy, M.A. (1990): Structure and functions of the digestive tract of *Alvinella pompejana,* a hydrothermal vent polychaete. *Canadian Journal of Zoology* 68: 722–732.

Shigeno, S., Ogura, A., Mori, T., Toyohara, H., Yoshida, T., Tsuchida, S. & Fujijura, K. (2014): Sensing deep extreme environments: The receptor cell types, brain center, and multi-layer neural packaging of hydrothermal vent endemic worms. *Frontiers in Zoology* 11: 82.

Sicot, FX, Mesnage, M., Masselot, M., Exposito, J.Y., Garrone, R., Deutsch, J. & Gaill, F. (2000): Molecular adaptation to an extreme environment: origin of the thermal stability of the Pompeii worm collagen. *Journal of Molecular Biology* 302: 811–820.

Stiller, J., Tilic, E., Rousset, V., Pleijel, F. & Rouse, G.W. (2020): Spaghetti to a tree: A robust phylogeny for Terebelliformia (Annelida) based on transcriptomes, molecular and morphological data. *Biology* 9:73: 1–29.

Taghon, G. (1988): Phospholipid fatty acid composition of the deep-sea hydrothermal vent polychaete Paralvinella palmiformis (Polychaeta-ampharetidae): effects of thermal regime and comparison with two shallow-water confamilial species. *Comparative Biochemistry and Physiology–Part B* 91(3): 593–596.

Tasiemski, A., Jung, S., Boidin-Wichlacz, C., Jollivet, D., Cuvillier-Hot, V., Pradillon, F., Vetriani, C., Hecht, O., Sönnichsen, F.D., Gelhaus, C. and Hung, C.W. (2014): Characterization and function of the first antibiotic isolated from a vent organism: the extremophile metazoan Alvinella pompejana. *PLoS One,* 9(4): p.e95737.

Terwilliger, N.B. & Terwilliger, R.C. (1984): Hemoglobin from the "Pompeii worm," *Alvinella pompejana*, an annelid from a deep sea hot hydrothermal vent environment. *Marine Biology Letters* 5: 191–201.

Thomas-Bulle, C., Bertrand, D., Nigarajan, N., Copley, R., Corre E., Hourdez, S., Bonnivard, E., Claridge-Chang, A. & Jollivet, D. (2020): Genomic patterns of divergence in the early and late steps of speciation of the deep-sea thermophilic worms of the genus *Alvinella*. Submitted.

Toulmond, A., El Idrissi Slitine, F., De Frescheville, J. & Jouin, C. (1990): Extracellular hemoglobins of hydrothermal vent annelids: Structural and functional characteristics in three alvinellid species. *Biological Bulletin* 179: 366–373.

Tunnicliffe, V. (1988): Biogeography and evolution of the hydrothermal vent fauna in the eastern Pacific Ocean. *Proceedings of the Royal Society of London B* 223: 347–366.

Tunnicliffe, V. & Jensen, R.G. (1987): Distribution and behaviour of the spider crab *Macroregonia macrochira* Sakai (Brachyura) around the hydrothermal vents of the northeast Pacific. *Canadian Journal of Zoology* 65: 2443–2449.

Tunnicliffe, V., Desbruyères, D., Jollivet, D. & Laubier, L. (1993): Systematic and ecological characteristics of *Paralvinella sulfincola* Desbruyères and Laubier, a new polychaete (family Alvinellidae) from northeast Pacific hydrothermal vents. *Canadian Journal of Zoology* 71: 286–297.

Vrijenhoek, R.C. (2013): On the instability and evolutionary age of deep-sea chemosynthetic communities. *Deep Sea Research Part II: Topical Studies in Oceanography 92*: 189–200.

Watanabe, H. & Beedessee, G. (2015): Vent fauna on the central Indian Ridge. In: Ishibashi J.-I., Okino, K. & Sunamura, M. (eds), *Subseafloor Biosphere Linked to Hydrothermal Systems: TAIGA Concept*. SpringerOpen: 205–212.

Zal, F., Desbruyères, D. & Jouin-Toulmond, C. (1994): Sexual dimorphism in *Paralvinella grasslei*, a polychaete annelid from deep-sea hydrothermal vents. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, Life Sciences* 317: 42–48.

Zal, F. Jollivet, D., Chevaldonné, P. & Desbruyères D. (1995): Reproductive biology and population structure of the deep-sea hydrothermal vent worm *Paralvinella grasslei* (Polychaeta: Alvinellidae) at 13° N on the East Pacific Rise. *Marine Biology* 122: 637–648.

Zhadan, A.E. & Tzetlin, A.B. (2002): Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta). *Cahiers de Biologie Marine* 43: 149–164.

Zhadan, A.E., Tzetlin, A.B. & Safronova, M.A. (2000): Anatomy of some representatives from the family Alvinellidae (Polychaeta, Terebellida) from the Pacific hydrothermal habitats [in Russian]. *Zoologiceskij Zhurnal 79*: 159–160.

Zhong, M., Hansen, B., Nesnidal, M., Golombek, A., Halanych, K.M. & Struck, T.H. (2011): Detecting the symplesiomorphy trap: A multigene phylogenetic analysis of terebelliform annelids. *BMC Evolutionary Biology* 11: 369.

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Teresa Darbyshire

7.7.5 Arenicolidae Johnston, 1835

Introduction

The family Arenicolidae Johnston, 1835 includes some of the best-known polychaete species in the world, the "lugworms", due to their commercial exploitation and visible presence on many beaches (Fig. 7.7.5.1A–C). It comprises four genera: *Arenicola* Lamarck, 1801, *Abarenicola* Wells, 1959, *Arenicolides* Mesnil, 1898, and *Branchiomaldane* Langerhans, 1881, between them containing nearly 30 species and subspecies. Together, *Arenicola* and *Abarenicola* comprise the majority of the species (including several subspecies, but see Darbyshire 2017 for a review of *Abarenicola* subspecies) and are the genera to which the term "lugworm" refers (Wells 1980). Species in these genera are large in form (Fig. 7.7.5.1D), create burrows in sandy areas from high to low tide (Fig. 7.7.5.1A, C), and are exposed to predation when they move their tail toward the surface for defecation. The specialized tail has no vital organs and is renewed via backward growth from where it joins the trunk, meaning that losses through predation can be accommodated more readily without severely affecting the worm (Wells 1980). The remaining genera, *Arenicolides* and *Branchiomaldane*, currently contain two and four species, respectively, are much smaller in form and less commonly encountered, and lack the specialized tails of the aforementioned lugworms.

The family was regarded as "tentatively" monophyletic by Rouse and Fauchald (1997), but more recent morphological and molecular analyses (Bartolomaeus and Meyer 1997, Bleidorn et al. 2003, 2005, Darbyshire 2017) have presented further evidence to support monophyly, whereas a sister-group relationship with Maldanidae has long been supported (Bartolomaeus and Meyer 1997, Rouse and Fauchald 1997, Rouse and Pleijel 2001, Bleidorn et al. 2003, 2005, Bartolomaeus et al. 2005, Zrzavý et al.



Fig. 7.7.5.1: A, Shore in South Wales (UK) with small population of *Arenicola marina* (Linnaeus, 1758); B, bait digging for *Arenicola defodiens* Cadman & Nelson-Smith, 1993 in South Wales using an Alvey bait pump (courtesy of A.S.Y. Mackie); C, (left) fecal cast of *A. defodiens* with feeding hole in center and (right) fecal cast of *A. marina* with nearby feeding depression (courtesy of A.S.Y. Mackie); D, large example of *A. defodiens* demonstrating mucus and pigment secretion when handled (courtesy of A.S.Y. Mackie).

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2009, De Assis and Christoffersen 2011, Weigert et al. 2014). *Branchiomaldane* is also strongly supported as belonging within the family (Bleidorn et al. 2005, Darbyshire 2017) despite past debate about its position (Rouse and Pleijel 2001).

Morphology

Color

Species of *Arenicola* and *Abarenicola* are generally pale brown to black in color and can vary significantly in shade within each species (Fig. 7.7.5.2A, B). *Arenicolides* have been described as ranging in color from dark green to dark red or yellowish red (Fig. 7.7.5.2C) (Gamble and Ashworth 1900). *Branchiomaldane* are distinct in its lack of pigmentation but may show a pinkish appearance due to the visibility of internal blood vessels through the translucent body wall (Ashworth 1912a).

External morphology

Body regions. The arenicolid body form is divided into three regions (Fig. 7.7.5.2A–D, 3A): an achaetous anterior region ("head"), a chaetigerous middle region ("body" or "trunk"), and a posterior region ("tail") that is achaetous in *Arenicola* and *Abarenicola* but chaetigerous in *Arenicolides* and *Branchiomaldane*. These differentiations follow those discussed by Wells in his various publications on Arenicolidae. Thus, the genera can be divided into two groups, those with differentiated, specialized tails — the lugworms, *Arenicola* and *Abarenicola* (Fig. 7.7.5.2A, B) and those with an undifferentiated posterior region that cannot be sacrificed — *Arenicolides* and *Branchiomaldane* (Fig. 7.7.5.2C, D). There are several features of gross morphology distinct to each group.

Prostomium and peristomium. The head of all arenicolids comprises three achaetous segments: the prostomium and the peristomium (both without palps, cirri or appendages of any kind) and a third segment. The prostomium of lugworm species is trilobate (Fig. 7.7.5.3C) and may (*Arenicola*) or may not (*Abarenicola*) be retractable into the nuchal pouch. A shallow groove marks the position of the X-shaped brain (Wells 1959). The prostomia of *Arenicolides* and *Branchiomaldane* species are a nonretractile, transverse band (Fig. 7.7.5.3D) with a comparatively large brain extending more laterally than in lugworm species (Wells 1959).

Statocysts are present in some species of all genera, except *Branchiomaldane*, with (*Abarenicola*, some *Arenicola*) or without (*Arenicolides*, some *Arenicola*) a tube to the exterior. The purpose of statocysts is believed to relate to orientation and, according to Buddenbrock (1912, 1913), used to guide *Arenicola* when burrowing into mud. The statocysts contain granules, statoliths (Fig. 7.7.5.3E), the origin of which may be secreted or foreign (such as sand grains) (Ashworth 1903, 1912a, b, Fauvel 1907, Wells 1950, 1963b, Nonato 1958, Purschke 2016). Those species without statocysts may instead possess otic grooves (some *Abarenicola*) (Wells 1950, 1963b), which can be protected by the prostomial lateral lobes and by the worm pressing together the dorsal and ventral borders of the groove (Wells 1950).

Eyes are present in all of Arenicolidae but not always visible in adults. Gamble and Ashworth (1900) described their presence as being "sunk even in early postlarval stages of *Arenicola marina* (Linnaeus, 1758) into the ganglionic layer of the brain". Two or more pairs of eyes have been described on larval and postlarval stages of all species studied (Wilson 1883, Gamble and Ashworth 1900, Okada 1941, Okuda 1946, Newell 1949, Southward and Southward 1958, Bailey-Brock 1984). They are confirmed as present in adults of *Arenicolides ecaudata* Johnston, 1835 and *Abarenicola claparedi* Levinsen, 1884 situated below the epidermis but not visible externally due to the pigment and thickness of the epidermis (Gamble and Ashworth 1900). In *Branchiomaldane*, eyes are discernible on adult worms of all species (Mesnil 1898, Gamble and Ashworth 1900, Ashworth 1912a, Fournier and Barrie 1987, Nogueira and Rizzo 2001). A brief account on their structure in *Clymenides* stage of *A. marina* is the given by Purschke et al. (2006, fig. 1C).

Arenicolidae possess a single, unpaired nuchal organ as a V-shaped, ciliated, groove formed by an invagination of the epidermis of the sides and posterior of the prostomium (Gamble and Ashworth 1900). The organ is present from the postlarval stage onward in those species of *Arenicola*, *Abarenicola*, and *Arenicolides* studied, although it may only be present as a weakly defined groove initially (Ashworth 1912a for *Arenicolides ecaudata*). In comparison, the nuchal organ of *Branchiomaldane*, although present, is only weakly developed and does not form the same deep invagination as in the other genera (Ashworth 1912a). The groove is lined with secretory and sensory cells (Gamble and Ashworth 1900, Purschke 1997), many ciliated and specific to arenicolids (Purschke 1997).

Trunk region. The "trunk" or "body" of arenicolids is divided into a number of chaetigerous segments, with branchiae present on a variable number of segments depending on species (Figs. 7.7.5.2A–D, 7.7.5.3A). Within the lugworm group, each species has a defined number of chaetigers and branchiae. However, in *Arenicolides* and *Branchiomaldane*, the number of chaetigerous segments shows more variation, with branchiae starting further

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back and occurring on a greater number of segments. In all species, segments are divided into several annuli, one of which, the chaetigerous annulus, bears the parapodia and branchiae (Wells 1950).

Parapodia. The parapodia of *Branchiomaldane* are poorly developed in relation to the other genera, being only slightly elevated from the body wall, but bear similar capillary notochaetae and neuropodial hooks (Ashworth 1912a). In the remaining genera, neuropodia are represented by a single dorsoventral row of hooked chaetae (Fig. 7.7.5.3F), each within their own epithelial follicle, all together termed the neuropodial plate (Wells 1950). Neuropodial plates increase in length, with an increase in number of neurochaetae, from anterior to posterior chaetigers in lugworm species. In *Arenicola,* the neuropodial chaetal rows may only approach the midventral line in the posterior region. The reverse is true for *Arenicolides*, however, where anterior neuropodia may extend up to or even above the notopodia (see Figs. 7.7.5.2C, 7.7.5.3D) and closely approach the midventral line in all segments (Wells 1959). In *Branchiomaldane,* no neuropodia approach close to the midventral line (Wells 1959). Wells (1950) considered the notopodium to be a modified neuropodium with a dorsoventrally flattened tip and thin-walled evaginable base. Long, slender capillary notochaetae are arranged in two, parallel rows (Fig. 7.7.5.3G) (*Arenicola* Wells, 1950). Notopodia and neuropodia are controlled by means of protractor and retractor muscles attached to the body wall and increase in size posteriorly. After the investigation of the musculature of the neuropodia of *Arenicola*, Wells (1950) hypothesized that movement of the neuropodial chaetae could have a ratchet or gripping function and be significant in the movement of the worm within the tube. Both notochaetae and neurochaetae are continually replaced with the oldest disintegrating and being discharged at the dorsal end of the series in the case of neurochaetae (Ashworth 1912a, b, Wells 1944b).

Chaetae. Ashworth (1912b) gave detailed accounts and drawings of the notochaetae and neurochaetae of *Arenicola*, *Abarenicola*, and *Arenicolides* at various stages of growth and for several species. Both notochaetae and neurochaetae change in form as the worm matures from larva through postlarva to adult. The notochaetae of adults are long, slender capillaries with or without a lamina along the distal edge and may also possess comb-like crests of fine teeth around the shaft of each capillary (Ashworth 1912b). The level of development of these crests, as well as the level of striation on the shaft, varies between species and is most developed in *Arenicola loveni* Kinberg, 1866, the only species in which they can be used as a distinguishing character (Ashworth 1912b, 1916). In other species of *Arenicola* and *Abarenicola*, the

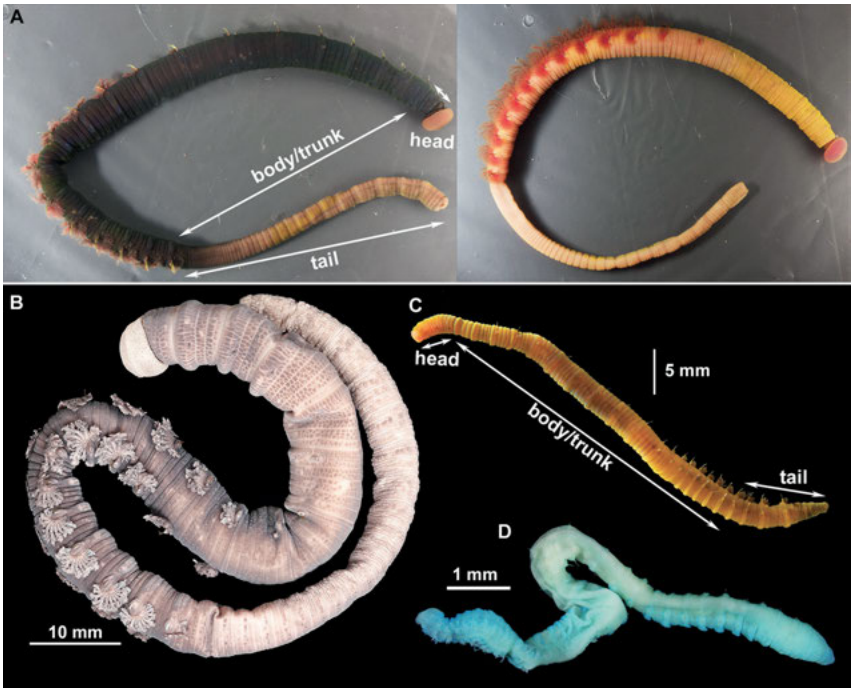


Fig. 7.7.5.2: A, *Arenicola defodiens*, live (courtesy of A.S.Y. Mackie), dark and pale examples; B, *Abarenicola wellsi* Darbyshire, 2017, preserved (NMW.Z.2011.039.181); C, *Arenicolides ecaudata*, live (courtesy of A.S.Y. Mackie); D, *Branchiomaldane vincenti*, preserved, stained with methyl green (NMW.Z.1987.050.4). NMW.Z., National Museum Wales, Cardiff.

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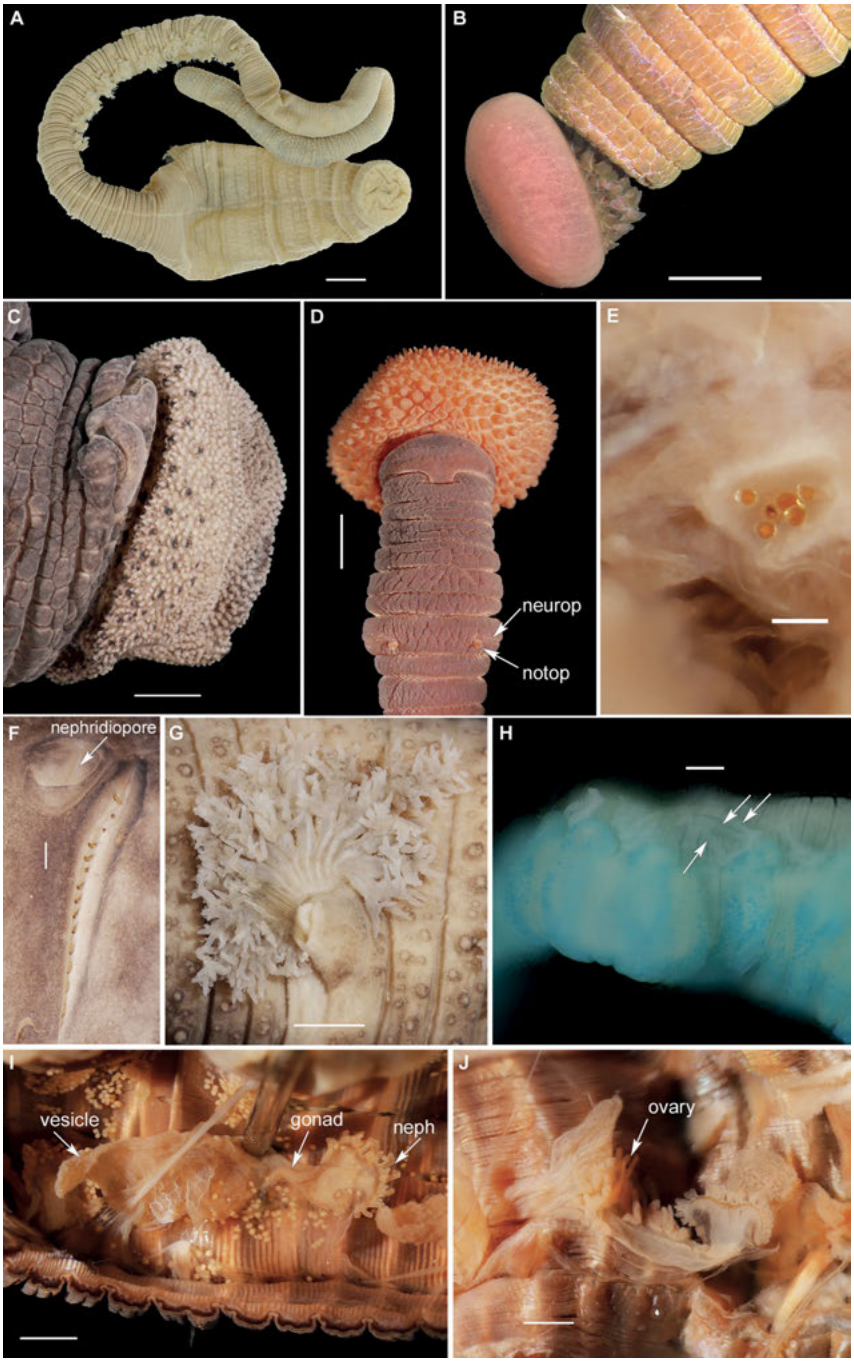


Fig. 7.7.5.3: A, *Abarenicola brevior* Wells, 1963, holotype (HZM V.4871a), ventral view; B, *Arenicola defodiens*, prostomium and proboscis, anterolateral view; C, *Abarenicola wellsi* (NMW.Z.2011.039.192), prostomium and proboscis, dorsolateral view; D, *Arenicolides branchialis* (NMW.Z.1989.139.73), anterior, dorsal view (notop, notopodium; neurop, neuropodium); E, *A. wellsi* (NMW.Z.2012.082.103), statoliths in statocyst; F, *A. wellsi* (NMW.Z.2011.039.192), nephridiopore and neuropodium, chaetiger 7; G, *A. brevior* (NMW.Z.2011.039.0181), gill, chaetiger 14; H, *Branchiomaldane vincenti* (NMW.Z.1987.050.4), filamentous gills (arrows indicate branchial filaments); I, *A. branchialis* (NMW.Z.1988.069.150), third nephridium with associated gonad (neph, nephrostome); J, *Arenicolides ecaudata* (NMW.Z.1985.051), fourth nephridium with associated gonad. HZM, Zoological Museum Hamburg; Scales: A, B, 5 mm; C, D, F, G, I, 1 mm; E, H, 0.1 mm; J, 0.5 mm.

differences between notochaetae are not sufficient to characterize species (Ashworth 1912b, Wells 1963b). In *Arenicolides*, the notochaetae have a similar form to those of *Arenicola* and *Abarenicola* but are more slender distally and have a narrow lamina that quickly breaks up into fine teeth and weakly developed crests (Ashworth 1912b). Neurochaetae take the form of hooks, with the curvature of the rostrum and shaft varying by species, but again not distinctively so. Several teeth are present on the rostrum but become less distinct as the worm matures. Neurohooks of

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Arenicolides are similar to those of *Arenicola* and *Abarenicola* but smaller in size. Chaetae of *Branchiomaldane* are of a generally similar form to the rest of the family but with some small modifications. Notochaetae are bilimbate, plumose capillaries in the anterior and median region, with some geniculate capillaries in the posterior (Ashworth 1912a, Fournier and Barrie 1987, Imajima 1988, Nogueira and Rizzo 2001). The neurohooks, in contrast, resemble those of *Arenicola* but with a sharply pointed rostrum (Ashworth 1912a) and with more clearly defined rostrum teeth (Day 1967).

Branchiae. The branchiae are hollow, highly vascularized structures situated on the chaetigerous annulus behind the notopodium (Wells 1950). They are present to some degree on all arenicolids, from the seventh chaetiger or later, although the number of segments on which they occur varies by species. In *Arenicola*, *Abarenicola*, and *Arenicolides*, the branchiae are highly branched (Figs. 7.7.5.2A–C, 7.7.5.3G) and contractile, but in *Branchiomaldane* they occur as up to five filaments (Fig. 7.7.5.3H) (Fournier and Barrie 1987). Arenicolid branchiae are not considered to be modified dorsal cirri as in some other groups, but specialized structures developed directly from the body wall, functioning immediately as respiratory structures upon formation (Gamble and Ashworth 1900). Their ultrastructure has been described by Jouin and Toulmond (1989).

Nephridiopores. The nephridiopores (Fig. 7.7.5.3F), in all species, are situated just posterior to the dorsal end of the neuropodia. Most species have four or five pairs of nephridia, although *Branchiomaldane* have only 2 pairs and *Arenicolides ecaudata* has 13 pairs, starting on either the fourth or fifth chaetigerous segment. Nephridia consist of a vascularized funnel (nephrostome) (Fig. 7.7.5.3I, J), which differs in form between the lugworms and the other two groups (Wells 1959), and a posterior terminal vesicle (Fig. 7.7.5.3I, J) or bladder (Gamble and Ashworth 1900), which functions in the excretion of metabolic waste (Wells 1961) and the release of gametes. The reproductive organs are situated immediately behind the posterior portion of the nephrostome (Fig. 7.7.5.3I, J) (except in *Branchiomaldane*) but are absent from the first pair. The nephridia of *A. ecaudata* differ from those of all other arenicolids in both their number (13 pairs) and the appearance of the associated gonads, which become enlarged and form a more complex structure (Fig. 7.7.5.3J) (Ashworth 1912b, Wells 1959).

Tail region. Although the genus *Arenicola* (originally comprising *Arenicola*, *Abarenicola*, and *Arenicolides* species) was split into "caudate" and "ecaudate" species by early authors, Wells (1950) detailed the presence of an undifferentiated tail in *Arenicolides* (Fig. 7.7.5.2C), previously described as "ecaudate", and distinguished it from the more obvious, differentiated tails in *Arenicola* and *Abarenicola* (Fig. 7.7.5.2A, B). The specialized tail of lugworm species, containing no vital organs, chaetae or branchiae, can be sacrificed via autotomy to aid escape when attacked by predators. The break occurs at the intersegmental boundary incurring minimal blood loss (Linke 1939). New segments are laid down by the pygidial growth zone with new trunk segments first and then very short achaetous tail segments that lengthen as the worm grows (Wells 1950). The number of tail segments laid down initially act as a "reserve" that lengthen to replace lost segments during the worms' life but are finite in number, with species of *Arenicola* appearing to possess more than those of *Abarenicola*. Tail segments are continually lost and replaced (in *Arenicola*) throughout a worm's lifetime, even if not lost through accident or predation (Wells 1966). In contrast, some tail segments of *Arenicolides* (distinguished from the trunk by the presence of internal septa and externally by the enlarging of the second, and sometimes third, intersegmental annuli) (Wells 1950) have both parapodia and branchiae and segments are grown to full size without further replacement throughout life. In *Branchiomaldane*, septa are also present throughout the branchial region with the last few segments being abranchiate but chaetigerous (Ashworth 1912a).

Anatomy

Early studies on arenicolid anatomy by Gamble and Ashworth (1898, 1900) and Ashworth (1904, 1912a, b) made comparisons between the three main genera *Arenicola*, *Abarenicola*, and *Arenicolides*, all classified within *Arenicola* at that time. Later studies by Wells (1944b, 1950, 1952) used mostly the same species but added additional details and made some corrections to the earlier observations.

Brain and nervous system. Within the head, the brain is that part of the central nervous system within the prostomium in close association with the epidermis (Wells 1950). It is considered as having been formed by the fusion of sensory areas derived from modified portions of the prostomial epidermis along with additional groups of cells that traverse the esophagus and extend into the nerve cord (Gamble and Ashworth 1900). The brain of *Arenicolides* is relatively large (Wells 1950), although Gamble and Ashworth (1900) regarded it as a simpler structure than that of the lugworm species. The brain of *Branchiomaldane* bears more relation to the lugworm form (Ashworth 1912a).

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The nervous system is most similar between *Arenicola* and *Arenicolides*, with *Abarenicola* presenting a more primitive condition. The rounded ventral nerve cord, with pairs of interannular nerves in each interannular groove that unite dorsally, encloses the body. *Arenicola* and *Arenicolides*, but not *Abarenicola* or *Branchiomaldane*, possess a giant fiber (axon) system as described by Gamble and Ashworth (1898, 1900), Ashworth (1904, 1912a), and Nicol (1948). Nicol (1948) proposed that such giant axons are directly involved in the impulses related to quick contraction and retraction from danger as exhibited by certain polychaetes, including *Arenicola*.

There are only a few studies that deal with the ultrastructure of sense organs in Arenicolidae. Besides a description of the statocysts (Titova and Kharkeevich 1973, Storch and Schlötzer-Schrehardt 1988) and some data on the eyes (Purschke et al. 2006), the sensory papillae of the caudal region have been described in detail by Jouin et al. (1985). These papillae contain two different types of receptor cells, which are considered to be involved in the control of tube ventilation. The statocysts are formed by an epidermal invagination that is connected to the exterior via a narrow canal. The epithelium comprises supportive cells, gland cells, and multiciliated receptor cells (Titova and Kharkeevich 1973, Kharkeevitch and Titova 1974).

Proboscis and intestine. All Arenicolidae possess an extrusible organ, the proboscis (Figs. 7.7.5.2A–C, 7.7.5.3A–D), which is used in both feeding and burrowing to varying extents depending on lifestyle. Juveniles of *Arenicola marina* prior to development of the proboscis possess a foregut structure known as dorsolateral ciliary folds along with a ventral pharyngeal organ (Purschke and Tzetlin 1996); in adults, the latter is replaced by the nonmuscular axial proboscis common to the group. Wells (1952) described the proboscis apparatus of *Arenicola*, *Abarenicola*, and *Arenicolides* in great detail. The proboscis apparatus includes the proboscis itself and the first part of the esophagus along with the retractor sheath and gular membrane. The proboscis is covered with hollow papillae derived from the body wall and hollowed by the development of the interstitial spaces between the cells. Different species possess papillae of different shapes and sizes. The retractor sheath and the gular membrane (Fig. 7.7.5.4A–D) together suspend the gut from the body wall of the head and consist of coelomic epithelium, connective tissue, and a layer of muscle. They play an important role in the extrusion of the proboscis; the more developed the gular membrane is, the more powerful that movement appears to be. The gular membrane varies between genera and species in its development, forming long, finger-shaped contractile sacs (septal pouches) in some (Gamble and Ashworth 1900). It is most developed in *Arenicolides* (Fig. 7.7.5.4C, D), which has an extensive, powerfully muscular membrane and large septal pouches. *Arenicola* have a less muscular membrane with a pair of small septal pouches (Fig. 7.7.5.4A), but the latter are absent in *Abarenicola* (Fig. 7.7.5.4B) (and *Branchiomaldane*) and the structure is more delicate (Wells 1980). No studies have been made of the proboscis in *Branchiomaldane*.

Beyond the esophagus and the hearts extends the gastric region with glandular walls and numerous blood vessels. The length the gastric region extends to is dependent on genus (longer in *Arenicolides* than *Arenicola* or *Abarenicola* but not documented in *Branchiomaldane*). A well-marked ventral groove occurs from the middle of the stomach to the anus and has oblique grooves opening into it from the side walls of the alimentary canal. Ciliated cells line the grooves producing currents toward the anus (Gamble and Ashworth 1900). The intestine continues from the stomach to the posterior end, terminating in the anus, which is bordered by papillae or lobes (Gamble and Ashworth 1900, Ashworth 1912a).

Gular membrane and coelom. Posterior to the gular membrane (the "first diaphragm" of Gamble and Ashworth 1900) (see Wells 1952 for a discussion of origin and terminology) are a further two diaphragms (the second and the third; Fig. 7.7.5.4A–D), forming septa at the anterior borders of the third and fourth chaetigers, respectively. Further septa are absent in *Arenicola* and *Abarenicola* until the most posterior branchial pair and are then present between each tail segment. In *Arenicolides* and *Branchiomaldane*, septa exist throughout the branchial region and, in *Arenicolides*, to the end of the body (Gamble and Ashworth 1900, Ashworth 1912a). At the posterior end of the esophagus are a pair of hollow glands, the esophageal ceca (Fig. 7.7.5.4A–D), with either separate (*Arenicola*, *Abarenicola*, and *Arenicolides*) or a common (*Branchiomaldane*) narrow duct(s). In *Abarenicola*, these esophageal ceca proliferate into a variable number of small ceca (Fig. 7.7.5.4B) and a single pair of longer ceca and can be used as a diagnostic character for some species.

The coelom contains coelomic cells (Figs. 7.7.5.3I, 7.7.5.4D) and reproductive products, and circulation is maintained through peristaltic waves that pass along the body. Pressure created through the movement of the coelomic fluid maintains the hydrostatic skeleton of the worm and, in combination with the musculature, is essential in all aspects of its life. The movement of coelomic fluid plays a particular role in the control of the proboscis and the

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resulting actions of burrowing and feeding (Chapman and Newell 1947, Wells 1952, 1954) as well as the irrigation of the tube (Wells 1945, 1949). Before the burrowing activity, coelomic fluid is forced into the anterior end of the worm, and there is a mechanism for providing temporary "bulkheads" across the body cavity to control varying pressure within the worm (Chapman and Newell 1947, Trueman 1966). Even at rest, the body wall muscles of a worm exert positive pressure on the coelomic fluid, maintaining form (Chapman and Newell 1947).

Blood vascular system. Between the esophageal ceca and the stomach of arenicolids lie a pair of hearts (Fig. 7.7.5.4A–D), documented in *Arenicola*, *Abarenicola*, and *Arenicolides* but not conclusively in *Branchiomaldane* due to inadequate material (Ashworth 1912a). A "heart-body", the purpose of which is to ensure blood flow from lateral vessels into the ventral vessel via the muscular ventricle (Dales and Cummings 1987), is not present in all species but has been documented as well developed in both species of *Arenicolides* (Gamble and Ashworth 1900, Ashworth 1904), absent in *Abarenicola claparedi* (Levinsen, 1884) and *Arenicola cristata* Stimpson, 1856, and present in *Arenicola marina* although absent in juveniles (Dales and Cummings 1987). The dorsal vessel has no direct communication with the heart (Gamble and Ashworth 1900). The heart-body is not a hemopoietic organ (producing blood cells) as in some other polychaetes this function is carried out by extravasal tissue (Braunbeck and Dales 1985, Dales and Cummings 1987).

Body wall. The body wall is divided externally into annuli, and the position of the nerve cord is visible externally as a pale ventral groove (Fig. 7.7.5.3A) (*Arenicola* and *Abarenicola*, not *Arenicolides*). Internally, septa or septal blood vessels indicate the division between segments (septal plane) and roughly correspond to the second groove behind each chaetigerous annulus (*Arenicola* Wells, 1950). Layers of different muscle fibers and connective tissue are present within the body wall, which is highly vascularized. The separation of longitudinal muscle fibers can be used to indicate the position of the ventral nerve cord, nephridiopores (more variable in presence and distinction), and notopodia as well as the dorsal mesentery where present.

The stomatogastric nervous system consists of nerves connecting the central nervous system of the head region with ganglionic masses in the gut wall (Whitear 1953). Some early works were done on part of the system in *Arenicola marina* by Wells (1937), showing interrelations between the neuromuscular structures in the front part of the gut and those of the anterior body wall, but the complete structure of the system in *A. marina* was described by Whitear in 1953. The arrangement of the systems in *Abarenicola* (*claparedii*) and *Arenicolides* (*ecaudata*) have been found to be essentially the same, with the exception that the ring ganglion, considered a specialized part of the esophageal plexus, is situated at the junction of the postpharynx and esophagus as opposed to immediately behind the junction as in *A. marina*.

Musculature. Oblique muscles run from the sides of the nerve cord to the notopodial line and the end of the body. They are absent from the head and the first 3 (*Arenicola* and *Abarenicola*) or 16 or 17 (*Arenicolides*) body segments, except where they attach to the notopodia.

In *Arenicola*, the anterior abranchiate chaetigerous segments that play a role in gripping the wall of the tube to assist in pulling the body in can distend in such a way as to strongly hold the body in place to prevent enforced withdrawal by a predator and also help draw surface sand down into the head end of the burrow (Wells 1944b, 1950). These anterior chaetigers have additional musculature as part of the "parapodial girdle", a group of special features that are only found as far back as chaetiger 8. The parapodial girdle is better developed in *Abarenicola* than *Arenicola* but more poorly so in *Arenicolides* (Wells 1950). The amount of musculature present (both longitudinal and circular) may also enable different species to inhabit different sediment types. A recent study on two lugworm species in False Bay, USA (Crane and Merz 2017) reported that *Abarenicola pacifica* Healy & Wells, 1959, which inhabits firmer sediments than *Abarenicola claparedi*, showed thicker body wall musculature and held their bodies more rigidly than *A. claparedi*, with additional differences also noted in proboscidial papillae morphology.

Pigment and mucus. The handling of arenicolids induces the production of mucus accompanied by a yellow or green secretion that stains the hands (Fig. 7.7.5.1D). Investigations by Dales (1963) on arenicolid pigments concluded that the dark color of *Arenicola marina* and *Abarenicola claparedi vagabunda* Healy & Wells, 1959 (as *A. vagabunda*) was due to a combination of the pigments haematin and melanin and, possibly, arenicochrome. Arenicochrome, a yellow green fluorescent pigment, was first described from epithelial cells of *A. marina* (Lignac 1945, van Duijn et al. 1951). Patel and Spencer (1963 a, b) studied the properties of the respiratory pigment hemoglobin found in *A. marina*. They determined that the oxyhemoglobin formed carboxyhemoglobin and nitric oxide hemoglobin, which were very similar to analogous derivatives of the mammalian respiratory pigment, but that the invertebrate pigment did

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not form a choleglobin or sulfemoglobin. The absence of the latter probably affords considerable protection against the toxic effects of sulfides, a tolerance to which has been demonstrated (see also later section on respiration p170). Paper chromatography results also suggested that the same porphyrin was present in both *Arenicola* and mammalian hemoglobins. Modern biotechnology techniques are now being used to investigate *A. marina* hemoglobin as a potential extracellular blood substitute for humans (Rousselot et al. 2006). Bacteria have also been used for high-level production of recombinant *A. marina* globin chains for potential therapeutic applications (Harnois et al. 2009).

Biology and ecology

Arenicolidae are mostly intertidal or shallow sublittoral species burrowing in sediments or, in the case of *Branchiomaldane*, inhabiting sand tubes (Rouse and Pleijel 2001). Wells (1963a) considered the distribution of lugworm genera (*Arenicola* and *Abarenicola*) to be mainly governed by surface water temperatures, bounded by the 20°C summer isotherms with some limits imposed by the 10°C southern isotherm also. *Arenicola* species predominantly inhabit northern cold water and warm water areas and are mostly absent below the southern 20°C isotherm. Cysted (with statocysts) *Abarenicola* species occur in the northern cold waters with cyst-less species found in the southern cold zone. *Arenicolides* species are restricted to Europe, whereas *Branchiomaldane* has a worldwide distribution (Rouse and Pleijel 2001).

In some areas, lugworms can be locally abundant (Fig. 7.7.5.1A), with estimates of up to 100 *Arenicola* individuals/m^2 accounting for 10% to 20% of the benthic biomass in the Wadden Sea (Flach and Beukema 1994), for example. Worms are generally large with adults ranging from 10 to 80 cm long, although *Branchiomaldane* species may only reach 25 mm long (Rouse and Pleijel 2001). *Arenicola* and *Abarenicola* species generally have their own preferences for sand type, and habitats can range from clean sand

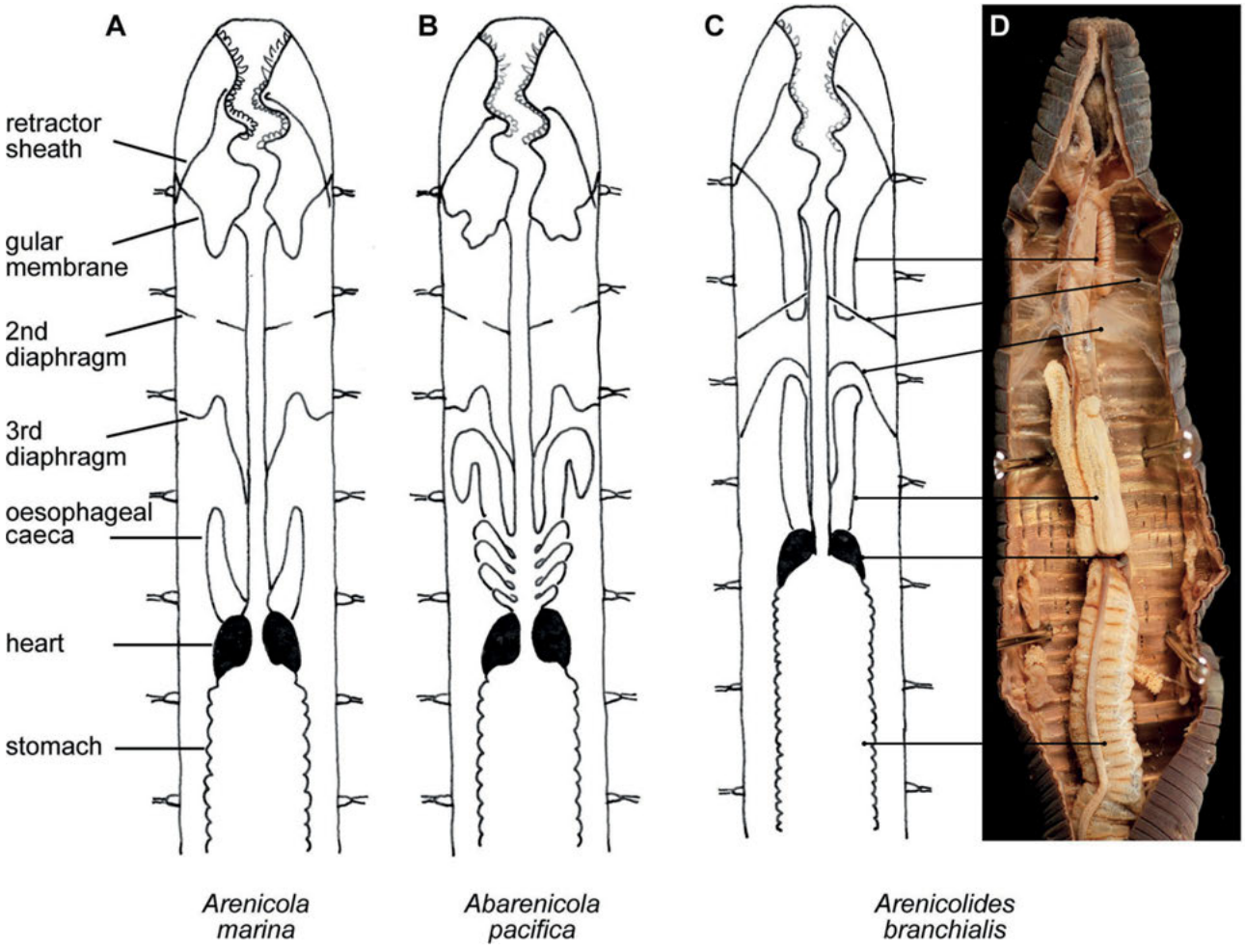


Fig. 7.7.5.4: A–C, Diagram showing the characters of the proboscis apparatus and esophageal glands; D, Image of a dissected *Arenicolides branchialis* (NMW.Z.1988.069.150) showing internal structures for comparison to the illustrations. A, B, Reprinted from Wells 1963a, fig. 4, with permission from the Systematics Association. See reference list for full citation.

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(*Abarenicola gilchristi* Wells, 1963b as *Arenicola* var. *affinis* (Day, 1955)) to black muddy sand (*Abarenicola affinis africana* Wells, 1963b). *Arenicolides* species inhabit gravel or understones (Southward and Southward 1958), and *Branchiomaldane* appears to be the least selective of the genera for habitat, inhabiting tubes among algae, underneath calcareous algae, among eelgrass, in fine sand, or on rocky beaches (Fournier and Barrie 1987).

Their density, accessibility, and size have made lugworms an ideal bait species for fishermen (Fig. 7.7.5.1B), with *Arenicola defodiens* Cadman & Nelson-Smith, 1993 recently classed as one of the top five most valuable polychaete species worldwide (Watson et al. 2016). However, exploitation pressure can severely impact populations if not managed. An area (200 m × 2 km) in northeast England set aside for bait digging was completely denuded of all lugworms within 6 weeks of the onset of bait digging, an estimated removal of 4 million worms (Olive 1993). Olive (1994) suggested that a system of progressive exploitation, allowing the migration of worms into depleted areas from unexploited neighboring areas, could be an effective management technique. The migration of both juvenile and adult *Arenicola marina* into unoccupied areas has been demonstrated by several authors (Newell 1948, 1949, Beukema and de Vlas 1979, Olive 1993, Flach and Beukema 1994).

Lugworms (*Arenicola* and *Abarenicola*) play an important part in tidal flat ecology both as a prey species and through reworking of the sediment. They are a food source for Platyhelminthes, ragworms, and crabs, whereas juvenile and adult tails are "nipped" by flatfish and wading birds (de Vlas 1979, Reise 1985). In turn, *Arenicola marina* has been identified as having significant impact through "predation by ingestion" on *Macoma balthica* spat on tidal flats of the Wadden Sea (Hiddinck et al. 2002) and can both enhance and reduce the bacterial content of the sediment (Hylleberg 1975, Grossmann and Reichardt 1991). First discovered and published by Reise and Ax (1979), lugworm burrows also provide an oxygenated microhabitat for a rich meiofauna. These meiofauna communities are characterized by extraordinary diversity and high abundance (Reise 1981, 1987, 2002).

The effect of lugworms on the shore by the reworking of sand through burrowing and ingestion has been estimated as equivalent to a sediment depth of up to 33 cm/year, with a large lugworm able to ingest up to 80 cm^3 sediments/day (Cadée 1976 for *Arenicola marina*). Increases in organic matter, organic carbon, and chlorophyll *a* at 20 to 30 cm sediment depth have been shown to result from *Arenicola* activity as well as an increase in grain size due to the preferential selection of smaller particles for ingestion (Cadée 1976). The irrigation of the burrow, through peristaltic motion forward along the body, promotes oxygen input below the sand surface (although lugworms themselves can absorb oxygen from either the water or from air) as well as the removal of excretory products and entry of food particles into the tube (Wells 1945, 1966). Actual water content of the sediment, however, is unaffected by lugworm activity (Cadée 1976).

Detailed reviews of the feeding in arenicolid species were published by Fauchald and Jumars in 1977 and updated in 2015 (Jumars et al. 2015). The majority of work has focused on *Arenicola marina* (according to Jumars et al. 2015, in 1979, *A. marina* was the most studied polychaete species in the world with regard to feeding), with some additional work on *Abarenicola affinis africana* Wells, 1963, *Abarenicola gilchristi* and *Arenicola loveni* (see Day 1967), and *Abarenicola pacifica* and *Abarenicola claparedi vagabunda* (as *A. vagabunda*) (see Hobson, 1967, Hylleberg 1975). There are no specific feeding studies published on *Arenicolides* or *Branchiomaldane*. *A. marina* was characterized as a "nonselective surface deposit feeder", as the material it ingests slumps or is deposited into the burrow due to the action of removing sand from the base of the head shaft. The same action was detailed for both *A. pacifica* and *Abarenicola vagabunda*. However, suspension feeding has been shown to be possible in some species, although the predominant mode was surface feeding (Hobson 1967) and selectivity has also been demonstrated in *A. marina* with a bias toward ingesting smaller grain sizes. Digestive selectivity by *A. pacifica* and *A. vagabunda* (Hobson 1967, Hylleberg 1975) was also demonstrated with both species digesting certain types of organic material but not others. Feeding rates increased as protein concentrations of food increased but then decreased at the highest values. This was attributed to the digestive system operating to maximize the rate of absorption of nutrients produced by digestion (Jumars 2000). Jumars et al. (2015) classified *Arenicola*, *Abarenicola*, and *Arenicolides* species as "discretely motile funnel feeders" (feeding below the sediment-water interface in sand-silt mixtures but ingesting surficial deposits along with variable amounts of subsurface sediments). *Branchiomaldane* species were speculatively determined as "subsurface deposit feeders". Despite extensive studies on feeding behavior, little has been published on the mechanisms of feeding. Wells (1954) suggested that, on the extrusion of the proboscis, the emerging buccal teeth exert a rasping action on the sand (*A. marina*) but that this would not be possible in the case of *Arenicolides ecaudata* due to the shape of the papillae (see below). Feeding and burrowing occur exclusively with no sand ingestion during the latter (Wells 1954). Defecation occurs by the worm moving backward in the burrow (*A. marina*) until the tip of the tail is just at the surface of the sand (Wells 1945). Fecal cylinders are ejected, often at speed, to pile

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up on the surface, leaving the characteristic piles associated with lugworms (Fig. 7.7.5.1A, C). The shape of the fecal cast and the relative position of the feeding depression/hole can, in some regions, be distinct enough to permit determination between local species, e.g., *A. marina* and *Arenicola defodiens* in the United Kingdom (Fig. 7.7.5.1C).

Recent studies on ingestion of microplastics by *Arenicola marina* have shown that they affect both the health and the behavior of lugworms (Green et al. 2016), although an earlier study by van Cauwenberghe et al. (2015) showed no adverse effect on the overall energy budget of the animals. The bioaccumulation of metals, such as selenium, thallium (Turner 2013, Turner et al. 2013), and arsenic (Casado-Martinez et al. 2013), have also been investigated and shown to accumulate in tissues although not necessarily with any discernible toxic effect. Other studies, however, have shown that a potential increase in copper bioavailability due to, and combined with, effects from ocean acidification could adversely affect the early stages of *A. marina* by reducing sperm motility and larval survival (Campbell et al. 2014).

Wells (1952) provided a detailed study of the proboscis apparatus of *Arenicola marina*, *Abarenicola pacifica* (as *A. claparedii*), and *Arenicolides ecaudata*. The proboscis apparatus was defined as comprising the proboscis itself, the first part of the esophagus, the retractor sheath and the gular membrane and is covered in hollow papillae that form conical teeth in *Arenicola* (Fig. 7.7.5.3B, C) and *Abarenicola* but are sucker shaped in *Arenicolides* (Fig. 7.7.5.3D). The form and mechanism of the proboscis are more similar between *Arenicola* and *Abarenicola* than in *Arenicolides*. In *Arenicolides*, the gular membrane is more extensive and muscular than in the other two genera and is the primary force behind the extrusion of the proboscis. In *Abarenicola*, extrusion is mainly through fluid driven forward by muscles of the body wall, whereas, in *Arenicola*, extrusion is achieved through a combination of the gular membrane and the body wall contracting. Extrusion also occurs more fully in both *Arenicola* (Figs. 7.7.5.2A, 7.7.5.3B) and *Abarenicola* (Figs. 7.7.5.2B, 7.7.5.3C), with the proboscis distended into a fuller, more spherical form than in *Arenicolides* (Fig. 7.7.5.3D). The proboscis is integral to the process of burrowing with varying hypotheses proposed as to the precise mechanisms involved (Chapman and Newell 1947, Wells 1944a, 1948). The variation in the timing of proboscis retraction is probably the distinction between feeding and burrowing (Wells 1954).

The irrigation of the burrow by *Arenicola marina* is managed via special waves traveling forward along the body (Wells 1945). Water currents created by the movement might be important in softening the sand in the head shaft. Spontaneous activity cycles have been shown in *A. marina*, which correspond to feeding, irrigation, and defecation cycles (Wells and Albrecht 1951a). The feeding rhythm originated in the esophagus, but the defecation-irrigation rhythm appeared in the body wall and tail. Similar experiments with *Arenicolides ecaudata* did not show such regulated cycles of activity as in *A. marina* (Wells and Albrecht 1951b).

Lugworms can absorb oxygen either from the water or from air (Wells 1945). At high tide, the irrigation of the burrow maintains an oxygen supply in the water; at low tide, when the burrow may be drained and air enters, the worm can draw oxygen from the air. At times during low tide, when stagnant water may fill the burrow, experiments have shown *Arenicola marina* to partake in "bubble trapping" in which the worm rises backward in the burrow to the water surface and draws air bubbles down between its dorsal surface and the tube and holds them there, often covering several pairs of gills and thus enabling aerial respiration (Wells 1945). Moreover, lugworms show specific adaptations and mechanisms to tolerate high concentrations of sulfide (Völkel and Grieshaber 1992, Völkel 1995), including a highly specialized hemoglobin that is involved in the detoxification of sulfide by immobilization (Zal et al. 1997). (see also previous section on pigments p167–8)

Reproduction, ontogeny, and larval life

Species within *Arenicola*, *Abarenicola*, and *Arenicolides* are gonochoristic (Benham 1893, Mesnil 1898, 1899, Fauvel 1899, Gamble and Ashworth 1900, Ashworth 1912b, Guberlet 1934, Newell 1948, Southward and Southward 1958, Healy and Wells 1959, Bailey-Brock 1984, Watson et al. 1998), although information on reproduction is not recorded for every species. *Branchiomaldane vincenti* Langerhans, 1881 is hermaphroditic (Mesnil 1899, Ashworth 1912a), and Linton and Taghon (2000) questioned as to whether there might be some occurrence of hermaphroditism within *A. pacifica*. Reproductive maturity in *Arenicola marina* is recorded as occurring at about 2 years old (Newell 1948).

In *Arenicola*, *Abarenicola*, and *Arenicolides*, the reproductive organs are closely associated with the nephridia (Ashworth 1912b). The gonads are a small ovoid, club-shaped, or cylindrical mass of cells (Gamble and Ashworth 1900, Ashworth 1912b), which is present behind the funnel of each nephridium (Fig. 7.7.5.3I) and sheds immature oocytes or spermatogonia into the coelom where they continue to mature and grow. In *Branchiomaldane*, the gonads are not associated directly with the nephridia but are instead located on the coelomic epithelium of the oblique muscles and septa and lateral body wall near the insertion of the oblique septum (Ashworth 1912a). They

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do not occur anterior to the third septum. Shedding and maturation of the gametes occur as in the other genera. In the two species of *Arenicolides*, the gonads vary in appearance and location, with those of *Arenicolides branchialis* (Audouin & Milne Edwards, 1833) like those in *Arenicola* and *Abarenicola*, but those of *Arenicolides ecaudata* are quite different (Fig. 7.7.5.3I, J) (Ashworth 1912b). In *A. ecaudata*, the reproductive organs are much larger and more complex than in the other Arenicolidae. In females, the gonads are divided into conical "processes" (Fig. 7.7.5.3J), each of which contains oocytes of up to 120 µm. Males have several outgrowths from the gonad, up to 6 mm long, containing all phases of male cells up to nearly mature spermatozoa. Gametes are therefore retained by the gonads of *A. ecaudata* to a much later stage of development and are then shed into the coelom through rupture of the gonad wall for final maturation just before spawning (Gamble and Ashworth 1900, Ashworth 1912b). Gamete maturation and spawning have been shown to be under hormonal control (see below).

Although the process of gamete production and spawning appears similar across the species, the morphology and development of the spermatozoa and oocytes show some variation, and most of our knowledge is restricted to a few, very well studied species, particularly *Arenicola marina* and *Arenicola defodiens* (Ashworth 1912b, Newell 1948, Howie 1959, 1961, 1963, 1966, Bentley 1985, Bentley et al. 1990, Pacey and Bentley 1992a, b, Bentley and Hardege 1996, Watson and Bentley 1997, 1998, Watson et al. 1998, 2000, 2008) but also *Arenicola brasiliensis* Nonato, 1958 (see Okada 1941 (as *A. cristata*) Sawada 1975), *Abarenicola pacifica* (see Okuda 1946 as *A. claparedi*), *Arenicola loveni* (see Lewis 2005a, b as *A. loveni loveni*), and *Arenicolides ecaudata* (see Ashworth 1912b, Southward and Southward 1958).

Oocytes are shed from the ovaries when they reach 12 to 20 µm in diameter (Ashworth 1912b), and vitellogenesis completes in the coelom (*Arenicola defodiens*, *Arenicola marina*, *Arenicola brasiliensis*, *Branchiomaldane vincenti*, and *Arenicolides branchialis*), except in *Arenicolides ecaudata*, which exhibits intraovarian vitellogenesis (Rouse 1992). Mature ova are circular or oval, biconvex or biconcave, and about 120 to 190 µm and may be yellow, orange, brown, or black (Gamble and Ashworth 1900, Ashworth 1912b, Newell 1948, Healy and Wells 1959, Watson et al. 1998, Linton and Taghon 2000). Ova have a clear vitelline membrane of between 1 and 6 µm, varying in thickness with species (Ashworth 1912b). The membrane is covered with numerous microvilli that withdraw during maturation, a modification that may have an important role in subsequent spawning and fertilization (Meijer 1979a, observed in *A. marina*, although Watson and Bentley 1997 since considered his work to have actually been based on *A. defodiens*). The process of oocyte maturation and spawning is hormonally controlled from the prostomium and has been studied in depth in both *A. defodiens* and *A. marina* (Howie 1961, 1963, 1966, Meijer 1979a, Bentley 1985, Pacey and Bentley 1992b, Watson and Bentley 1997, 1998, Watson et al. 1998). It involves first the production of a prostomium maturation hormone (PMH), which itself induces, in *A. marina*, production of the coelomic maturation factor (CMF) that is detectable in coelomic fluid just before spawning (Watson and Bentley 1997). In *A. marina*, CMF is essential for oocytes to mature, but in *A. defodiens*, CMF is not produced, and oocyte maturation only requires the presence of PMH (Watson et al. 1998).

In *Arenicola marina* (or *defodiens* where referenced to Meijer 1979b), spermatogonia are released from the gonads and form clusters of spermatocytes (still undergoing proliferative mitotic division) and spermatids (final mitotic division complete) (Pacey and Bentley 1992b). As development continues, spermatids form disc-like masses that become sperm "morulae", discs of mature spermatozoa in which individual spermatozoa are cytoplasmically connected to a central mass of cytoplasm (cytophore) (Ashworth 1912b, Newell 1948, Pacey and Bentley 1992b). Spermatozoa are composed of four parts: the acrosome (anterior, narrow, complex part), an enlarged region containing the nucleus, a narrow region containing the centriole, flagellum basis, and mitochondria, and the flagellum (Meijer 1979b). Although part of sperm morulae, the flagella of the spermatozoa are not moving or do so only slightly (Meijer 1979b) and they are not available for spawning or use in fertilization (Meijer 1979b, Pacey and Bentley 1992b). Before spawning, the morulae must therefore dissociate, a process under endocrine control (Howie 1963, 1966) of a fatty acid hormone secreted by the prostomium, termed "sperm maturation factor" (Bentley 1985), and putatively identified as 8,11,14-eicosatrienoic acid (Bentley et al. 1990, Pacey and Bentley 1992a, b, Bentley and Hardege 1996). Once free, the individual spermatozoa are released via the nephridia. Not many studies have compared sperm morphology and size between species, but size appears to be comparable between *A. marina* (see Ashworth 1912b) and *Arenicola brasiliensis* (see Okada 1941 as *A. cristata*), whereas those of *Arenicolides* are slightly smaller (Gamble and Ashworth 1900). Morphology, however, does vary slightly between the two *Arenicola* species studied (Ashworth 1912b, Okada 1941, Newell 1948). The actual appearance of spawning also seems to have some variation, with *A. marina* producing sperm "puddles" (Fig. 7.7.5.5A) (Duncan 1960, Williams et al. 1997, Watson et al. 1998, Watson personal communication) and *Abarenicola pacifica* ejecting individual "spermatophores" as oval pellets enveloped in a gelatinous

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membrane (Okuda 1946 as *A. claparedii*). The latter spermatophores then sink into the burrow of an adjacent female and "burst" into individual spermatozoa on contact with chaetae, stimulating oviposition by the female (Okuda 1946). In *A. vagabunda*, spawning relies on an incoming tide to bring eggs and sperm together (Guberlet 1934 as *A. claparedii*). Up to 40% mortality was recorded in adult *A. marina* following spawning (Newell 1948).

The timing of spawning varies and, in some cases, has been related to temperature (Howie 1959) or lunar cycle (Newell 1948, Duncan 1960, Bailey-Brock 1984). However, Watson et al. (2000), studying *Arenicola marina* populations in the United Kingdom, found that a combination of clement weather (high pressure, low rainfall, and wind speed) in conjunction with spring tides led to successful spawning, whereas inclement weather at the time of the spring tides would result in population-wide spawning being aborted. Sympatric species, such as *Abarenicola pacifica*/*Abarenicola vagabunda* in False Bay, WA, USA, and *Arenicola defodiens*/*Arenicola marina* in the United Kingdom, have been found to spawn in different seasons (Newell 1948, Healy and Wells 1959, Watson et al. 1998, 2000), possibly ensuring that no cross-fertilization can occur, although variability in the breeding seasons of *A. marina* and *A. defodiens* can cause spawning to overlap (Watson et al. 2008). Attempts to cross-fertilize the two latter species in the laboratory (Watson et al. 2008) found that an advance or delay in spawning by a few weeks resulted in a significant reduction in the numbers of competent larvae produced. In addition, an asymmetrical gamete incompatibility either prevented fertilization or the development of the resultant larvae in most cases. Those hybrid larvae that did result were only grown for 5 days, and it was unclear as to whether they would develop intermediate characteristics or be fertile on maturity. Previous studies on populations in the field (Cadman and Nelson-Smith 1990, 1993, Cadman 1997) did not indicate whether intermediate forms or hybrids were present.

Only one species of Arenicolidae, *Abarenicola vagabunda*, has been found to have "simple" broadcast spawning (Rouse 1992), thereafter the eggs become adhesive and stick to the sand (Guberlet 1934 as *A. claparedii*). Extratubular brooding in the form of a jelly mass (Fig. 7.7.5.5B) is exhibited by both *Arenicola brasiliensis* and *A. cristata* (Rouse 1992). In *A. brasiliensis*, larvae develop to three or more chaetigers within the mass before dispersing for a brief pelagic phase, settling by five chaetigers and able to feed at seven chaetigers (Okada 1941, Wu and Sun 1979, Bailey-Brock 1984, Rouse 1992). The remaining species utilize intratubular brooding (Rouse 1992), although few specifics of brooding have been published, except for the detailed study by Okuda (1946) on *Abarenicola pacifica*, wherein the fertilized eggs form a gelatinous "egg tube" around the body of the female. In the other species, larvae hatch at the 1- to 4-chaetiger stage and may have a short, nonfeeding, pelagic phase before settling a few days later with feeding possible from about 6 to 7 chaetigers (*Abarenicola claparedii* (see Ashworth 1904 as *Arenicola pusilla*), *Arenicola cristata* (see Wilson 1883, Okada 1941), *Abarenicola pacifica* (see Okuda 1946 as *A. claparedii*), and *Arenicola brasiliensis* (see Bailey-Brock 1984)). Newell (1948) cast doubt on previous suggestions (Thamdrup 1935) that *Arenicola marina* larvae had a pelagic phase with further evidence published in 1949 of 3- to 4-chaetiger larvae that were already benthic. Farke and Berghuis (1979b), in observations on populations of *A. marina* in the western Wadden Sea, found 0- to 3-chaetiger larvae both in and around burrows, but later larval stages (> 3 chaetigers) were found to migrate into sheltered areas where juvenile and adult lugworms were absent, suggesting at least a brief pelagic phase where tidal currents transport the larvae to such "nursery" areas. After further development, postlarvae were found to secrete a gelatinous tube and migrate, via passive transport by water currents (reported from laboratory experiments and plankton hauls) (Benham 1893, Farke and Berghuis 1979a, b), and resettle in those areas inhabited by juveniles and adults. Proboscis, stomach, gut, and anus are developed by the 5-chaetiger stage, implying that feeding is possible (Farke and Berghuis 1979a). In *Arenicolides ecaudata*, eggs are also both released and fertilized within the burrow, but larvae hatch at the 1-chaetiger stage, do not appear to have any pelagic phase, and can feed by the 4-chaetiger stage (Southward and Southward 1958).

Despite differences in the rate of development, early ciliated larvae of *Arenicola*, *Abarenicola*, and *Arenicolides* have the same form, with a well-developed prototroch and telotroch with long cilia and a ventral neurotroch between with shorter cilia (Fig. 7.7.5.6A–D). The ciliary trochs diminish as the larvae metamorphose and become benthic, being completely lost in *Arenicola brasiliensis* by the 6-chaetiger stage (Okuda 1943, Bailey-Brock 1984). The precise stage of loss is not detailed for *Arenicola* or *Arenicolides* but likely occurs at around the same stage or slightly earlier (Newell 1949, Southward and Southward 1958). Southward and Southward (1958) found that the larvae of *Arenicolides ecaudata* were slow to develop compared to those of other species of *Arenicola* (and *Abarenicola*) but that otherwise those of all species were very much alike.

Little is known about the reproductive biology of *Branchiomaldane* beyond the early studies published by Mesnil (1898) and Ashworth (1912a, b). It is the only genus within Arenicolidae known to be hermaphroditic, although

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this has only truly been confirmed for the original species described, *Branchiomaldane vincenti*. Reproduction has not been detailed for the other three described species. Oocytes are released from the gonads directly into the coelomic fluid where they grow to maturity (Ashworth 1912a, b). When mature, the "milk-white" eggs are 200 × 300 µm in size and markedly fewer in relation to body size than for *Arenicola* Mesnil, 1898. Ashworth reported a mature specimen found to contain about 120 eggs, judged at nearly the maximum the body could contain. Unlike the other Arenicolidae, which spawn via the nephridia, release is via rupture of the body wall in the posterior. Spermatogenesis was reported to be similar to that in *Arenicola* with all stages of spermatozoa present at any time in the coelom. As with many of the other Arenicolidae, *B. vincenti* exhibits intratubular brooding, but larvae undergo direct development with 4-chaetiger larvae hatching from eggs found around the tubes of adult worms and remaining benthic (Mesnil 1899).

In those lugworm species studied, branchiae begin to develop once the juveniles have attained the full number of adult chaetigers and the caudal region has started development, although it may take several months before all pairs have appeared (Benham 1893, Ashworth 1912b, Bailey-Brock 1984). Bailey-Brock (1984) found that, in *Arenicola brasiliensis*, the full complement of adult chaetigers was developed by 6.5 weeks along with the start of a caudal region (Fig. 7.7.5.6E), statocysts and internal organs by 10.5 weeks (Fig. 7.7.5.6F), and branchiae by 14.5 weeks. Burrowing is possible once the proboscis is fully eversible, and *A. brasiliensis* larvae began to burrow from the 7-chaetiger stage (Bailey-Brock 1984). In *Arenicolides* (see Ashworth 1912b) and *Branchiomaldane* (see Mesnil 1899), branchiae begin development before the worm attains the full number of segments.

Associations with other species

Commensal species

Several species of the pea crab *Pinnixa* have been reported as having commensal association with *Abarenicola* and *Arenicola* species. *Pinnixa eburna* Wells, 1928 and *Pinnixa schmitti* Rathbun, 1918 have been reported as cohabiting with *Abarenicola pacifica* and *Abarenicola vagabunda* in False Bay, WA, USA (Wells 1959), whereas *Austinixa cristata* Rathbun, 1900, *Pinnixa cylindrica* Say, 1818, and *Pinnixa retinens* Rathbun, 1918 have all been recorded from *A. cristata* burrows in the Gulf of Mexico (Britton and Morton 1989).

Certain scaleworm species have also been reported as living in *Arenicola marina* burrows: *Malmgrenia arenicolae* Saint-Joseph, 1888 (Hartmann-Schröder 1996 as *Malmgreniella*; Chambers and Muir 1997), *Malmgrenia lunulata* Chiaje, 1830 (MBA 1957 as *Harmothoe*; Hartmann-Schröder 1996 as *Malmgreniella*), *Bylgides sarsi* (Kinberg in Malmgren, 1866) (as *Antinoella sarsi*: Wolff 1973, Reise 2002), *Gattyana cirrhosa* Pallas, 1766 (Newell 1954, Jepsen 1965), *Lepidonotus squamatus* Linnaeus, 1758 (Newell 1954), *Lepidonotus clava* Montagu, 1808 (Newell 1954), and *Harmothoe longisetis* Grube, 1863 (Newell 1954, MBA 1957, Hartmann-Schröder 1971). Some records of the latter may, however, be confused with *Harmothoe glabra* (Malmgren, 1866) due to the misapplication of the name (Tebble and Chambers 1982).

The copepod *Clausia antiqua* Kim, 2001 was described from intertidal sands in Korea, living in association with *Arenicola brasiliensis* (see Kim 2001). All members of the Clausiidae family live in association with polychaetes



Fig. 7.7.5.5: A, Sperm puddles of *Arenicola marina* (courtesy of G. Watson); B, Egg mass of *Arenicola* sp., showing size (top) and attachment into the sediment (bottom) (courtesy of P. Barfield).

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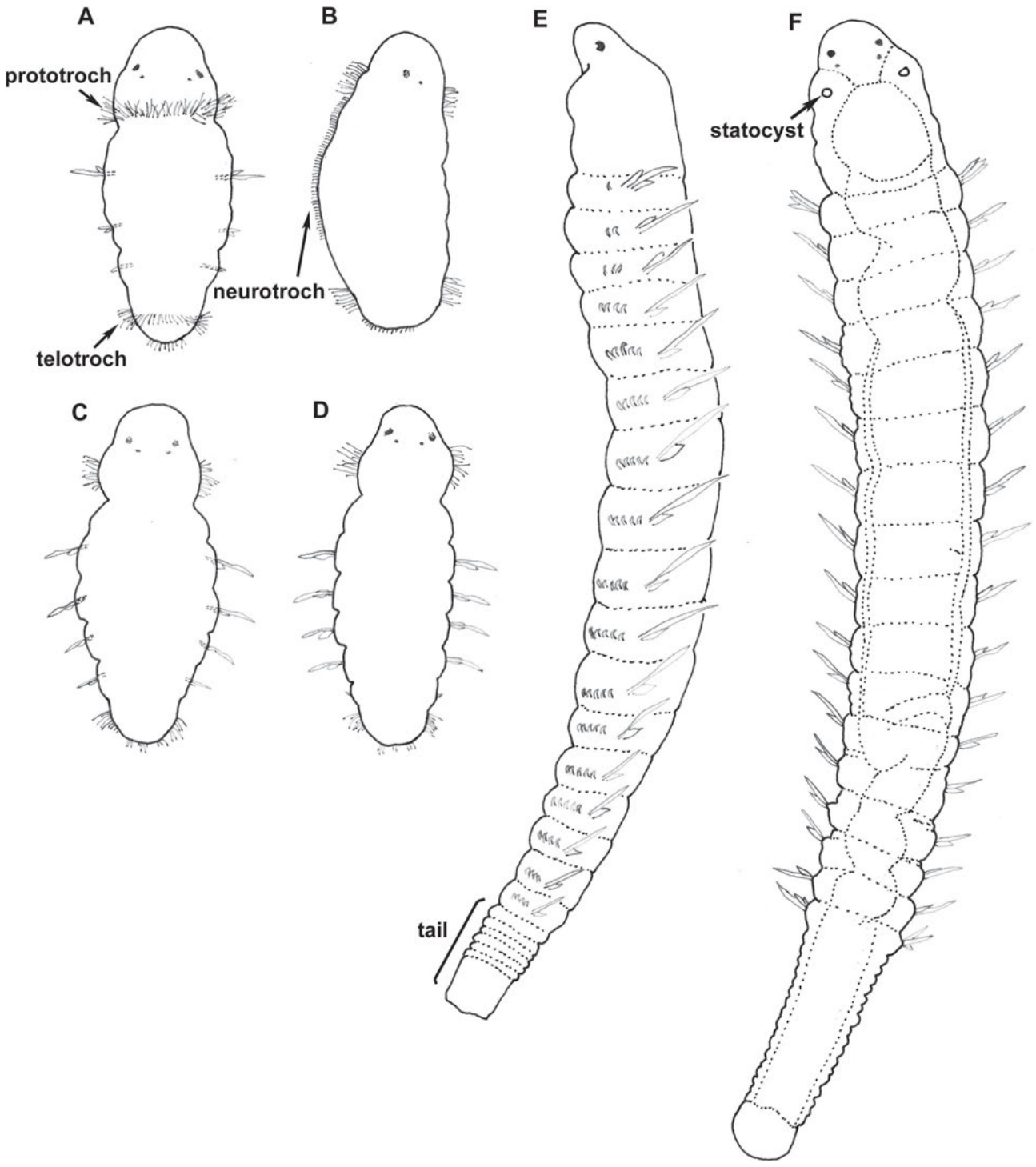


Fig. 7.7.5.6: Progression of larval development of *A. brasiliensis* (redrawn from Bailey-Brock 1984): A, Newly released 3-chaetiger larva, dorsal view; B, As A, lateral view, chaetae omitted; C, 4-chaetiger larva; D, Early 5-chaetiger larva; E, Early 17-chaetiger stage; F, 10.5-week-old juvenile with statocysts, dorsal view. Lengths: A–D, 0.35 to 0.4 mm; E, 2.0 mm; F, 5 to 6 mm. Reprinted from Bailey-Brock 1984, fig. 2 (A–D), fig. 4C (E), and fig. 5A (F), with permission from the Linnean Society of New South Wales. See reference list for full citation.

(Ho and Kim 2003), although *C. antiqua* was the first to be recorded among Arenicolidae. No further details of the association were given in the paper.

There have been several records of protists associating with species of Arenicolidae, some benign and some parasitic. The ciliate *Rhabdostyla arenicola* Fabre-Domergue,

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1888 was described from the gills of *Arenicola marina* in France (Cuénot 1891) and the United Kingdom (Southward and Southward 1958) but has also been recorded from the branchiae of *Arenicola branchialis* (Southward and Southward 1958). The association appears to have no adverse effect on the host and can therefore be viewed as epizooic or commensal (Southward and Southward 1958).

Parasites

Internal sporozoan parasites have been recorded from *Arenicolides ecaudata* in Plymouth, UK (Cunningham 1907, Goodrich and Pixell-Goodrich 1920, Southward and Southward 1958). Trophozoites of *Gonospora arenicolae* Cunningham, 1907 live attached to the nephridia of both sexes of *A. ecaudata*, and trophozoites of *Gonospora minchini* Goodrich & Pixell-Goodrich, 1920 can infect and reside within oocytes that have been released from the gonads into the coelom (Southward and Southward 1958). Although the trophozoites of *G. arenicolae* do not appear to affect gamete development, the growth and release of those of *G. minchini* destroys the oocytes affected (Southward and Southward 1958).

Phylogeny and taxonomy

Phylogeny

Historically, Arenicolidae have been consistently placed with Maldanidae in phylogenetic analyses using morphological (Bartolomaeus and Meyer 1997, Rouse and Fauchald 1997, Rouse and Pleijel 2001, Bartolomaeus et al. 2005, De Assis and Christoffersen 2011) or molecular data (Bleidorn et al. 2003, 2005, Weigert et al. 2014) or a combination of the two (Zrzavý et al. 2009). However, which families or groups may form a sister-group relationship with an Arenicolidae-Maldanidae clade have been debated. Morphological analyses have often placed Capitellidae as the sister group to both Arenicolidae and Maldanidae based on internal morphology (Orrhage 1973, Dales 1977, Tzetlin and Purschke 2005); however, investigations of chaetal morphology and development (Bartolomaeus and Meyer 1997, Bartolomaeus 1998, Hausen 2001, Bartolomaeus et al. 2005) have proposed a closer relationship to Psammodrilidae, with Capitellidae in a completely separate clade. This relationship was also observed by De Assis and Christoffersen in their 2011 morphological analysis of Maldanidae in which they also confirmed the relationship between Arenicolidae and Maldanidae using the characters of inverted formative site of tori, a larger number of denticules on *capitium*, and capillary notochaetae with an ornamented limb as apomorphies. Molecular analyses by Bleidorn et al. (2003) and Persson and Pleijel (2005) both suggested a possible sister-group relationship with Scalibregmatidae. In 2007, using both nuclear and mitochondrial genes, Struck et al. proposed a phylogeny that, once again, recovered Capitellidae, along with Echiurida, as a sister group to Arenicolidae-Maldanidae. The same relationship was recovered by Zrzavý et al. (2009) using both morphological and molecular data, although some trees included Terebelliformia as well. Most recently, Weigert et al. (2014) similarly recovered a Terebelliformia sister-group relationship for Arenicolidae (Maldanidae were not included in the analysis) but placed Capitellidae elsewhere.

Within Arenicolidae itself, only the placement of the genus *Branchiomaldane* has been particularly debated. In his original description, Langerhans (1881) placed *Branchiomaldane* with *Arenicola* in Telethusae (Arenicolidae) but stated that it showed "unmistakeable" affinity with Maldanidae. Both Fauvel (1899) and Mesnil (1899) viewed it as a juvenile stage of *Arenicola*, but Ashworth (1912a) resurrected the genus within Arenicolidae. Berkeley and Berkeley (1932) described a new species of *Branchiomaldane* within Capitellidae as *Protocapitella simplex* Berkeley & Berkeley, 1932, although the species was later transferred to *Branchiomaldane* (Berkeley and Berkeley 1950, Fournier and Barrie 1987). Despite remaining in the family, the position of the genus has continued to be uncertain. In 2001, Rouse and Pleijel suggested that *Branchiomaldane* may either belong within Maldanidae or that its position may make Arenicolidae paraphyletic. However, a molecular study of the family by Bleidorn et al. (2005, fig. 7) showed strong support for the inclusion of *Branchiomaldane* within Arenicolidae as a monophyletic genus, substantiated morphologically by hermaphroditism, reduction of nephridia, and an extreme elongation of the caudal nephridia. A hypothesis of the progenetic evolution for the genus has been proposed (Bartolomaeus and Meyer 1998, Bleidorn et al. 2005) as explanation for the presence of the genus in the family and the persistent juvenile characters exhibited. Its relationship with the other genera is, however, unclear. With regard to the other genera, all were recovered as monophyletic (Bleidorn et al. 2005), although only *Abarenicola* received strong support. The monophyly of *Arenicola* received no bootstrap support, whereas *Arenicolides* was represented by only one species. An updated analysis of the data by Darbyshire (2017), including three additional species, recovered a similar tree topology, also with strong support for the monophyly of the family as a whole and within that *Abarenicola*, but not *Arenicola*, as monophyletic genera.

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Taxonomy

Fossil records

Three fossil specimens from the same area were attributed to Arenicolidae by Horwood in 1912, although doubts have been casted on their validity. *Archarenicola rhaetica* Horwood, 1912, the only "Arenicolidae" fossils known, were discovered in Leicestershire, UK, in 1910 in Lower Rhaetic black shales. The deposits date them to the Rhaetian period of the late Triassic (209–201 million years ago). Although the specimens were not found *in situ*, Horwood stated that burrows, which he believed "undoubtedly" belonged to them, were commonly found in the area from which the material came (Horwood 1911, 1912). He provided a detailed description of the specimens and a strong argument for their placement in Arenicolidae. According to Horwood (1912), the fossils showed evidence of chaetae, a papillated epidermis, and brown staining around the specimens that he attributed to an exudate "such as that exhibited by modern lugworms" (Fig. 7.7.5.8). The fossils, are however, now considered more likely to be trace evidence of worm activity rather than fossils of actual worms (M. Evans, curator of Leicester Museum, personal communication).

More recently, annulated worm-like fossils were described from China by Wang (1982) and Hong et al. (1991) and comprised five species within three genera: *Pararenicola* Wang, 1982, *Protoarenicola* Wang, 1982, and *Pseudoarenicola* Liu & Huang, 1991. All were later placed into the fossil family Protoarenicolidae Hofmann, 1994. Dating back to the Neoproterozoic period of the Pre-Cambrian (541–1000 million years ago), these would not only be some of the earliest known polychaete fossils (Rouse and Pleijel 2001) but also the earliest bilaterian animals

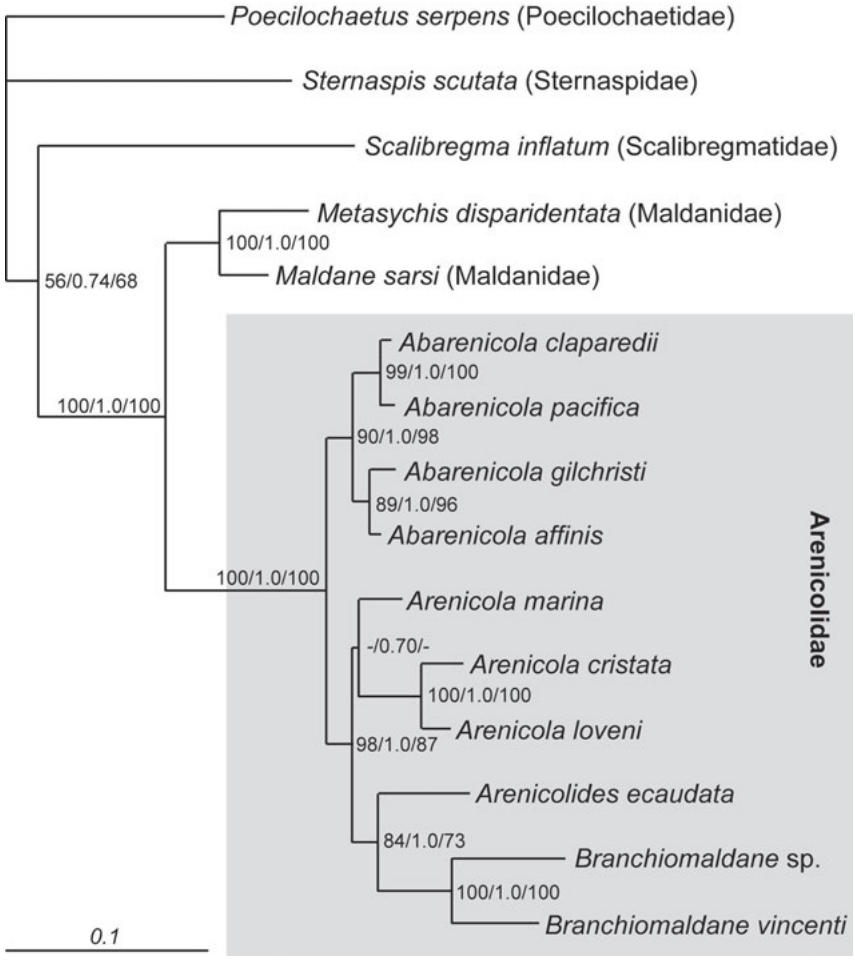


Fig. 7.7.5.7: Phylogenetic tree of relationships within Arenicolidae (Bleidorn et al. 2005). First value at the node represents the maximum likelihood bootstrap support, second represent Bayesian posterior probabilities, and third represent the maximum parsimony bootstrap support. Reprinted from Bleidorn et al. 2005, fig. 2, with permission from Elsevier. See reference list for full citation.

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(Dong et al. 2008). Despite their given names, they were not specifically attributed to any known living group; in 2008, Dong et al. cast doubt on the identification of the fossils as animals, instead reinterpreting the forms as "erect epibenthic organisms", possibly algae. Many of the fossils were found to be incompletely preserved or with no diagnostic features, and some were determined to be invalid or were synonymized (Dong et al. 2008).

Extant species

Family Arenicolidae Johnston, 1835

Type genus: *Arenicola* Lamarck, 1801

Synonyms: Telethusae Savigny, 1820; Arénicoliens Audouin & Edwards, 1833

Diagnosis (Wells 1959): Polychaeta of elongate, cylindrical form. The achaetous anterior region or "head" is composed of a prostomium without tentacles or palps, a peristomium without cirri, and another achaetous segment. The chaetigers follow, each divided into secondary annuli, one of which is the chaetigerous annulus and bears on each side a notopodium with capillary chaetae and a neuropodium with a single row of crotchets. In some species, the number of chaetigers is restricted, usually to 19, and the remaining segments are specialized to form an achaetous "tail". Gills are borne, in the adult, on a number of successive chaetigers. The eversible proboscis is jawless. Glandular ceca, one pair or more, are present on the posterior part of the esophagous. There is a single pair of hearts, at the sides of the junction of the esophagous and the stomach. Coelomic septa have disappeared from many consecutive segments in the middle region of the body but are present at the anterior border of the first, third, and fourth chaetigers and also to a greater or less extent in the intestinal region. In many species, the first septum bears a pair of backwardly projecting septal pouches. Nerve cord not ganglionated.

Genus *Abarenicola* Wells, 1959 (Fig. 7.7.5.9A)

Type species: *Arenicola claparedii* Levinsen, 1884

11 species.

Diagnosis (Wells 1959): Arenicolidae with an achaetous tail. Prostomium nonretractile, in the form of a

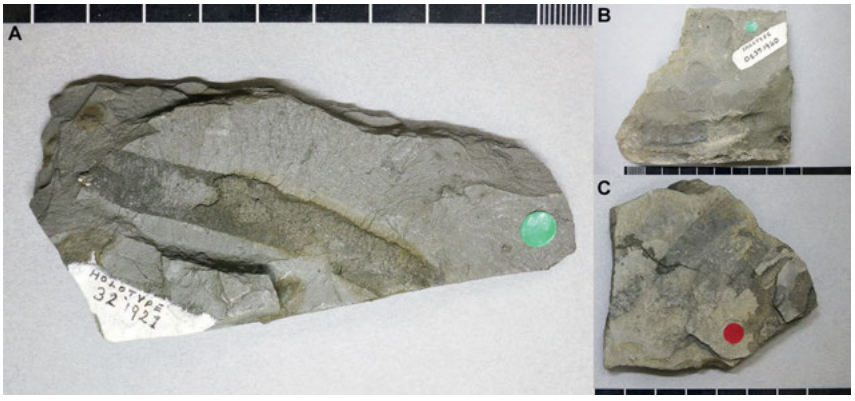


Fig. 7.7.5.8: Fossil-type specimens of *Archarenicola rhaetica* (Leicester Arts & Museum Service): A, Holotype, G.32.1921; B, Paratype, G.37.1960; C, Paratype, G.38.1960.

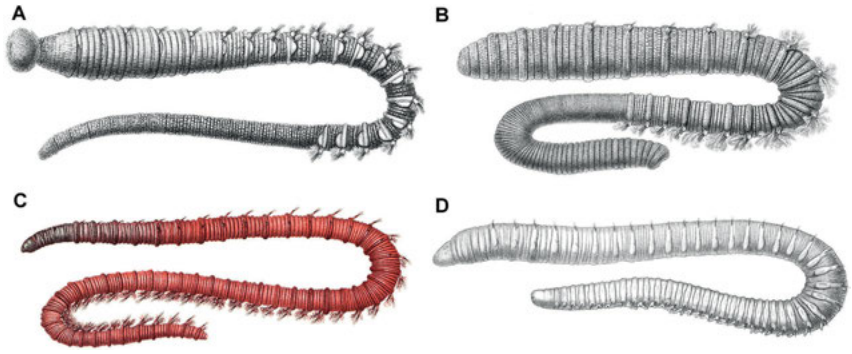


Fig. 7.7.5.9: Drawings from Ashworth 1912b: A, *Abarenicola assimilis*; B, *Arenicola loveni*; C, *Arenicolides ecaudata*; D, *Branchiomaldane vincenti*.

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triangle with lateral extensions of its (anterior) base; with a shallow groove marking the attachment of the brain. Statocysts either present, with a tube to the exterior, or absent. Chaetigers (except the first two or three) subdivided into five annuli. Gills branched, the first (which may be reduced or absent) on chaetiger 7 or 8. None of the neuropodia approaches close to the midventral line. Esophageal ceca more than one pair. Gular membrane very thin; septal pouches absent. Nephridia five or six pairs, the first opening on chaetiger 4 or 5. Dioecious; gonads on the nephridia.

Genus *Arenicola* Lamarck, 1801 (Fig. 7.7.5.9B)
Type species: *Lumbricus marinus* Linnaeus, 1758
Synonyms: *Chorizobranchus* Quatrefages, 1866
7 species.
Diagnosis (Wells 1959): Arenicolidae with an achaetous tail. Prostomium small, retractile, in the form of a triangle with the rounded base anterior; with a shallow groove marking the attachment of the brain. Statocysts present, with or without a tube to the exterior. Chaetigers (except the first two or three) subdivided into five annuli. Gills branched, the first (which may be reduced or absent) on chaetiger 7. The neuropodia of the hinder branchiate segments but not those of the more anterior segments, approach close to the midventral line. One pair of esophageal ceca, opening by separate ducts. Septal pouches present. Nephridia five to seven pairs, the first opening on chaetiger 4 or 5. Dioecious; gonads on the nephridia.

Genus *Arenicolides* Mesnil, 1898
Type species: *Arenicola ecaudata* Johnston, 1865 (Fig. 7.7.5.9C)
2 species.
Diagnosis (Wells 1959): Arenicolidae without an achaetous tail. Prostomium a nonretractile transverse band; brain large, transversely elongated. Statocysts present, without a tube leading to the exterior. Chaetigers (except the first two or three) subdivided into five annuli. Gills branched, the first (which may be reduced or absent) on chaetiger 12 or 16. All the neuropodia approach close to the midventral line. One pair of esophageal ceca, opening by separate ducts. Septal pouches present. Nephridia 5 or 13 pairs, the first opening on chaetiger 15. Dioecious; gonads on the nephridia.

Genus *Branchiomaldane* Langerhans, 1881
Type species: *Branchiomaldane vincenti* Langerhans, 1881, monotypic (Fig. 7.7.5.9D)
4 species.
Diagnosis (Nogueira and Rizzo 2001): Small worms, with unpigmented short body. Prostomium conical to round, usually provided with ocelli, scattered or coalesced in groups; lensed eyes present in one species, and in juveniles of two other species, at least. Peristomium fused to next segment, achaetous. Notopodia provided with capillary chaetae, neuropodia widely separated in the ventral side, with few long-handled hooked chaetae, each with hook to laterally directed rostrum and capitium with three to four rows of smaller teeth. Anterior segments abranchiate, posterior segments bearing one to five branchial filaments, and divided into annuli. Posterior achaetigerous region reduced to a few segments or totally absent; pygidium without appendages, entire or with rounded lobes.

References

Ashworth, J.H. (1903): The anatomy of *Arenicola assimilis* Ehlers, and of a new variety of the species, with some observations on the post-larval stages. *Quarterly Journal of Microscopical Science* 46: 737–783.

Ashworth, J.H. (1904): Memoir on *Arenicola*. The lugworm. *Proceedings and Transactions of the Liverpool Biological Society* 18: 209–326.

Ashworth, J.H. (1912a): Observations on the structure and affinities of *Branchiomaldane vincenti* Langerhans. *Proceedings of the Royal Society of Edinburgh* 32: 62–72.

Ashworth, J.H. (1912b): *Catalogue of the Chaetopoda in the British Museum*. A. *Polychaeta: Part 1. Arenicolidae*. British Museum of Natural History, London.

Ashworth, J.H. (1916): On the occurrence of *Arenicola loveni* Kinberg on the coast of South Australia. *Transactions of the Royal Society of South Australia* 40: 38–41.

Audouin, J.V. & Milne Edwards, H. (1833): Classification des Annélides et description de celles qui habitent les côtes de la France. *Annales des sciences naturelles, Paris. sér. 1*, 30: 411–425.

Bailey-Brock, J.H. (1984): Spawning and development of *Arenicola brasiliensis* (Nonato) in Hawaii (Polychaeta; Arenicolidae). In: Hutchings, P.A. (ed.), *Proceedings of the First International Polychaete Conference*, The Linnean Society of New South Wales, Sydney: 439–449.

Bartolomaeus, T. (1998): Chaetogenesis in polychaetous Annelida — Significance for annelid systematics and the position of the Pogonophora. *Zoology* 100: 348–364.

Bartolomaeus, T. & Meyer, K. (1997): Development and phylogenetic significance of hooked setae in Arenicolidae (Polychaeta, Annelida). *Invertebrate Biology* 116: 227–242.

Bartolomaeus, T., Purschke, G. & Hausen, H. (2005): Polychaete phylogeny based on morphological date: A comparison of current attempts. *Hydrobiologia* 535/536: 341–356.

Benham, W.B. (1893): The post-larval stages of *Arenicola marina* L. *Journal of the Marine Biological Association of the U.K.* 3: 48–53.

Bentley, M.G. (1985): Sperm maturation response in *Arenicola marina* (L.): *In vitro* assay for sperm maturation factor and its partial purification. *Invertebrate Reproduction and Development* 8: 139–148.

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Bentley, M.G. & Hardege, J.D. (1996): The role of a fatty acid hormone in the reproduction of the polychaete *Arenicola marina* (L.). *Invertebrate Reproduction and Development* 30: 159–165.

Bentley, M.G., Clark, S. & Pacey, A.A. (1990): The role of arachidonic acid and eicosatrienoic acids in the activation of spermatozoa in *Arenicola marina* L. (Annelida: Polychaeta). *Biological Bulletin* 178: 1–9.

Berkeley, E. & Berkeley, C. (1932): Some Capitellidae (Polychaeta) from the northeast Pacific with a description of a new genus. *Proceedings of the Zoological Society of London* 1932: 669–675.

Berkeley, E. & Berkeley, C. (1950): Notes on Polychaeta from the coast of western Canada. IV. Polychaeta Sedentaria. *Annals and Magazine of Natural History* 3: 50–69.

Beukema, J.J. & de Vlas, J. (1979). Population parameters of the lugworm, *Arenicola marina* living on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 13: 331–353.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003): New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 29: 279–288

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2005): Molecular phylogeny of lugworms (Annelida, Arenicolidae) inferred from three genes. *Molecular Phylogenetics and Evolution* 34: 673–679

Braunbeck, T. & Dales, R.P. (1985): The ultrastructure of the heart-body and extravasal tissue in the polychaete annelid *Neoamphitrite figulus* and *Arenicola marina*. *Journal of the Marine Biological Association of the U.K.* 65: 653–662.

Britton, J.C. & Morton, B. (1989): *Shore ecology of the Gulf of Mexico*. University of Texas Press: 1–396.

Buddenbrock, W. von. (1912): Über die Funktion der Statozysten im Sande grabender Meerestiere (*Arenicola* und *Synapta*). *Biologisches Centralblatt* 32: 564–585.

Buddenbrock, W. von. (1913): Über die Function der Statozysten im Sande grabender Meerestiere, II. Zoologische Jahrbücher. *Abteilung fuer Allgemeine Zoologie und Physiologie der Tiere* 33: 441–482.

Cadée, G.C. (1976): Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Netherlands Journal for Sea Research* 10: 440–460.

Cadman, P.S. (1997): Distribution of two species of lugworm (*Arenicola*) (Annelida: Polychaeta) in South Wales. *Journal of the Marine Biological Association of the U.K.* 77: 389–398.

Cadman, P.S. & Nelson-Smith, A. (1990): Genetic evidence for two species of lugworm (*Arenicola*) in South Wales. *Marine Ecology Progress Series* 64: 107–112.

Cadman, P.S. & Nelson-Smith, A. (1993): A new species of lugworm: *Arenicola defodiens* sp. nov. *Journal of the Marine Biological Association of the U.K.* 73: 213–223.

Campbell, A.L., Mangan, S., Ellis, R.P. & Lewis, C. (2014): Ocean acidification increases copper toxicity to the early life history stages of the polychaete *Arenicola marina* in artificial seawater. *Environmental Science & Technology* 48: 9745–9753.

Casado-Martinez, M.C., Smith, B.D. & Rainbow, P.S. (2013): Assessing metal bioaccumulation from estuarine sediments: Comparative experimental results for the polychaete *Arenicola marina*. *Journal of Soils and Sediments* 13: 429–440.

Chambers, S.J. & Muir, A.I. (1997): Polychaetes: British Chrysopetaloidea, Pisionoidea and Aphroditoidea. In: Barnes, R.S.K. & Crothers, J.H. (eds.): *Synopses of the British Fauna*. No. 54. Field Studies Council, Telford.

Chapman, G. & Newell, G.E. (1947): The role of the body fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola*. *Proceedings of the Royal Society B, Biological Sciences* 134: 431–455.

Chiaje, S. delle (1822 [1830]): *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*. Atlas. Napoli, 109 plates.

Crane, R.L. & Merz, R.A. (2017): Mechanical properties of sediment determine burrowing success and influence distribution of two lugworm species. *Journal of Experimental Biology* 220: 3248–3259.

Cuénot, L. (1891): Infusoires commensaux des Ligies, Patelles et Arénicoles. *Revue Biologique de Nord de la France* 3: 81–89.

Cunningham, J.J. (1907): On *Kalpidorhynchus arenicolae*, a new gregarine, parasitic in *Arenicola ecaudata*. *Arch. Protistenk*. 10: 199–215.

Dales, R.P. (1963): Pigments in the skins of the polychaetes *Arenicola*, *Abarenicola*, *Dodecaceria* and *Halla*. *Comparative Biochemistry and Physiology* 8: 99–108.

Dales, R.P. (1977): The polychaete stomodeum and phylogeny. *Essays on polychaetous annelids in memory of Dr. Olga Hartman. Los Angeles Allan Hancock Foundation* 23: 525–546.

Dales, R.P. & Cummings, M.O. (1987): The ultrastructure of the heart-body of the lugworm, *Arenicola marina*. *Journal of the Marine Biological Association of the U.K.* 67: 647–652.

Darbyshire, T. (2017): A re-evaluation of the *Abarenicola assimilis* group with a new species from the Falkland Islands and key to species. In: Holmes, A.M., Darbyshire, T., Mortimer, K. & Mackie, A.S.Y. (eds): Proceedings of the 12th International Polychaete Conference, Cardiff, Wales, 2016. *Journal of the Marine Biological Association of the U.K.* 97: 897–910.

Day, J.H. (1955): The Polychaeta of South Africa. Part 3. Sedentary species from Cape shores and estuaries. *Journal of the Linnean Society of London, Zoology* 42: 407–452.

Day, J.H. (1967): *A Monograph on the Polychaeta of South Africa. Part 2. Sedentaria.* British Museum of Natural History, London.

De Assis, J.E. & Christoffersen, M.L. (2011): Phylogenetic relationships within Maldanidae (Capitellida, Annelida), based on morphological characters. *Systematics and Biodiversity* 9: 233–245.

de Vlas, J. (1979): Secondary production by tail regeneration in a tidal flat population of lugworms (*Arenicola marina*), cropped by flatfish. *Netherlands Journal for Sea Research* 13: 362–393.

Dong, L., Xiao, S., Shen, B., Yuan, X., Yan, X. & Peng, Y. (2008): Restudy of the worm-like carbonaceous compression fossils *Protoarenicola*, *Pararenicola*, and *Sinosabellidites* from early Neoproterozoic successions in North China. *Palaeogeography Palaeoclimatology Palaeoecology* 258: 138–161.

Duncan, A. (1960): The spawning of *Arenicola marina* (L.) in the British Isles. *Journal of Zoology* 134: 137–155.

Farke, H. & Berghuis, E.M. (1979a): Spawning, larval development and migration behaviour of *Arenicola marina* in the laboratory. *Netherlands Journal of Sea Research* 13: 512–528.

Farke, H. & Berghuis, E.M. (1979b): Spawning, larval development and migration of *Arenicola marina* under field conditions in the western Wadden Sea. *Netherlands Journal of Sea Research* 13: 529–535.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193–284.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Fauvel, P. (1899): Sur les stades *Clymenides* et *Branchiomaldane* des Arénicoles. *Bulletin scientifique de la France et de la Belgique* 32: 283–316.

Fauvel, P. (1907): Recherches sur les otocystes des Annélides Polychètes. *Annales des sciences naturelles, Paris* 6: 1–149.

Flach, E.C. & Beukema, J.J. (1994): Density-governing mechanisms in populations of the lugworm *Arenicola marina* on tidal flats. *Marine Ecology Progress Series* 115: 139–149.

Fournier, J.A. & Barrie, J. (1987): Revisionary commentary on *Branchiomaldane* (Polychaeta: Arenicolidae) with description of a new species from Labrador. *Bulletin of the Biological Society of Washington* 7: 97–107.

Gamble, F.W. & Ashworth, J.H. (1898): The habits and structure of *Arenicola marina*. *Quarterly Journal of Microscopical Science* 41: 1–42.

Gamble, F.W. & Ashworth, J.H. (1900): The anatomy and classification of the Arenicolidae, with some observations on their postlarval stages. *Quarterly Journal of Microscopical Science* 43: 419–569.

Goodrich, E.S. & Pixell-Goodrich, H. (1920): *Gonospora minchini* n. sp., a gregarine inhabiting the egg of *Arenicola*. *Quarterly Journal of Microscopical Science* 65: 157–162.

Green, D.S., Boots, B., Sigwart, J., Jiang, S. & Rocha, C. (2016): Effects of conventional and biodegradable microplastics on a marine ecosystem engineer (*Arenicola marina*) and sediment nutrient recycling. *Environmental Pollution* 208: 426–434.

Grossmann, S. & Reichardt, W. (1991): Impact of *Arenicola marina* on bacteria on intertidal sediments. *Marine Ecology Progress Series* 77: 85–93.

Grube, A.-E. (1863): Beschreibung neuer oder wenig bekannter Anneliden. Sechster Beitrag. *Archiv für Naturgeschichte, Berlin* 29: 37–69, pl. 4–6.

Guberlet, J.E. (1934): Observations on the spawning and development of some Pacific annelids. *Proceedings of the 5th Pacific Science Congress* 5: 4213–4220.

Harnois, T., Rousselot, M., Rogniaux, H. & Zal, F. (2009): High-level production of recombinant *Arenicola marina* globin chains in *Escherichia coli*: A new generation of blood substitute. *Artificial Cells, Blood Substitutes and Biotechnology* 37: 106–116.

Hartmann-Schröder, G. (1971): *Annelida, Borstenwürmer, Polychaeta. Vol. 58. Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise.* Gustav Fischer, Jena: 1–594.

Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise*. Vol. 58. 2nd ed. Gustav Fischer. Jena: 1–648.

Hausen, H. (2001): *Untersuchungen zur Phylogenie "spiomorpher" Polychaeten (Annelida)*. Logos, Berlin: 1–142.

Healy, E.H. & Wells, G.P. (1959) Three new lugworms (Arenicolidae, Polychaeta) from the North Pacific area. *Proceedings of the Zoological Society of London* 133: 315–335.

Hiddinck, J.G., ter Hofstede, R. & Wolff, W.J. (2002): Predation of the endobenthic invertebrates *Nereis diversicolor* and *Arenicola marina* on *Macoma balthica* Spat. *Netherlands Journal for Sea Research* 47: 141–159.

Ho, J.-S. & Kim, I.-H. (2003): New clausiid copepods (Poecilostomatoida) associated with polychaetes of Korea, with cladistics analysis of the family Clausiidae. *Journal of Crustacean Biology* 23: 568–581.

Hobson, K.D. (1967): The feeding and ecology of two north pacific *Abarenicola* species (Arenicolidae, Polychaeta). *Biological Bulletin* 133: 343–354.

Hofmann, H.J. (1994): Proterozoic carbonaceous compressions ("metaphytes" and "worms"). In: Bengtson, S. (ed.) *Early Life on Earth.* Columbia University, New York: 342–357.

Hong, Z., Huang, Z. & Liu, X. (1991): *Upper Precambrian geology in southern Liaodong Peninsula.* China Ministry of Geology and Mineral Resources Geological Memoirs Series 2, vol. 14: 1–189.

Horwood, A.R. (1911): On some new Rhaetic fossils from Glen Parva, Leicestershire. *Report of the British Association for the Advancement of Science. 80th/81st meeting, Portsmouth, Transactions of Section C:* 388.

Horwood, A.R. (1912): On *Archarenicola rhaetica* sp. nov. *Geological Magazine* 9: 395–399, pl. 21, figs. 1–4.

Howie, D.I.D. (1959): The spawning of *Arenicola marina* (L.). I. The breeding season. *Journal of the Marine Biological Association of the U.K.* 28: 395–406.

Howie, D.I.D. (1961): The spawning of *Arenicola marina* (L.). II. Spawning under experimental conditions. *Journal of the Marine Biological Association of the U.K.* 41: 127–144.

Howie, D.I.D. (1963): Experimental evidence for the hormonal stimulation and ripening of the gametes and spawning in the polychaete *Arenicola marina* (L.). *General and Comparative Endocrinology* 3: 660–668.

Howie, D.I.D. (1966): Further data relating to the maturation hormone and its site of secretion in *Arenicola marina* (L.). *General and Comparative Endocrinology* 6: 347–361.

Hylleberg, J. (1975): Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola* and a concept of gardening in lugworms. *Ophelia* 14: 113–137.

Imajima, M. (1988): Occurrence of *Branchiomaldane simplex* (Polychaeta, Arenicolidae) from Hokkaido, Japan. *Bulletin of the National Science Museum Tokyo* 14: 23–26.

Jepsen, U. (1965): Die Struktur der Wattenbiozönosen im Vormündungsgebiet der Elbe. *Archiv fur Hydrobiologie* 29: 252–370 (Suppl. Elbe-Aestuar, 2).

Johnston, G. (1835): Illustrations in British Zoology (45 *Lernaea uncinata*, 46 *Arenicola ecaudata*). *Magazine of Natural History and Journal of Zoology, Botany, Mineralogy, Geology and Meteorology* 8: 565–569, figs. 53–54 (x–1835).

Johnston, G. (1865): *A catalogue of the British non-parasitical worms in the collection of the British Museum.* British Museum, London: 1–365.

Jouin, C. & Toulmond, A. (1989): The ultrastructure of the gill of the lugworm *Arenicola marina* (L.) (Annelida, Polychaeta). *Acta Zoologica (Stockholm)* 70: 121–129.

Jouin, C., Tchernigovtzeff, C., Baucher, M.F. & Toulmond, A. (1985): Fine structure of probable mechano- and chemoreceptors in the caudal epidermis of the lugworm *Arenicola marina* (Annelida, Polychaeta). *Zoomorphology* 105: 76–82.

Jumars, P.A. (2000): Animal guts as ideal chemical reactors: maximizing absorption rates. *American Naturalist* 155: 527–543.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Kharkeevitch, T.A. & Titova, L.K. (1974): Electron microscope studies of the structural organization of statocyst of *Arenicola marina*. *Zeitschrift für mikroskopisch-anatomische Forschung* 88: 382–392.

Kim, I.-H. (2001): A new species of *Clausia* (Copepoda, Poecilostomatoida, Clausiidae) associated with the polychaete *Arenicola brasilliensis* Nonato in Korea. *Hydrobiologia* 452: 217–223.

Lamarck, J.-B. (M. de). (1801): *Système des animaux sans vertèbres, ou tableau general des classes, des orders et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'apres la considération de leurs rapports naturelles et de leur organisation, et suivant l'arrangement* établi *dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; Précédé du discours d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République*. published by the author, and Deterville, Paris: pp. VIII + 432 + 8 pl.

Langerhans, P. (1881): Ueber einige canarische Anneliden. *Nova Acta der Kaiserlichen Leopold-Carolin Deutschen Akademie der Naturforscher, Halle*. 42: 95–124.

Levinsen, G.M.R. (1884): Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Köbenhavn* 1883: 92–350.

Lewis, C. (2005a): Fertilization, post-fertilization development and larval biology of the South African polychaete, *Arenicola loveni loveni* (Kinberg 1866). *Invertebrate Reproduction and Development* 48: 19–30.

Lewis, C. (2005b): Aspects of the reproductive biology of the South African polychaete, *Arenicola loveni loveni* (Kinberg 1866). *Invertebrate Reproduction and Development* 48: 147–160.

Lignac, G.O.E. (1945): About arenicochrome and its possible significance as a meso-catalyst. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 48: 406–410.

Linke, O. (1939): Die Biota des Jadebusenwattes. *Helgolander Wissenschaftliche Meeresuntersuchungen* 1: 201–348.

Linnaeus, C. (1758): *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Laurentius Salvius: Holmiae: 1–824.

Linton, D.L. & Taghon, G.L. (2000): Feeding, growth and fecundity of *Abarenicola pacifica* in relation to sediment organic concentration. *Journal of Experimental Marine Biology and Ecology* 254: 85–107.

Malmgren, A.J. (1866): Nordiska Hafs-Annulater. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 22: 355–410.

Marine Biological Association (MBA) (1957): *Plymouth Marine Fauna*, 3rd ed. 1–457.

Meijer, L. (1979a): Hormonal control of oocyte maturation in *Arenicola marina* (L.) (Annelida, Polychaeta). I. Morphological study of oocyte maturation. *Development, Growth and Differentiation* 21: 303-314.

Meijer, L. (1979b): Hormonal control of oocyte maturation in *Arenicola marina* L. (Annelida, Polychaeta). II. Maturation and fertilization. *Development, Growth and Differentiation* 21: 315–329.

Mesnil, F. (1898): Les genres *Clymenides* et *Branchiomaldane* et les stades post-larvaires des arenicoles. *Zoologischer Anzeiger* 21: 630–638.

Mesnil, F. (1899): Les genres *Clymenides* et *Branchiomaldane* et les stades postlarvaires des arenicoles. *Bulletin scientifique de la France et de la Belgique* 32: 317–328.

Montagu, G. (1808): Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London* 9: 81–114, pl. 2–8.

Newell, G.E. (1948): A contribution to our knowledge of the life history of *Arenicola marina* (L.). *Journal of the Marine Biological Association of the U.K.* 27: 554–580.

Newell, G.E. (1949): The later larval life of *Arenicola marina* (L.). *Journal of the Marine Biological Association of the U.K.* 28: 635–639.

Newell, G.E. (1954): The marine fauna of Whitstable. *Annals and Magazine of Natural History* 7: 321–350.

Nicol, J.A.C. (1948): The giant axons of annelids. *The Quarterly Review of Biology* 23: 291–323.

Nogueira, J. M. & Rizzo, A.E. (2001): A new species of *Branchiomaldane* (Polychaeta: Arenicolidae) from the State of Sao Paulo, south-eastern Brazil. *Journal of the Marine Biological Association of the U.K.* 81: 415–421.

Nonato, E. (1958): Sôbre duas Arenicolas da costa Brasileira (Annelida, Polychaeta). *Contribuiçoes Avulsas do Instituto Oceanográfico* 3: 1–6.

Okada, K. (1941): The gametogenesis, the breeding habits, and the early development of *Arenicola cristata* Stimpson, a tubicolous polychaete. *Science Reports of the Tôhoku Imperial University* 16: 99–145.

Okuda, S. (1946): Studies on the development of Annelida Polychaeta I. *Journal of the Faculty of Science, Hokkaido University* 9: 115–219.

Olive, P.J.W. (1993): Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3: 1–24.

Olive, P.J.W. (1994): Polychaeta as a world resource: A review of patterns of exploitation as sea angling baits and the potential for aquaculture based production. *Memoires du Museum National D'Histoire Naturelle* 162: 603–610.

Orrhage, L. (1973): Light electron microscope studies of some brachiopod and pogonophoran setae. With a discussion of the "annelid setae" as a phylogenetic-systematic character. *Zeitschrift für Morphologie de Tiere* 74: 253–270, pls. 1–26.

Pacey, A.A. & Bentley, M.G. (1992a): The fatty acid 8,11,14-eicosatrienoic acid induces spawning in the male lugworm *Arenicola marina*. *Journal of Experimental Biology* 173: 165–179.

Pacey, A.A. & Bentley, M.G. (1992b): An ultrastructural study of spermatogenesis and sperm morula breakdown in *Arenicola marina* (L.) (Annelida: Polychaeta). *Helgoländer Meeresuntersuchungen* 46: 185–199.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Pallas, P.S. (1766): *Miscellanea zoologica. Quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur.* Petrum van Cleef. Hagí Comitum., xii + 224 pp.; 14 pls.

Patel, S. & Spencer, C.P. (1963a): Studies on the haemoglobin of *Arenicola marina*. *Comparative Biochemistry and Physiology* 8: 65–82.

Patel, S. & Spencer, C.P. (1963b): The oxidation of sulphide by the haem compounds from the blood of *Arenicola marina*. *Journal of the Marine Biological Association of the U.K.* 43: 167–175.

Persson, J. & Pleijel, F. (2005): On the phylogenetic relationships of *Axiokebuita*, *Travisia* and Scalibregmatidae (Polychaeta). *Zootaxa* 998: 1–14.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica* 78: 123–143.

Purschke, G. & Tzetlin, A.B. (1996): Dorsolateral ciliary folds in the polychaete foregut: Structure, prevalence and phylogenetic significance. *Acta Zoologica* 77: 33–49.

Purschke, G. (2016): Annelida: Basal groups and Pleistoannelida. In: Schmidt-Rhaesa, A., Harzsch, S. & Purschke, G. (eds.), *Structure and Evolution of Invertebrate Nervous Systems*. Oxford University Press, Oxford: 254–312.

Purschke, G., Arendt, D., Hausen, H. & Müller, M.C.M. (2006): Photoreceptor cells and eyes in Annelida. *Arthropod Structure and Development* 35: 211–230.

Quatrefages, A. de (1866): *Histoire naturelle des Annelés marins et d'eau douce. Annélides et Géphyriens*. Volume 1. Librarie Encyclopédique de Roret. Paris: 1–588.

Rathbun, M.J. (1900): Synopses of North American invertebrates. XI. The catometopous or grapsoid crabs of North America. *American Naturalist* 34: 583–592.

Rathbun, M.J. (1918): The grapsoid crabs of America. *Bulletin of the United States National Museum* 97: 1–461.

Reise, K. (1981): Gnathostomulid abundant alongside polychaete burrows. *Marine Ecology Progress Series* 6: 329–333.

Reise, K. (1985): *Tidal flat ecology: An experimental approach to species interactions.* Ecological Studies 54. Springer, Berlin Heidelberg: 1–194.

Reise, K. (1987): Spatial niches and long-term performance in meiobenthic Platyhelminthes of an intertidal lugworm flat. *Marine Ecology* 38: 1–11.

Reise, K. (2002): Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48: 127–141.

Reise, K. & Ax, P. (1979): A meiofaunal "Thiobios" limited to the anaerobic sulfide system of marine sand does not exist. *Marine Biology* 54: 225–237.

Rouse, G.W. (1992): Oogenesis and larval development in *Micromaldane* (Polychaeta: Capitellida: Maldanidae). *Invertebrate Reproduction and Development* 21: 215–230.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, New York: 1–354.

Rousselot, M., Delpy, E., La Rochelle, C.D., Lagente, V., Pirow, R., Rees, J.-F., Hagege, A., Le Guen, D., Hourdez, S. & Zal, F. (2006): *Arenicola marina* extracellular hemoglobin: A new promising blood substitute. *Biotechnology Journal* 1: 333–345.

Saint-Joseph, A. d'A. de. (1888): Les annélides polychètes des côtes de Dinard. Seconde partie. *Annales des Sciences Naturelles, Zoologie et Paléontologie, Paris Série 7*, 5: 141–338, pl. VI–XIII.

Sawada, N. (1975): Electron microscope studies on sperm differentiation in marine annelid worms. II. Sperm formation in *Arenicola brasiliensis*. *Development, Growth and Differentiation* 17: 89–99.

Say, T. (1818): Observations on some of the animals described in the account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 1: 442–458.

Southward, E.C. & Southward, A.J. (1958): The breeding of *Arenicola ecaudata* Johnston and *A. branchialis* Aud. & Edw. at Plymouth. *Journal of the Marine Biological Association of the U.K.* 37: 267–286.

Storch, V. & Schlötzer-Schrehardt, U. (1988) Sensory structures. In: Westheide, W & Hermans, C.O. (eds) The ultrastructure of Polychaeta. *Microfauna Marina* 4: 121–133.

Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7: 57.

Tebble, N. & Chambers, S. (1982): Polychaetes from Scottish waters, Part 1. Family Polynoidae. Royal Scottish Museum, Edinburgh: 1–73.

Thamdrup, H.M. (1935): Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. *Meddelelser Kommn Danmarks Fiskeri-og Havundersogelser, Serie Fiskeri* 10: 1–125.

Titova, L.K. & Kharkeevich, T.A. (1973): Cytological and ultrastructural organisation of the statocyst in the polychaete *Arenicola marina*. *Journal of Evolutionary Biochemistry and Physiology* 9: 513–520.

Trueman, E.R. (1966): Observations on the burrowing of *Arenicola marina* (L.). *Journal of Experimental Biology* 44: 93–118.

Turner, A. (2013): Selenium in sediments and biota from estuaries of southwest England. *Marine Pollution Bulletin* 73: 192–198.

Turner, A., Turner, D. & Braungardt, C. (2013): Biomonitoring of thallium availability in two estuaries of southwest England. *Marine Pollution Bulletin* 69: 172–177.

Tzetlin, A.B. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535: 199–225.

van Cauwenberghe, L., Claessens, M., Vandegehuchte, M.B., & Janssen, C.R. (2015): Microplastics are taken up by mussels (*Mytilus edulis*) and lugworms (*Arenicola marina*) living in natural habitats. *Environmental Pollution* 199: 10e17.

van Duijn, P., Havinga, E. & Lignac, G.O.E. (1951): Arenicochrome, a new pigment from *Arenicola marina* L. *Experientia* 7: 376–378.

Völkel, S. (1995): Sulfide tolerance and detoxification in *Arenicola marina* and *Sipunculus nudus*. *American Zoologist* 35: 145–153.

Völkel, S. & Grieshaber, M.K. (1992): Mechanisms of sulphide tolerance in the peanut worm *Sipunculus nudus* (Sipunculidae) and in the lugworm *Arenicola marina* (Polychaeta). *Journal of Comparative Physiology and Biochemistry* 162: 469–477.

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Wang, G. (1982): Late Precambrian Annelida and Pogonophora from the Huainan of Anhui Province. *Bulletin of the Tianjin Institute of Geology and Mineral Resources, Chinese Academy of Geological Science* 6: 9–22.

Watson, G.J. & Bentley, M.G. (1997): Evidence for a coelomic maturation factor controlling oocyte maturation in the polychaete *Arenicola marina* (L.). *Invertebrate Reproduction and Development* 31: 297–306.

Watson, G.J. & Bentley, M.G. (1998): Oocyte maturation and post fertilization development of *Arenicola marina* (L.) (Annelida: Polychaeta). *Invertebrate Reproduction and Development* 33: 35–46,

Watson, G.J., Cadman, P.S., Paterson, L.A., Bentley, M.G. & Auckland, M.F. (1998): Control of oocyte maturation, sperm activation and spawning in two lugworm species: *Arenicola marina* and *A. defodiens*. *Marine Ecology Progress Series* 175: 167–176.

Watson, G.J., Williams, M.E. & Bentley, M.G. (2000): Can synchronous spawning be predicted from environmental parameters? A case study of the lugworm *Arenicola marina*. *Marine Biology* 136: 1003–1017.

Watson, G.J., Hannah, L.C., Gaudron, S.M., Betteley, K.A. & Bentley, M.G. (2008): Extension of the breeding season and its effects on fertilization and development in two species of lugworm (*Arenicola marina* and *A. defodiens*). *Journal of Experimental Marine Biology and Ecology* 354: 17–27.

Watson, G.J., Murray, J.M., Schafer, M. & Bonner, A. (2016): Bait worms: A valuable and important fishery with implications for fisheries and conservation management. *Fish and Fisheries* 18: 374–388.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Wells, G.P. (1937): Studies on the physiology of *Arenicola marina* L. I. The pace-maker role of the oesophagus, and the action of adrenaline and acetylcholine. *Journal of Experimental Biology* 14: 117–157, 26 figures.

Wells, G.P. (1944a): Mechanism of burrowing in *Arenicola marina* L. *Nature* 154: 396.

Wells, G.P. (1944b): The parapodia of *Arenicola marina* L. (Polychaeta). *Proceedings of the Zoological Society of London* 114: 100–116.

Wells, G.P. (1945): The mode of life of *Arenicola marina* L. *Journal of the Marine Biological Association of the U.K.* 26: 170–207, 10 figures.

Wells, G.P. (1948): Thixotropy and the mechanism of burrowing in the lugworm (*Arenicola marina* L.). *Nature* 162: 652–653.

Wells, G.P. (1949): Respiratory movements of *Arenicola marina* L.: intermittent irrigation of the tube, and intermittent aerial respiration. *Journal of the Marine Biological Association of the U.K.* 28: 447–464.

Wells, G.P. (1950): The anatomy of the body wall and appendages in *Arenicola marina* L., *Arenicola claparedii* Levinsen and *Arenicola ecaudata* Johnston. *Journal of the Marine Biological Association of the U.K.* 29: 1–44.

Wells, G.P. (1952): The proboscis apparatus of *Arenicola*. *Journal of the Marine Biological Association of the U.K.* 31: 1–28.

Wells, G.P. (1954): The mechanism of proboscis movement in *Arenicola*. *Quarterly Journal of Microscopical Science* 95: 251–270.

Wells, G.P. (1958): Giant nerve cells and fibers in *Arenicola claparedii* (Polychaeta). *Nature* 182: 1609–1610.

Wells, G.P. (1959): The genera of Arenicolidae (Polychaeta). *Proceedings of the Zoological Society of London* 133: 301–314.

Wells, G.P. (1961): How lugworms move. In: J.A. Ramsay & V.B. Wigglesworth (eds.): *The Cell and the Organism.* Cambridge University Press, Cambridge: 209–233.

Wells, G.P. (1963a): Barriers and speciation in lugworms (*Arenicola*, Polychaeta). In: J.P. Harding & N. Tebble (eds.): *Speciation in the sea.* Systematics Association, London: 79–98.

Wells, G.P. (1963b): The lugworms of the southern cold temperate zone (Arenicolidae, Polychaeta). *Proceedings of the Zoological Society of London* 140: 121–159.

Wells, G.P. (1966): The lugworm (*Arenicola*) — A study in adaptation. *Netherlands Journal of Sea Research* 3: 294–313.

Wells, G.P. (1980): The species problem in lugworms and other Polychaeta. In: Gunawardana T.T.P., Prematilleka L. & Silva R. (eds). *P.E.P. Deraniyagala Commemoration Volume*. Lake House Investments Ltd., Colombo: 355–366.

Wells, G.P. & Albrecht, E.B. (1951a): The integration of actitivity cycles in the behaviour of *Arenicola marina* L. *Journal of Experimental Biology* 28: 41–50.

Wells, G.P. & Albrecht, E.B. (1951b): The role of oesophageal rhythms in the behaviour of *Arenicola ecaudata*. *Journal of Experimental Biology* 28: 51–56.

Whitear, M. (1953): The stomatogastric nervous system of *Arenicola*. *Quarterly Journal of Microscopical Science* 94: 293–302.

Williams, M.E., Bentley, M.G. & Hardege, J.D. (1997): Assessment of field fertilization success in the infaunal polychaete *Arenicola marina* (L.). *Invertebrate Reproduction and Development* 31: 189–197.

Wilson, E.B. (1883): Observations on the early developmental stages of some polychaetous annelids. *Studies of the Biological Laboratory, Johns Hopkins University* 2: 271–299.

Wolff, W.J. (1973): The estuary as a habitat. An analysis of the data in the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. *Zoologische Verhandelingen* 126: 1–242.

Wu, B.L. & Sun, R. (1979): Studies of *Arenicola brasiliensis* Nonato in the Bohai and the Yellow Sea. *Oceanologia et Limnologia Sinica* 10: 257–272.

Zal, F., Green, B.N., Lallier, F.H., Vinogradov, S.N. & Toulmond, A. (1997): Quaternary structure of the extracellular haemoglobin of the lugworm *Arenicola marina*. *European Journal of Biochemistry* 243: 85–92.

Zrzavý, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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José Eriberto De Assis, Christoph Bleidorn, and
Martin Lindsey Christoffersen

7.7.6 Maldanidae Malmgren, 1867

Introduction

Maldanidae, commonly known as bamboo worms (Fig. 7.7.6.1), comprise a group of sedentary polychaetes that include 6 subfamilies, 31 genera, and more than 200 described species. However, some genera are in need of revision (Tab. 7.7.6.1). These worms are found in all marine regions, and some species even occur in estuarine areas. They are benthic organisms and tube builders and live under rocks or fixed on sand or mud.

The body of maldanids can be divided into a head, formed by the prostomium fused to the peristomium, sometimes with a flattened cephalic plate; a thorax, formed by the first four chaetigers, usually have strong spines; an abdomen, with several longer chaetigers and often followed by a number of achaetous segments; and a posterior end, with a pygidium that bears the anus (Fauchald 1977, De Assis and Christoffersen 2011).

Maldanids are considered to be consumers of organic material (Day 1967, Imajima and Shiraki 1982a, De Assis et al. 2007b). Most are head-down feeders and transport subsurface sediments upward, although some species are known to drag surface material down their tube into a feeding cavity (Levin et al. 1997). Their food is largely composed of detritus (Mangum 1964, Day 1967, Fauchald and Jumars 1979). Diatoms and protozoans have been identified in the gut of some species (Ullman and Bookhout 1949, Wolf 1984). During feeding, animals extend their eversible proboscis, which is globular and covered with papillae, by increasing the coelomic pressure in the first four chaetigers (Pilgrim 1966a, Jiménez-Cueto and Salazar-Vallejo 1997). An enhanced bacterial growth within the tube wall has been reported for *Maldane sarsi* Malmgren, 1865, which might also be exploited for nutritional benefits (Dufour et al. 2008). Another feeding mode was investigated in *Praxillura maculata* Moore, 1923, which bears stiff particle-collecting spokes attached to the tube end to collect algae and particles of organic matter, and then transported to the gut and ingested (McDaniel and Banse 1979).

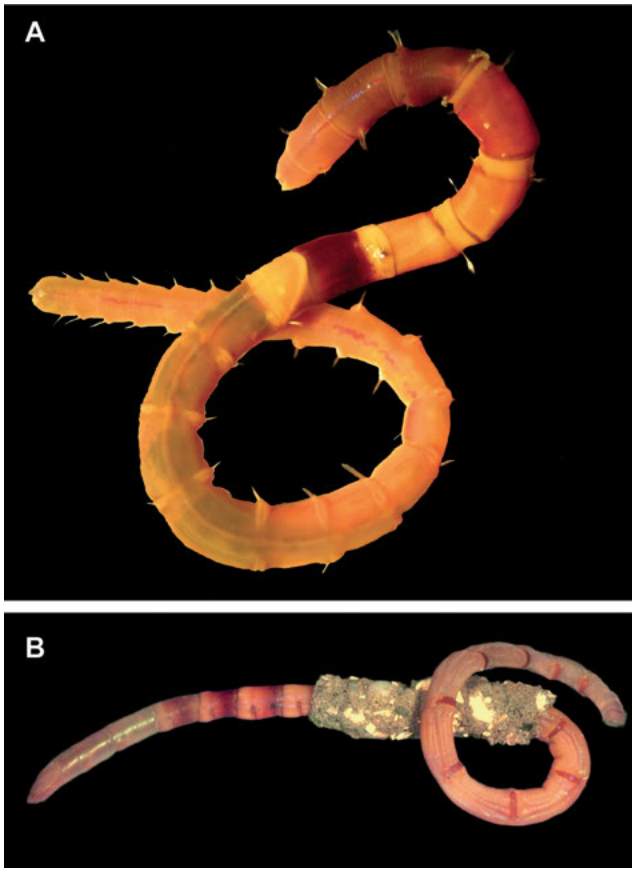


Fig. 7.7.6.1: Habitus of maldanid polychaetes. A, *Leiochone leiopygos* Grube, 1860, whole animal. Note the ventral glandular shield on segment 8, which represents a diagnostic character for the genus *Leiochone*. Picture by Anne Zrakzewski (Bergen). B, *Euclymene* sp., showing an animal in its tube. Picture by Wilfried Westheide (Osnabrück).

Morphology

Color. Living maldanids can be variously colored in shades of red, brown, green, or yellow. They may also be transparent as in some species of *Micromaldane* (Rouse 1990). They have a cylindrical body, which is normally truncated at both ends; many taxa bear well-developed cephalic and pygidial plates (Fig. 7.7.6.2A, B). In Nicomachinae, only the pygidial plate is present (Fig. 7.7.6.2C), and in Rhodininae and Lumbriclymeninae, both cephalic and pygidial plates are absent. Most species have a fixed number of 16 to 24 chaetigers (Day 1967, Imajima and Shiraki 1982a, b, De Assis and Christoffersen 2010); although the species of *Micromaldane* have a fixed number of 17 chaetigers, only some of which have prepygidial achaetous segments. Species of *Macroclymenella* bear 28 to 32 chaetigers, and *Gravierella* and *Macroclymene* may have 30 to 70 chaetigers (Day 1967, Fauchald 1977). Many species show a fixed number of prepygidial achaetous segments. Species lengths vary from 3 mm in some species of *Micromaldane* to more than 200 mm in some species of *Nicomache*, *Petaloproctus*, *Gravierella*, and *Macroclymene* (Rouse 2001). As a rule, midbody segments tend to be longer than those at the anterior or posterior end.

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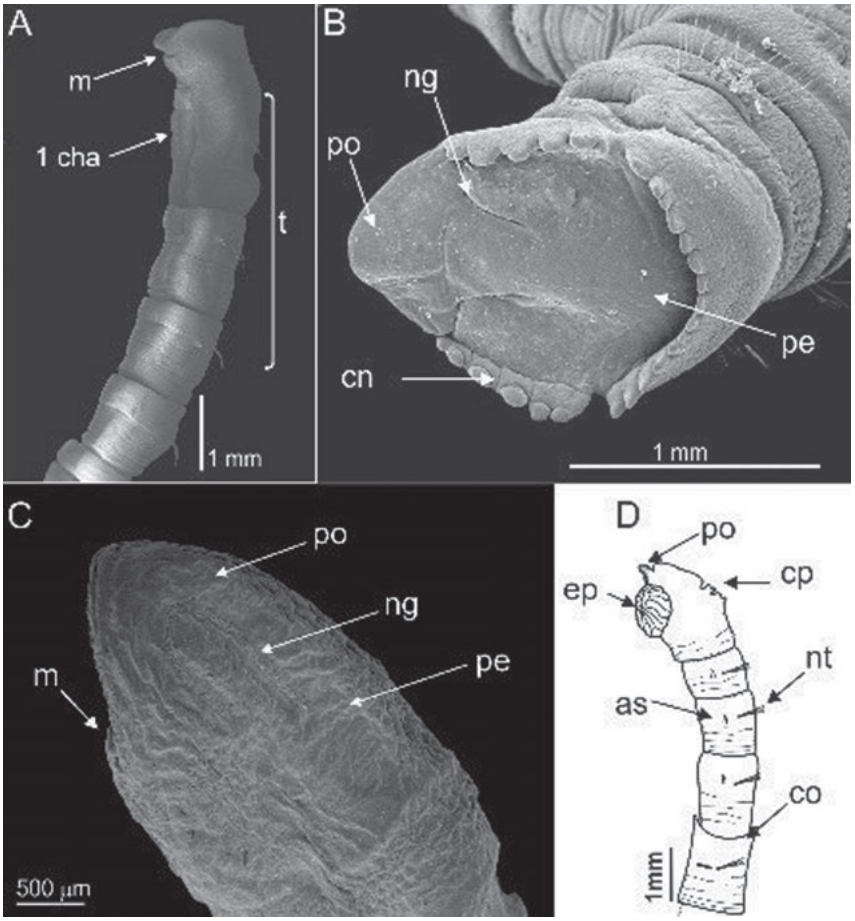


Fig. 7.7.6.2: A, Anterior end of *Johnstonia* sp., showing the head and the first four chaetigers; B, Cephalic plate of *Metasychis disparidentatus* Moore, 1904, showing the prostomium and nuchal grooves; C, Head of *Nicomache (Nicomache) brasiliensis* De Assis et al., 2007a, b, showing cephalic keel and nuchal grooves; D, Drawing of the anterior end of *Clymenella zonalis* Verrill, 1874, showing the first four chaetigers. 1 cha, first chaetiger; as, acicular spine; cn, crenulations; co, collar; cp, cephalic plate; ep, eversible proboscis; m, mouth; ng, nuchal grooves; nt, notopodium; pe, peristomium; po, prostomium; t, thorax.

Prostomium. The prostomium is fused to the peristomium, forming a well-defined head, with the prostomium extending forward as a palpode (Fauchald and Rouse 1997). The head may be truncated, funnel-shaped, or rounded at the anterior end. A keel is not conspicuous in Notoproctinae and Euclymeninae but elevated and arched in species of Nicomachinae, Lumbriclymeninae, Maldaninae, and some Rhodininae (Figs. 7.7.6.2B–D, 7.7.6.6A) (Arwidsson 1906, Hartmann-Schröder 1971, De Assis et al. 2010).

The paired nuchal organs, ciliated furrows on each side of the prostomium, may be parallel, curved, or divergent (Fig. 7.7.6.2B, C) (Pettibone 1954, De Assis et al. 2007a). The peristomium forms the ventral buccal lips (which, in many species, are thick and wrinkled), the roof of the mouth, and the peristomial rings, between the prostomium and the first chaetiger (Fig. 7.7.6.2D). Prostomial pigment-spots have been described for some species (e.g., *Euclymene oerstedi* (Claparède, 1863) and *L. leiopygos*) but are lacking in other species (Pilgrim 1966b, Read 2011). Their ultrastructure has not been investigated yet. In Maldaninae and Euclymeninae, the flattened cephalic plate is bordered by a rim that may be smooth, with grooves, or crenulated posteriorly and/or laterally (Day 1967, Wolf 1984). The ventral mouth leads to an eversible pharynx. Tzetlin (1991) investigated the foregut of several maldanids and found taxa with a ventral pharyngeal organ in some species (e.g., *Nicomache*), a nonmuscular axial proboscis in some others (e.g., *Axiothella*), and a combination of ventral and axial proboscis in others (e.g., *Praxillella*). As in other taxa, such as Orbiniidae, it was concluded that the presence of a ventral pharynx might represent a progenetic structure only present in individuals of small species (Tzetlin and Purschke 2005). Moreover, during development, individuals of larger species pass through a stage possessing a ventral buccal organ and dorsolateral ciliary folds, which can be observed in individuals of the closely related lugworm *Arenicola marina* (Linnaeus, 1758) as well. Some species have a gular membrane (Fig. 7.7.6.2D) (Green 1994).

Lateral organs. In maldanids, lateral organs have been described for *Euclymene oerstedi* using scanning electron microscopy (Purschke and Hausen 2007). Lateral organs or interramal organs are sense organs that occur between the rami of parapodia in many sedentary polychaetes

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(Purschke 2005). Usually, they are made up of rows of densely arranged uniciliated receptor cells.

Parapodia. Biramous parapodia usually occur in all chaetigers posteriorly (Fig. 7.7.6.3A), but in some taxa neurochaetae are absent from a number of anterior chaetigers. The notopodia are cylindrical, truncate, or cone-shaped, with chaetae in two rows, all capillaries. Capillaries are of different types, including limbate (Fig. 7.7.6.3D) and nonlimbate (Light 1991) forms, simple chaetae (Fig. 7.7.6.3B), spirally fringed forms, with a proximal shaft or crenulated blade (Fig. 7.7.6.3C), ruffled chaetae (Fig. 7.7.6.3C), or spatulate and geniculate chaetae (Mesnil 1897, Rioja 1925).

Chaetae. Neuropodial chaetae are often acicular spines or reduced rostrate uncini in the first three or more chaetigers (Fig. 7.7.6.3D). The following chaetigers have single rows of uncini or double rows in Rhodininae. The uncini are of three types: (a) rostrate hooks, with strongly or slightly curved shafts, the main manubrium with a series of teeth and the subrostral tooth with a tuft of fibrils or subrostral processes (Fig. 7.7.6.4A, B); (b) avicular hooks,

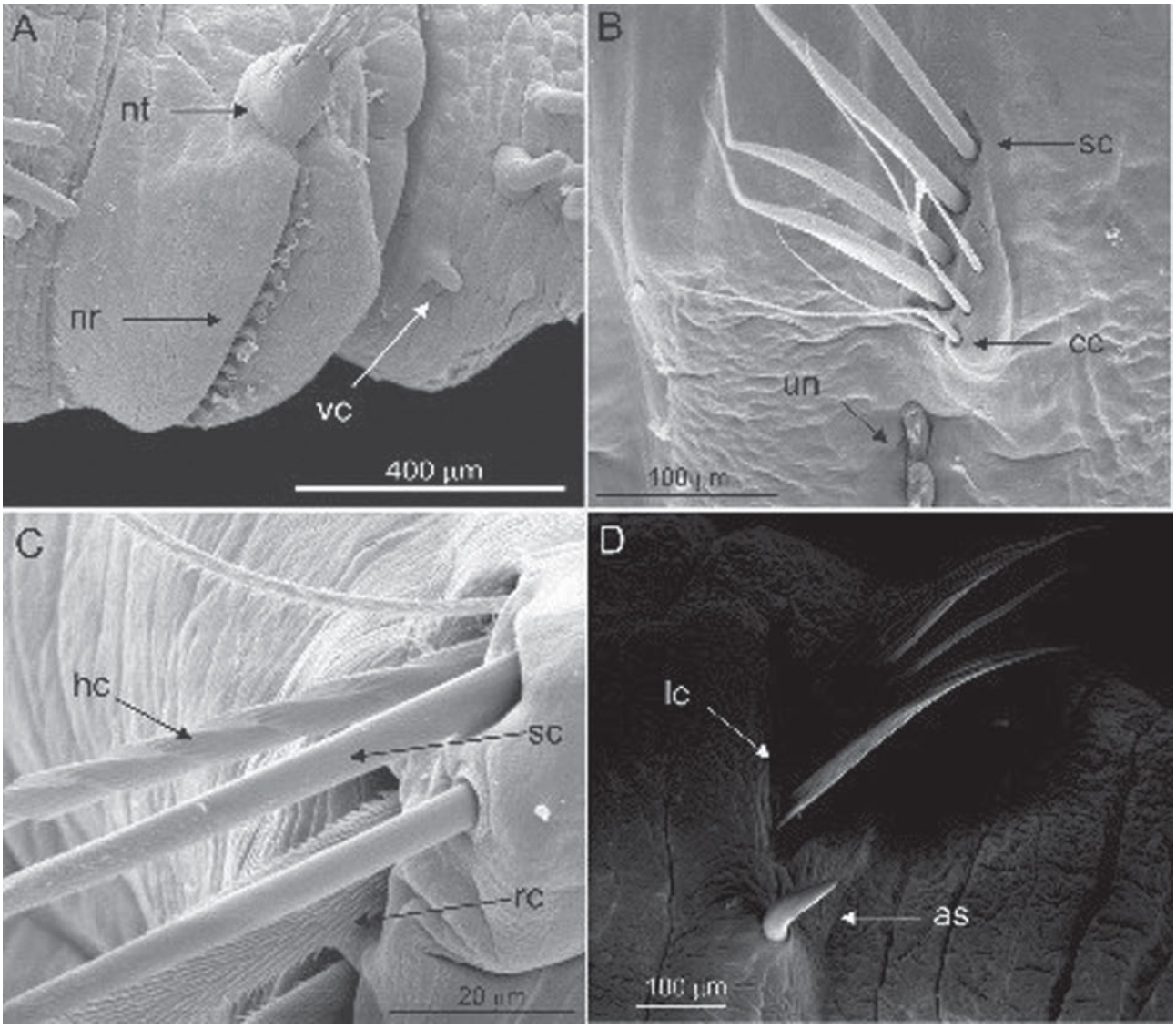


Fig. 7.7.6.3: A, Fragment of the median body region of *Johnstonia clymenoides* Quatrefages, 1866, showing parapodia and the vascular cirri; B, Anterior parapodia of *Metasychis disparidentatus* Moore, 1904, with two types of notochaetae and neuropodial uncini; C, Median notopodia of *M. disparidentatus* Moore, 1904, showing three types of notochaetae; D, parapodia of the first chaetiger of *Johnstonia* sp., showing acicular spines, limbate, and bilimbate chaetae. as, acicular spine; cc, companion chaetae; hs, helicoidal chaetae; lc, limbate chaetae; nr, neuropodium; nt, notopodium; rc, ruffled chaetae; sc, simple chaetae; un, uncinus; vc, vascular cirrus.

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with a row of teeth on the main fringe; and (c) terebelloid uncini (Fig. 7.7.6.4C). The neurochaetae remain perpendicular to the body axis, forming an elevated torus (Fig. 7.7.6.4A). A shift in chaetal arrangement of the notopodial chaetal rows from a transverse direction in anterior segments to a longitudinal one in posterior segments can be observed in species of *Axiothella*, *Clymenella*, *Clymenura*, *Euclymene*, and *Johnstonia* (Hausen and Bleidorn 2006, Bleidorn and Hausen 2007), although not in members of Maldaninae and Nicomachinae. The possible taxonomic significance of the pattern of neuropodial chaetae was pointed out by Pilgrim (1977).

The prepygidial achaetigerous segments have been much used to differentiate species within genera. Some species of *Rhodine* have up to five prepygidial segments, whereas *Boguella* and *Boguea* have one and two achaetous prepygidial segments, respectively. Species of Lumbriclymeninae, in particular *Lumbriclymene* and *Praxillura*, usually have more than two prepygidial achaetous segments. Maldaninae, Notoproctinae, and Nicomachinae have up to two prepygidial achaetous segments, although these may be absent in some species. Euclymeninae contains a majority of species with more than three prepygidial achaetous segments.

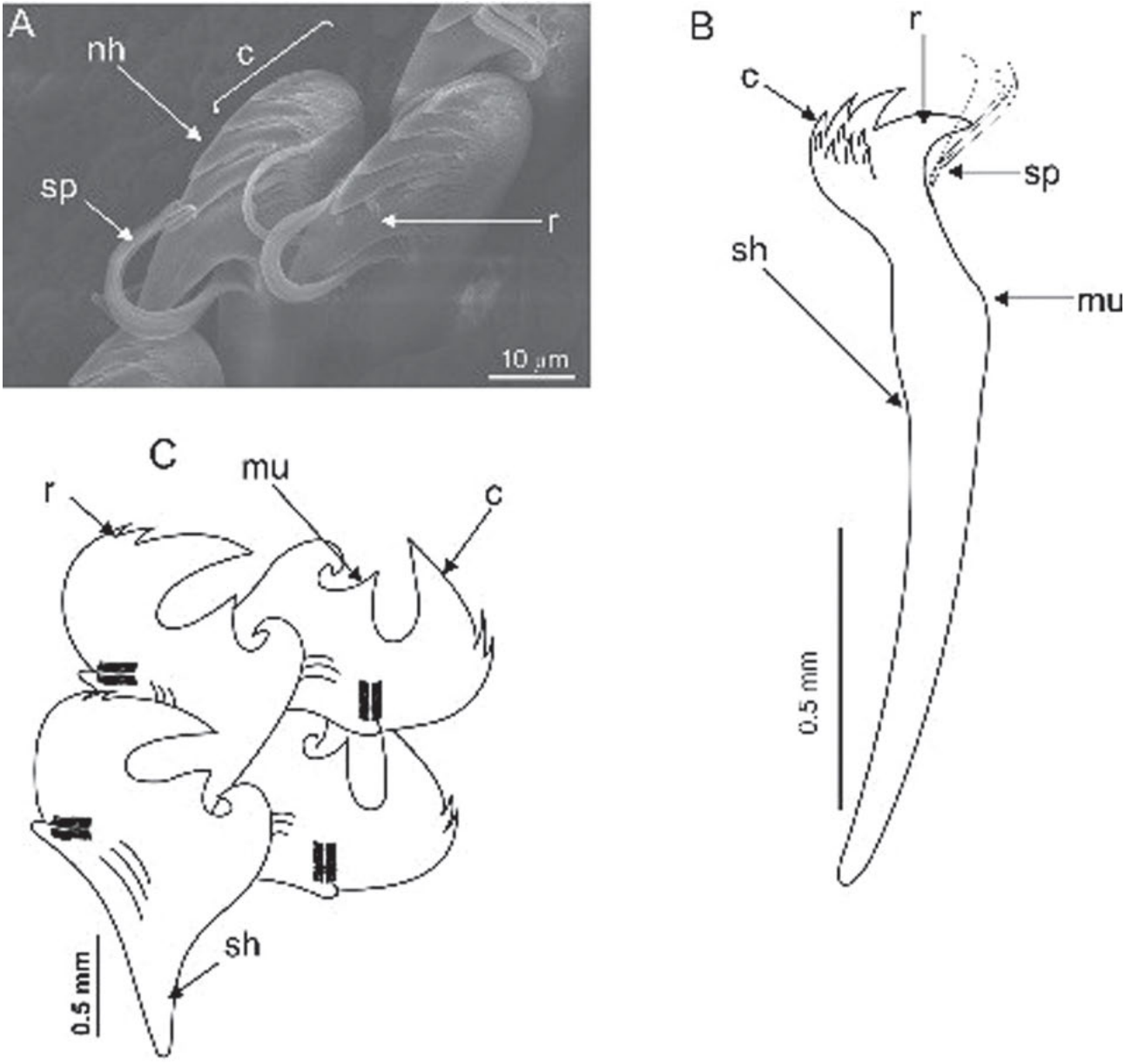


Fig. 7.7.6.4: A, Neuropodial uncini from chaetiger 5 of *Johnstonia* sp., showing anterior structure of uncini; B, Complete uncinus of *Lumbriclymene interstricta* Ehlers, 1908) C, Double row of terebelloid uncini of *Rhodine loveni* Malmgren, 1865. c, capitium; m, manubrium; nh, neuropodial hook; r, rostrum; s, shaft; sp, subrostral process.

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Pygidium. The pygidium is of various forms and bears the anus. In taxa without pygidial plates, the anus is terminal or subdorsal (Lumbriclymeninae and Rhodininae) (Fig. 7.7.6.5A). Four subfamilies have a pygidial plate and are united as Maldanoplaca (De Assis and Christoffersen 2011). In Euclymeninae and Nicomachinae, the anus is terminally located within an anal funnel bordered by cirri or crenulations (Fig. 7.7.6.5B). In Maldaninae and Notoproctinae, the anus is dorsally placed, outside the pygidial plate. This plate can have petaloid borders or lateral slits in Maldaninae (Fig. 7.7.6.5C).

Musculature. Maldanids bear an inner longitudinal and an outer circular muscle ring (Fig. 7.7.6.6C, D). The longitudinal muscles are much more prominent (Fig. 7.7.6.6B) than the circular muscles, but the latter still form complete rings.

Blood vascular system and nephridia. The circulatory system is closed, without a heart-body (Rouse 2001). It was described in detail by Pilgrim (1966b) and includes chloragogenous and iron-bearing tissue associated with the ventral vessel. A gut sinus is associated with the stomach and the intestine. Respiration is through the body wall, although some taxa bear gill-like epidermal structures, such as the members of the genera *Johnstonia* (Fig. 7.7.6.3A) and *Sabaco* (Light 1991). Excretion and gamete release are facilitated by metanephridia. Green (2000) reported four

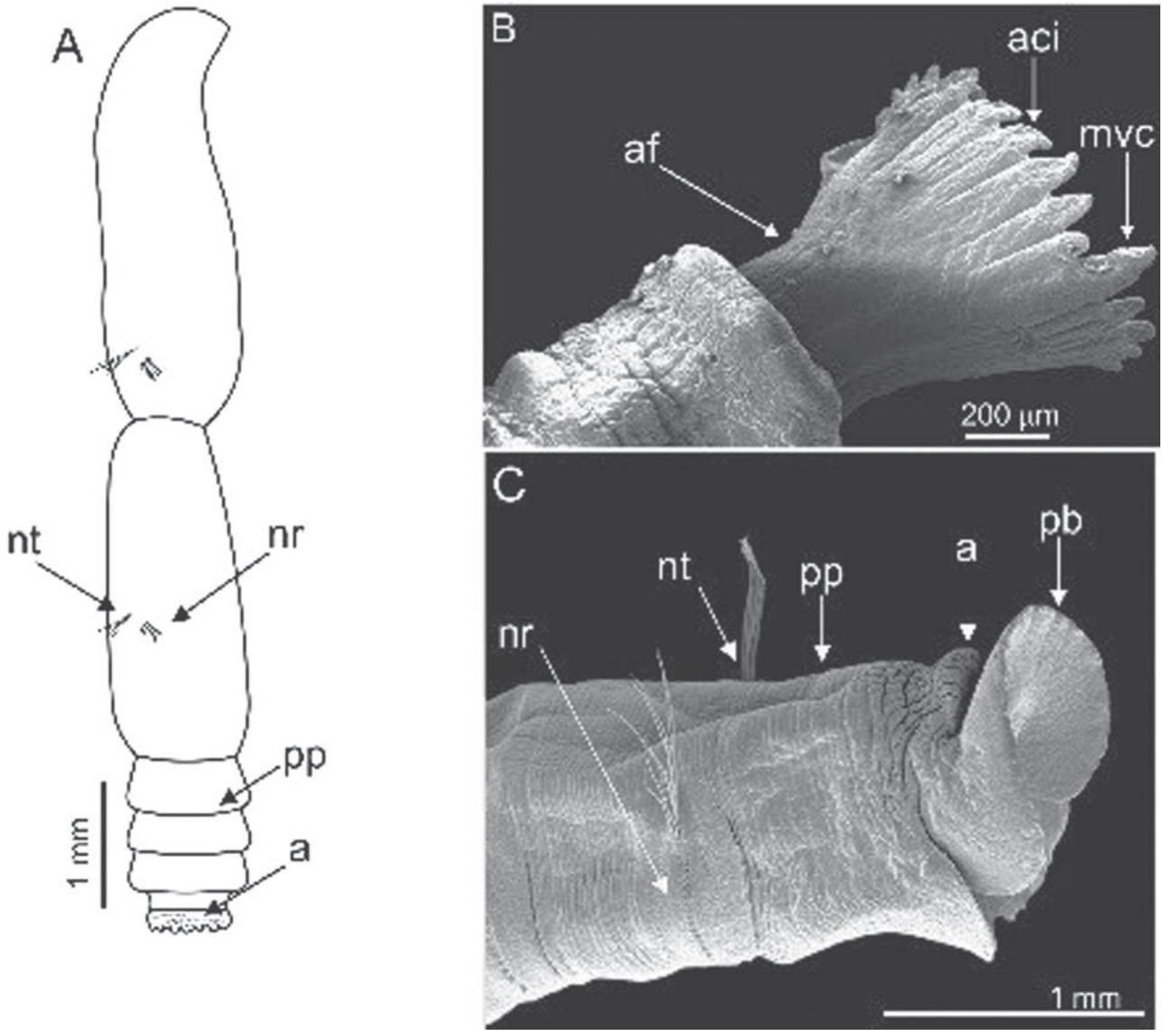


Fig. 7.7.6.5: A, Posterior end of *Lumbriclymene interstricta* Ehlers, 1908, showing prepygidial achaetigers and anus; B, Posterior end of *Johnstonia* sp., showing anal funnel and cirri; C, posterior end of *Metasychis disparidentatus* Moore, 1904, showing a dorsal anus and petaloid borders. a, anus; af, anal funnel; aci, anal cirri; nr, neuropodium; nt, notopodium; mvc, medioventral cirrus; pb, petaloid borders; pp, prepygidial achaetigers.

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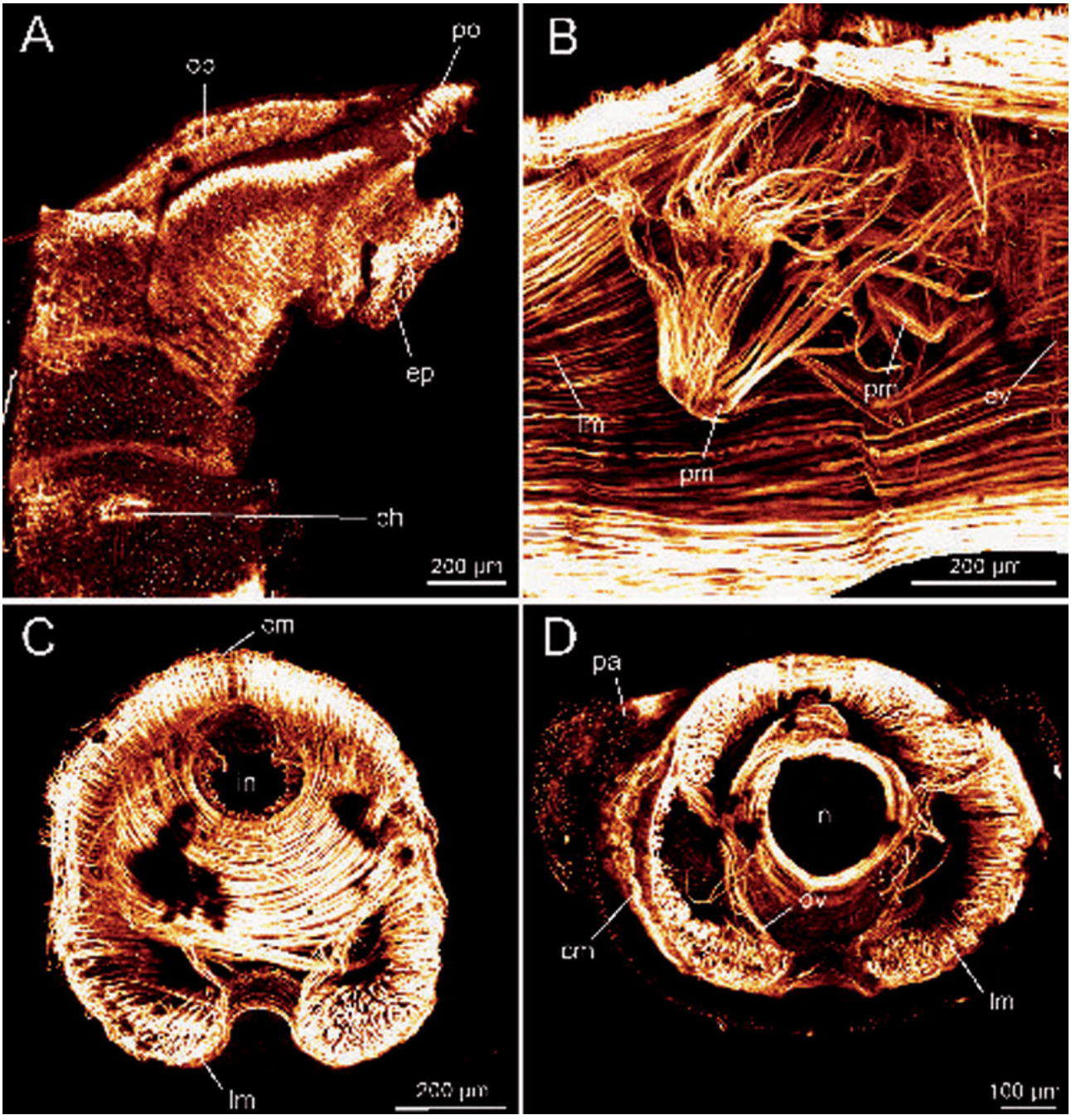


Fig. 7.7.6.6: Organization of musculature in *Maldane sarsi* Malmgren, 1865. Phalloidin-rhodamine labeling; confocal maximum projections. A, Prostomial region with everted pharynx, anterior is up; B, Detailed view of the inner musculature of the midbody region, anterior is left, note the prominent longitudinal musculature in the body wall; C, Posterior cross-section, dorsal is up, note the continuous circular musculature; D, Anterior cross-section, dorsal is up. ch, chaetiger; cm, circular muscle fibers; dv, dorsoventral muscle fibers; in, intestine; lm, longitudinal muscle fibers; pa, parapodium; pe, peristomium; ph, pharynx; po, prostomium.

pairs of metanephridia in Euclymeninae and three pairs in Maldaninae.

Nervous system. The adult nervous system is composed of simple circumoesophaegal connectives, a stomatogastric nerve ring, and a single ventral connective (Brinkmann and Wanninger 2010). The brain includes ganglia sending nerves to the prostomium, nuchal organ, and buccal organ. The nervous system shows traces of metamerism in the presence of larger collections of neurons at the level of the parapodia and in an enlargement of the nerve cord at the segmental boundaries (Pilgrim 1978). The presence of multicellular giant fibers has been reported in the ventral nerve cord (Pilgrim 1978), which were described as

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myelinated by Nicol (1948). However, subsequent studies based on transmission electron microscopy failed to confirm the presence of myelin (Hartline and Kong 2009).

Biology and ecology

Species are distributed in all marine regions of the world, and many have a relatively fragile body. They are easily fragmented during collection. Following natural damage, they are capable of anterior and posterior regeneration. Maldanids may be difficult to identify to species level, particularly when specimens are incomplete. Clavier (1984) investigated a population of *Euclymene oerstedi* in Brittany (France) and found that 22% of the examined individuals were regenerating anterior segments and 41% were regenerating posterior segments of the body. No fossils attributable to Maldanidae have been described (Rouse 2001).

Maldanidae occur from the intertidal regions to deep waters (Arwidsson 1906, Chamberlin 1919, De Assis et al. 2007b, 2010), and some species may be very abundant in estuarine habitats, in which their tubes lie in mud or sand banks (e.g., species of *Johnstonia* Quatrefages, 1866). Some species are reported from hydrothermal vents and may be associated with other organisms (Blake and Hilbig 1990, Kongsrud and Rapp 2012). Maldanids are benthic animals that construct their tubes with mineral particles of diverse sizes and textures (Dufour et al. 2008). Tubes may be fixed to stones, shells, or algal holdfasts by a thin and transparent mucous matrix, which begins to be produced after the end of the larval period. Many species build their tubes under rocks and frequently form horizontal galleries, as in the species of *Nicomache* (De Assis et al. 2007a), or vertical galleries in sand or mud bottoms of estuarine regions, as in the species *Euclymene* (Jiménez-Cueto and Salazar-Vallejo 1997, De Assis et al. 2007a, b). *Axiothella rubrocincta* Johnson, 1901 builds a U-shaped tube in sand bottoms, which is similar to the tubes constructed by some species of arenicolids (Kudenov 1978, Wilson 1983). Mass assemblages of *Clymenella torquata* (Leidy, 1855) in Vancouver Island have been shown to create a spongy and porous type of sediment that negatively impacts commercial oyster faming (Mach et al. 2012).

Maldanidae are usually gonochoristic worms with a variety of reproductive modes. Wilson (1983) showed that closely related species of the *Axiothella rubrocincta* complex may spawn their gametes into seawater where fertilization occurs or brood the eggs in the adult tube. Several *Micromaldane* species have also been reported to brood directly, developing larvae in their tubes (Rouse 1990). Spiral cleavage is observed in these animals, and as is typical for many polychaetes, the larvae bear a prototroch, neurotroch, and telotroch (Bookhout and Horn 1949, Brinkmann and Wanninger 2010). The larval period is short, and the development is of lecitotrophic or direct developing mode (Newell 1951, Rouse 1992). After fertilization, some species construct a cocoon of mucus, which adheres to the tube, opening until juveniles start to construct their own tubes (Day 1967). Maldanids are able to regenerate lost segments, and an asexual reproducing maldanid species has been described (Tzetlin and Markelova 1986).

The only population genetic analysis of maldanids was undertaken for *Clymenella torquata*. Jennings and Halanych (2005) sequenced the mitochondrial genome of this species to provide molecular markers for subsequent studies. In a phylogeographic study using two mitochondrial genes from 10 populations around Cape Cod (Massachusetts, USA), Jennings et al. (2009) found low levels of gene flow between populations. Their analysis indicated a clear phylogenetic break in this region, with a cline of haplotype frequencies from north to south. Recent molecular studies revealed a widespread occurrence of cryptic species within annelids (e.g., Bleidorn et al. 2006), although no such studies have been conducted for maldanids to date. However, 133 maldanid barcodes (a defined region of the *cox1* gene) were available in the Barcode of Life database in September 2012 (Ratnasingham and Hebert 2007). A first study on Canadian polychaetes, in general, showed a conspicuous genetic distance also for the maldanid *Praxillella praetermissa* (Malmgren, 1865) between populations sampled in the Pacific and Arctic oceans (Carr et al. 2011).

Phylogeny and taxonomy

Phylogeny. Lamarck (1818) first established maldanids as part of Polychaeta Sedentaria. Later, Savigny (1822) placed Maldaninae as part of Serpuleae, whereas Blainville (1828) included Maldanies-Maldanids and Télethuses-Arenicolids as part of the group Paromocriniens. Grube (1850) considered them part of Limivora, which was maintained by Johnson (1865). Finally, Malmgren (1867) established the basis of the nomenclature presently in use. The main proposal for the classification within Maldanidae is contained in the study of Arwidsson (1906), in which five subfamilies were established: Rhodininae, Lumbriclymeninae, Nicomachinae, Maldaninae, and Euclymeninae. Imajima and Shiraki (1982a) proposed Clymenurinae based on the presence of a large ventral triangular glandular shield on the eighth chaetiger. However, Jiménez-Cueto and Salazar-Vallejo (1997) disagreed with this proposal, suggesting that *Axiothella mucosa* Andrews, 1891, which belongs to Euclymeninae, also bears this character, the position of which varies from chaetigers 5 to 8. These

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authors inferred that *Clymenura* should be included in Euclymeninae. Wolf (1983) reduced the family Bogueidae Hartman and Fauchald, 1971 to the subfamily Bogueinae and included them in Maldanidae based on morphological and ontogenetic criteria of *Boguea enigmatica* Hartman, 1945 and *Boguella ornata* Hartman & Fauchald, 1971. Detinova (1985) proposed Notoproctinae to contain the genus *Notoproctus*, previously placed in Lumbriclymeninae. She argued that the species of *Notoproctus* have a smooth pygidial plate and a dorsal anus, whereas, in the genera of Lumbriclymeninae, a pygidial plate is absent, with a conical pygidium and a terminal anus. These designations were accepted by Green (1994) and Jiménez-Cueto and Salazar-Vallejo (1997).

Parallel to these classification attempts, several taxonomic works were published worldwide, with the aim of recording or describing new taxa. Fauvel (1927) studied maldanids from France and Day (1967), updated the South African maldanids. Imajima and Shiraki (1982a, b) revised and described maldanids from Japan. Lee and Paik (1986a, b) recorded maldanids from Korea, and Wolf (1984) and Jiménez-Cueto and Salazar-Vallejo (1997) both recorded the maldanid fauna of the Gulf of Mexico.

The genus *Leiochone* has been synonymized by Fauchald (1977), but Read (2011) presented a detailed discussion on the genera and concluded that both are valid. The subfamily Clymenurinae Imajima and Shiraki, 1982a and the subgenus *Cephalata* were treated as invalid taxa (Tab. 7.7.6.1) (Fauchald 1977).

Fauchald and Rouse (1997) provided the first evidence for the monophyly of Maldanidae based on morphological characters. Several phylogenetic hypotheses have been offered based on various data sets (morphological, ontogenetic, and molecular) in an attempt to determine the proximity to Capitellidae and primarily Arenicolidae (Bartolomaeus and Meyer 1997, Rouse and Fauchald 1997, Bartolomaeus et al. 2005, Rousset et al. 2007). A preliminary maldanid phylogeny has been presented for some genera and species as a part of a detailed analysis of arenicolid phylogeny by Bleidorn et al. (2005). In this paper, mitochondrial 16S rRNA genes, nuclear 18S rRNA, and a small fraction of nuclear 28S rRNA established the relationships between selected species and demonstrated the polyphyly of Euclymeninae. Maldaninae was found to be monophyletic as the sister taxon of Arenicolidae.

Using morphological characters, De Assis et al. (2010) analyzed relationships within *Petaloproctus* and demonstrated the monophyly of Nicomachinae. In this study, Euclymeninae appeared as the sister group of Nicomachinae. De Assis and Christoffersen (2011) undertook a phylogenetic study of Maldanidae, including species of most genera (Fig. 7.7.6.7). The monophyly of the six higher-ranked taxa previously referred to as subfamilies (Euclymeninae, Lumbriclymeninae, Nicomachinae, Notoproctinae, Maldaninae, and Rhodininae) was supported. *Boguea* and *Boguella* represent the sister group to *Rhodine*. Consistent with molecular data (Bleidorn et al. 2005), *Clymenura* was included in Euclymeninae, confirming the abandonment of Clymenurinae. A new clade Maldanoplaca was proposed (including Notoproctinae, Maldaninae, Nicomachinae, and Euclymeninae) for taxa bearing pygidial and cephalic plates. However, the cephalic plate has been lost in Nicomachinae and in the genus *Leiochone* of Euclymeninae. The new proposed classification, based on morphological data, is provided herein. A brief diagnosis for all taxa of Maldanidae currently considered valid (see also Tab. 7.7.6.1) according to De Assis and Christoffersen (2011) follows.

Taxonomy and classification

Family Maldanidae Malmgren, 1867

Diagnosis: Long and cylindrical body, usually truncate at one or both ends; prostomium localized dorsally, fused to the peristomium; peristomium forming lips and postprostomial rings; parapodia generally biramous, median chaetigers elongate; notochaetae as various forms of capillaries; neurochaetae as various forms of uncini, sometimes replaced by acicular spines in some anterior segments; a number of prepygidial achaetous segments may be present; pygidium in a wide variety of forms, conical, plate-shaped, or funnel-shaped.

Rhodininae Arwidsson, 1906

Diagnosis: No cephalic or pygidial plate; posterior chaetigerous segments with posteriorly directed collars in one genus; prostomium forms a short low keel; notochaetae may include acicular spines; neurochaetae absent from a number of anterior chaetigers then double row of terebelloid uncini on some chaetigers; subrostral processes without barbules, chaetiger number not fixed; pygidium conical.

Boguea Hartman, 1945

Type species: *Boguea enigmatica* Hartmann, 1945
2 species.
Diagnosis: Notochaetae include acicular spines on far posterior chaetigers and may be present on a specific anterior segment; neurochaetae from chaetiger 5 onward, in double rows in median and posterior chaetigers; 22 to 24 chaetigers.

Boguella Hartman & Fauchald, 1971

Type species: *Boguella ornata* Hartmann & Fauchald, 1971
1 species.

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Tab. 7.7.6.1: Valid and invalid taxa within Maldanidae, with respective number of species. Taxa with asterisk denote genera that need revision. Indeterminable or invalid genera, with asterisk, are not described in the text.

Genera within Maldanidae	Synonymized genera within Maldanidae or indeterminable	Number of species
Rhodininae Arwidsson, 1906		
Rhodine Malmgren, 1865		7
Boguea Hartman, 1945		2
Boguella Hartman & Fauchald, 1971		1
Lumbriclymeninae Arwidsson, 1906		
Lumbriclymene Sars, 1872		10
Lumbriclymenella Arwidsson, 1906		2
Clymenopsis Verrill, 1900		4
Praxillura Verrill, 1880		6
Notoproctinae Detinova, 1982		
Notoproctus Arwidsson, 1906		9
Maldaninae Malmgren, 1867		
Asychis Kinberg, 1867	*Maldanopsis* Verrill, 1900; *Branchioasychis* Monro, 1939	~5
Bathyasychis Detinova, 1982		1
Chirimia Light, 1991	*Chrysothemis* Kinberg, 1867	~5
Maldane Grube, 1860	*Heteromaldane* Ehlers, 1908; *Sonatsa* Chamberlin, 1919	18
Metasychis Light, 1991		4
Sabaco Kinberg, 1867	*Maldanopsis* Verrill, 1900; *Branchioasychis* Monro, 1939 (see Light 1991)	9
Euclymeninae Arwidsson, 1906		
Aclymene Buzhinskaja, 1995		1
Axiothella Verrill, 1900	*Axiotheia* Malmgren, 1865	19
Clymenella Verrill, 1873	*Paraxiothea* Webster, 1879	19
Clymenura Verrill, 1900		9
Euclymene Verrill, 1900	*Arwidssonia* McIntosh, 1914; *Caecisirrus* Arwidsson, 1911; *Leiocephalus* Quatrefages, 1885	~30
*Eupraxillella** Hartmann-Schröder & Rosenfeldt, 1989		1
Gravierella Fauvel, 1919		1
*Heteroclymene** Arwidsson, 1906		2
Isocirrus Arwidsson, 1906		7
Johnstonia Quatrefages, 1866		~5
Leiochone Grube, 1868		6
Macroclymene Verrill, 1900		~5
*Macroclymenella** Augener, 1926		1
Maldanella McIntosh, 1885	*Abyssoclymene* Hartman, 1967	12
Microclymene Arwidsson, 1906		5
*Minusculisquama** Pettibone, 1983		1
*Mylitta** Kinberg, 1866		1
Petaloclymene Augener, 1918		2
Praxillella Verrill, 1881	*Iphianissa* Kinberg, 1867; *Praxilla* Malmgren, 1865	~15
*Pseudoclymene** Arwidsson, 1906		1
*Proclymene** Arwidsson, 1906		1
Nicomachinae Arwidsson, 1906		
Micromaldane Mesnil, 1897		7
Nicomache Malmgren, 1865	*Sabella* Linnaeus, 1767; *Clymene* Savigny, 1818	17
Petalopoctus Quatrefages, 1865	*Nicomachella* Levinsen, 1883	~10
Clymene Oken 1815,	Indeterminable	
Clymene Savigny, 1818	Indeterminable	
Chaponella Rullier, 1972	Referred to Sabellidae	
Neco Kinberg, 1867	Referred to *Mylitta*	
Mandrocles Kinberg, 1867	Indeterminable	
Promaldane Mesnil, 1897	Hypothetical	

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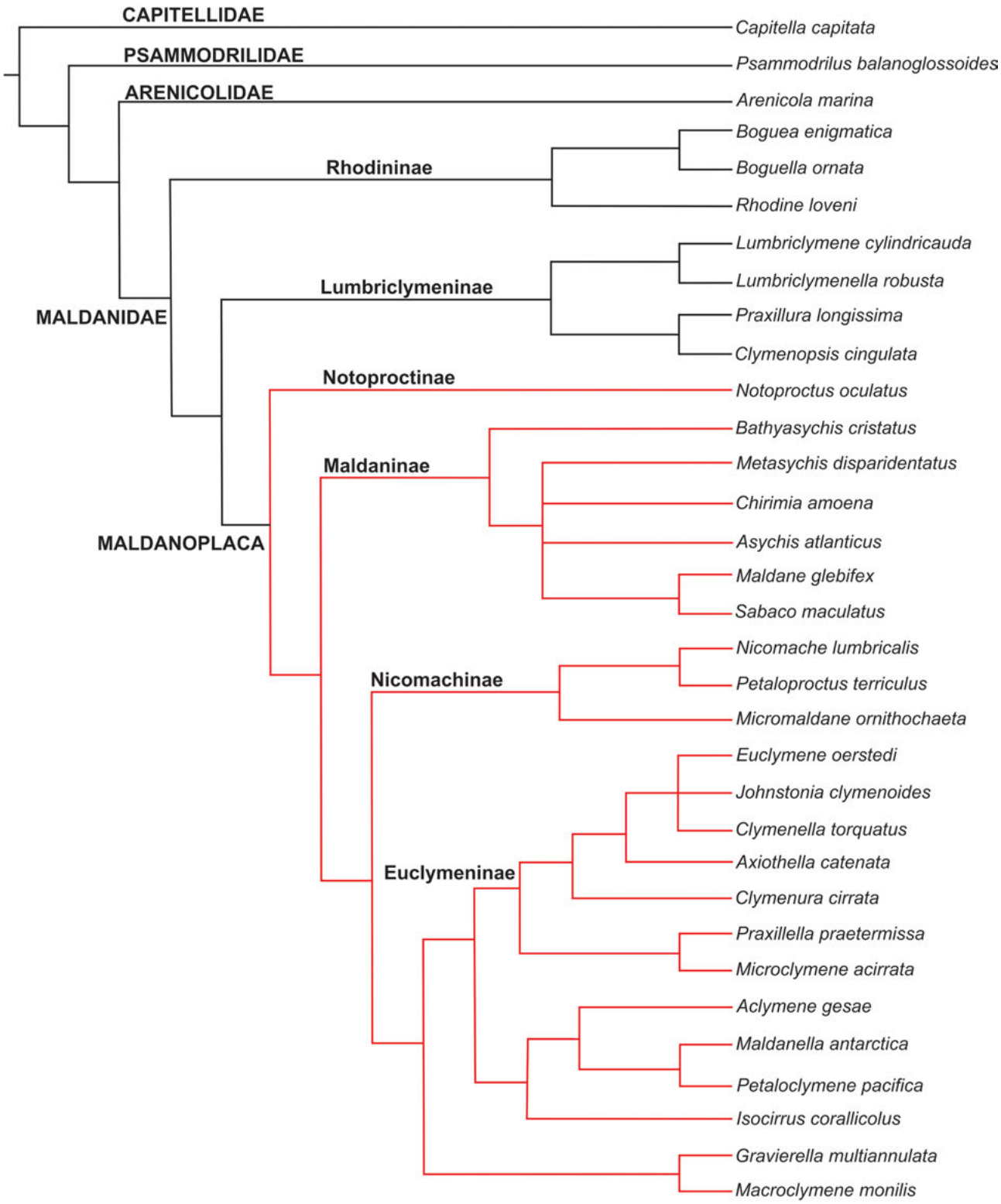


Fig. 7.7.6.7: Proposal of phylogenetic relationships within Maldanidae based on morphological data (modified from De Assis and Christoffersen 2011).

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Diagnosis: Notopodial acicular spines absent; neurochaetae from chaetiger 4 in single or double rows; 22 chaetigers.

***Rhodine* Malmgren, 1865**
Type species: *Rhodine loveni* Malmgren, 1865
7 species.
Diagnosis: Head with transverse ridge on posterior part of peristomium; neurochaetae beginning on chaetiger 5; double rows of uncini in median to posterior chaetigers; chaetiger number not fixed; posterior segments with posteriorly directed collars.

Lumbriclymeninae Arwidsson, 1906
Diagnosis: No cephalic or pygidial plates; prostomium forming a keel; nuchal grooves short and curved; notochaetae of a variety of forms; anterior neurochaetae as acicular spines in anterior chaetigers and rostrate uncini in posterior ones; pygidium conical and long, with many transversal striae, and dark circular rings.

***Lumbriclymene* Sars, 1872**
Type species: *Lumbriclymene cylindricaudata* Sars, 1872
10 species.
Diagnosis: Neurochaetae in the first four chaetigers as acicular spines; 19 or 20 chaetigers and some achaetous prepygidial segments; pygidium forms a long and symmetrical anal cone; with irregular transversal striation in cross-section.

***Lumbriclymenella* Arwidsson, 1911**
Type species: *Lumbriclymenella robusta* Arwidsson, 1911
2 species.
Diagnosis: Neurochaetae in the first four chaetigers as acicular spines; 19 chaetigers and some achaetous prepygidial segments; pygidium forms a simple, flattened cone, curved upward.

***Clymenopsis* Verrill, 1900**
Type species: *Clymene cingulata* Ehlers, 1887 accepted as *Clymenopsis cingulata* (Ehlers, 1887)
4 species.
Diagnosis: Neurochaetae in first three chaetigers as acicular spines; 19 chaetigers and some achaetous prepygidial segments; anteriorly projecting collar on chaetiger 4; pygidium forms a narrow anal cone with numerous narrow rings.

***Praxillura* Verrill, 1880**
Type species: *Praxillura ornata* Verrill, 1880
6 species.
Diagnosis: Neurochaetae in first few chaetigers as acicular spines; their number variable within a species and probably size dependent; neurochaetae may include acicular spines in posterior segments; chaetiger number not fixed; pygidium a short cone.

Notoproctinae Detinova, 1985
Monotypic.
Diagnosis: see *Notoproctus*

***Notoproctus* Arwidsson, 1906**
Type species: *Notoproctus oculatus* Arwidsson, 1906
9 species.
Diagnosis: Cephalic and pygidial plate present; cephalic plate with low rim; prostomium wide, forming a low keel; nuchal grooves strongly curved; notochaetae include thick and long capillaries; neurochaetae as acicular spines or reduced uncini on first four chaetigers; subsequent chaetigers with a row of rostrate uncini; 10 to 17 chaetigers and some achaetous prepygidial segments; pygidium with flat pygidial plate with low rim, anus dorsal to plate.

Maldaninae Malmgren, 1867
Diagnosis: Cephalic and pygidial plate present; cephalic plate large, disc-like, with low rim; prostomium broad, mushroom-shaped, or spade-shaped; forming a low keel and auricular lateral cephalic lobules or low lateral lobules; nuchal grooves strongly curved; notochaetae include thick and long capillaries; neurochaetae with reduced uncini on first four chaetigers; subsequent chaetigers with row of rostrate uncini; 16 to 19 chaetigers and some achaetous prepygidial segments; pygidium with a posterior pygidial plate with well-developed rim, ornamented; anus dorsal to the plate.

***Bathyasychis* Detinova, 1982**
Type species: *Bathyasychis cristatus* Detinova, 1982
1 species.
Diagnosis: Cephalic plate broad; prostomium broad, mushroom-shaped; lateral cephalic lobes suboval, margin entire; keel low and wide; no collar on chaetiger 1; first two chaetiger segments lacking neuropodial uncini; 19 chaetigers and 2 achaetigers; pygidium rudimentary, posterior surface flat or somewhat concave, lacking rim, forming right angle with body axis; no anal valve.

***Metasychis* Light, 1991**
Type species: *Maldane disparidentata* Moore, 1904 accepted as *Metasychis disparidentata* (Moore, 1904)
4 species.
Diagnosis: Cephalic plate mushroom-shaped; prostomium broad, lateral cephalic lobules crenulated or well-developed, with slender cirri; nuchal grooves J- or U-shaped; complete collar on chaetiger 1, sometimes reduced to a thick ventral roll of tissue; notochaetae spirally fringed;

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one achaetous prepygidial segment; 19 chaetigers; pygidium hood-like, with or without cirri, posterior surface with funnel-like pocket; dorsal anus without anal valve.

Chirimia Light, 1991

Type species: *Chrysothemis amoena* Kinberg, 1867 accepted as *Chirimia amoena* (Kinberg, 1866)
5 species.
Diagnosis: Cephalic plate with lateral lobules subrectangular, with entire to dentate margins; prostomium mushroom-shaped; nuchal grooves U-shaped; complete collar on chaetiger 1; notochaetae of spirally fringed type; with one or two achaetous prepygidial segments; 19 chaetigers; pygidium with slight furrow, not foliose but forming a shallow pocket on ventral side; no pygidial cirri.

Asychis Kinberg, 1867

Type species: *Asychis atlanticus* Kinberg, 1867
5 species.
Diagnosis: Lateral cephalic lobules subtriangular or auricular; prostomium prow-like; nuchal grooves J- or U-shaped; posterior surface of cephalic plate with rugose papillae; no collar on chaetiger 1; notochaetae of spirally fringed type; anal mound typically vase-shaped and heavily sculptured; 19 chaetigers and 1 achaetiger; pygidium foliaceous, dorsal lobe cordate, with one to three simple or branched cirri; pygidial lobules form a deep, funnel-like pocket; posterior wall of dorsal lobule bulbous, mushroom-like; no anal valve.

Maldane Grube, 1860

Type species: *Maldane glebifex* Grube, 1860
18 species.
Diagnosis: Prostomium spade-like; lateral cephalic lobules low and entire; nuchal organs straight to slightly curved; no collar on chaetiger 1; notochaetae of spirally fringed type; 19 chaetigers and some achaetous prepygidial segments; pygidium reduced, with anal valve, posterior surface flat, plate-like, no pygidial cirri.

Sabaco Kinberg, 1866

Type species: *Sabaco maculatus* Kinberg, 1866
9 species.
Diagnosis: Cephalic plate with lateral cephalic lobes reduced, forming an entire rim; prostomium spade-like; nuchal organs small, crescentic, separated from cephalic rim; complete collar on chaetiger 1; notochaetae spirally fringed; companion chaetae, with proximal keel; neuropodia with rostrate hooks; no achaetous prepygidial segments or anal valve; chaetiger number not fixed; pygidium trumpet-shaped; no pygidial cirri, but with two large, subtriangular lappets on dorsal lobule.

Euclymeninae Arwidsson, 1906

Diagnosis: Cephalic plate usually present; prostomium may form a low cephalic keel with variously developed rim; nuchal organs straight and parallel; notochaetae include many forms of capillaries; tufts of median notochaetae disposed longitudinally; neurochaetae are acicular spines or reduced uncini on first three chaetigers or more, subsequent ones with uncini; with 18 to 70 chaetigers; segment numbers often fixed; pygidium with anus sunken into a funnel and bordered by cirri; pygidial plate present; anus terminal, sometimes provided with a ventral valve.

Clymenura Verrill, 1900

Type species: *Clymene cirrata* Ehlers, 1887 accepted as *Clymenura cirrata* (Ehlers, 1887)
9 species.
Diagnosis: Cephalic and pygidial plate present; ventral glandular shield on eighth chaetigerous segment; notochaetae include both winged capillaries and feathered forms; the first three chaetigers may be rudimentary uncini or acicular spines; 18 to 19 chaetigers; pygidium forms a projected cone with an anal funnel, bordered by cirri.

Leiochone Grube, 1868

Type species: *Clymene leiopygos* Grube, 1860 accepted as *Leiochone leiopygos* (Grube, 1860)
6 species.
Diagnosis: Cephalic plate absent; nuchal organs straight, length variable, palpode tip bluntly oval; cephalic ocelli usually present; eighth chaetiger with a large ventral glandular shield; notochaetae winged capillaries only; neurochaetae reduced uncini in the first three chaetigers; 19 to 29 chaetigers; up to five achaetous prepygidial segments; pygidium without anal funnel, anal cone prominent, with anal valve peg usually present.

Maldanella McIntosh, 1885

Type species: *Maldanella antarctica* McIntosh, 1885
12 species.
Diagnosis: Cephalic plate present, with a raised margin and several striae on surface; nuchal organs short; notochaetae as winged capillaries, often including feathered forms; chaetiger 1 without neurochaetae and chaetigers 2 and 3 with a reduced number of uncini; 19 chaetigers; pygidium funnel-shaped, with short cirri; anus sunk into the funnel.

Axiothella Verrill, 1900

Type species: *Axiothella catenata* Verrill, 1900
19 species.
Diagnosis: Cephalic plate flattened, with a raised rim; prostomium small, forming a straight keel; notochaetae are winged capillaries and often include feathered forms;

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neurochaetae similar throughout, from the first chaetiger onward, with numerous (6–15 on chaetigers 1–3) avicular and rostrate hooks; 19 to 22 chaetigers; pygidium funnel-shaped; anus sunk into a funnel rimmed with cirri or mere crenulations; no ventral valve.

***Gravierella* Fauvel, 1919**
Type species: *Gravierella multiannulata* Fauvel, 1919
1 species.
Diagnosis: Cephalic plate with a raised rim; prostomium narrow; body with very numerous segments, the posterior ones are campanulate; notochaetae are winged capillaries and often include feathered forms; neurochaetae are rostrate hooks, reduced on first three chaetigers, and similar to all succeeding ones; 60 to 70 chaetigers; pygidium funnel-shaped, with marginal cirri.

***Johnstonia* Quatrefages, 1866**
Type species: *Johnstonia clymenoides* Quatrefages, 1866
Jonhstonia clymenoide is unaccepted, printer error misspelling
5 species.
Diagnosis: Cephalic plate bordered by a raised rim; prostomium large; last few chaetigerous segments bearing rows of vascular cirri; anterior segments with glandular rings and posterior ones with longitudinal belts; notochaetae include winged capillaries and feathered forms; neuropodia of chaetigers 1 to 3 with acicular spines, subsequent ones with rostrate hooks; with 19 to 22 chaetigers; pygidium funnel-shaped, with marginal cirri; anus within funnel.

***Macroclymene* Verrill, 1900**
Type species: *Clymene producta* Lewis, 1897 accepted as *Macroclymene producta* (Lewis, 1897)
5 species.
Diagnosis: Slanting cephalic plate with a raised rim; prostomium narrow; notochaetae include limbate capillaries, slender feathered forms in posterior segments; neuropodia of first three chaetigers with acicular spines with smooth tips; subsequently uncini; body with more than 30 chaetigers; posterior segments short, often campanulate; pygidium funnel-shaped; anus within funnel, with marginal cirri.

***Euclymene* Verrill, 1900**
Type species: *Clymene oerstedii* Claparède, 1863 accepted as *Euclymene oerstedii* (Claparède, 1863)
30 species.
Diagnosis: Slanting cephalic margin with a raised rim; prostomium narrow, nuchal organs straight and parallel; notochaetae include limbate capillaries and slender feathered forms; neuropodia of first three chaetigers with acicular spines on neuropodia; subsequent neurochaetae with uncini; usually a number of achaetous prepygidial segments; 19 to 25 achaetigers; pygidium funnel-shaped, with cirri; anus within anal funnel.

***Praxillella* Verrill, 1881**
Type species: *Praxillella praetermissa* Malmgren, 1865
15 species.
Diagnosis: Cephalic plate with smooth margin and two posterolateral incisions; prostomium narrow, sometimes forming long cirrus; notochaetae include limbate capillaries and slender feathered forms; chaetigers 1 to 3 with acicular spines or reduced uncini; subsequent neurochaetae uncini; a number of achaetous prepygidial segments; 18 to 19 achaetigers; pygidium with a short anal funnel, bordered by cirri; medioventral cirrus long; anus on a protuberant cone and with an enlarged ventral valve.

***Microclymene* Arwidsson, 1906**
Type species: *Microclymene acirrata* Arwidsson, 1906
1 species.
Diagnosis: Cephalic plate entire; prostomium narrow; notochaetae include limbate capillaries and geniculate chaetae; neuropodia of first three chaetigers with acicular spines; subsequent neuropodia with rostrate hooks; 18 to 20 chaetigers; pygidium forming a truncate plate with short border; anus on a protuberant cone; a long cirrus may be present.

***Clymenella* Verrill, 1873**
Type species: *Clymene torquatus* Leidy, 1855 accepted as *Clymenella torquata* (Leidy, 1855)
19 species.
Diagnosis: Cephalic usually entire; prostomium short and broad; nuchal organs long; notochaetae include limbate, bilimbate, and spinulose capillaries; neuropodia of first three chaetigers often with one acicular spine or uncinus; subsequent neuropodia with uncini; chaetiger 4 with deep encircling anterior collar; 18 to 20 chaetigers; pygidium funnel-shaped, with cirri of various lengths; anus within funnel.

***Isocirrus* Arwidsson, 1906**
Type species: *Clymene planiceps* Sars, 1872 accepted as *Isocirrus planiceps* (Sars, 1872)
7 species.
Diagnosis: Cephalic plate oval; prostomium short and broad; nuchal organs straight and parallel, forming a thick furrow; notochaetae include limbate capillaries and spinulose chaetae; neuropodia of first three chaetigers with acicular spines; subsequent neuropodia with uncini; 19 to 20 chaetigers; pygidium funnel-shaped, with cirri of equal lengths; anus within funnel.

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Aclymene Buzhinskaja, 1995

Type species: *Aclymene gesae* Buzhinskaja, 1995
1 species.
Diagnosis: Cephalic plate oval, with crenulated margin; prostomium narrow; notochaetae include limbate capillaries and feathered forms; with reduced uncini on first three neuropodia; subsequent neuropodia with uncini; achaetous prepygidial segments with large tongue-like paired lobules; 18 chaetigers; pygidium funnel-shaped, with cirri; anus within funnel, forming a low cone.

Petaloclymene Augener, 1918

Type species: *Petaloclymene notocera* Augener, 1918
2 species.
Diagnosis: Cephalic plate oval; prostomium short with smooth margin; notochaetae include winged capillaries and feathered forms; with reduced uncini on first three neuropodia; subsequent neuropodia with uncini; two achaetous prepygidial segments; 19 chaetigers; pygidium funnel-shaped, flattened, with well-developed ventral border; dorsal border strongly reduced, with a deep furrow; anus on protuberant cone.

Nicomachinae Arwidsson, 1906

Diagnosis: Prostomium forming a strongly arched cephalic keel; cephalic plate absent; nuchal organs short, slightly curved; notochaetae include limbate capillaries, with serrate blade, extremely elongated spirally coiled chaetae, or geniculate chaetae; neurochaetae acicular spines on first three or four chaetigers or with reduced uncini; subsequent neuropodia with uncini; pygidial plate present; 19 to 37 chaetigers; pygidium funnel-shaped; anus within funnel with smooth rim or bordered by cirri or papillae; anal pore located on level with pygidial plate, no ventral valve.

Petaloproctus Quatrefages, 1865

Type species: *Petaloproctus terricolus* Quatrefages, 1865
10 species.
Diagnosis: Prostomium long cephalic keel; nuchal organs short, strongly curved; anterior chaetigers short, with anterior glandular rings; notochaetae include limbate, spinulous, and very long filamentous pinnate capillaries; neurochaetae acicular spines on first three or more chaetigers, subsequent neuropodia with uncini; 19 to 23 chaetigers, achaetous prepygidial segments may be present; pygidium funnel-shaped, with well-developed ventral border; dorsal border strongly reduced; anus in center of plate.

Micromaldane Mesnil, 1897

Type species: *Micromaldane ornithochaeta* Mesnil, 1897
7 species.
Diagnosis: Prostomium short, cephalic keel strongly arched; nuchal organs strongly curved; notochaetae include stout limbate capillary chaetae, spatulate or straight lancet-type chaetae, and geniculate chaetae; avicular, rostrate hooks strongly curved on all neuropodia; 17 to 19 chaetigers; achaetous prepygidial segments may be present; pygidium funnel-shaped, bordered by crenulations; anus in center of plate; body very small.

Nicomache Malmgren, 1865

Type species: *Sabella lumbricalis* Fabricius, 1780 accepted as *Nicomache lumbricalis* (Fabricius, 1780)
17 species.
Diagnosis: Prostomium long cephalic keel; nuchal organs long and curved; notochaetae include limbate, spinulous, and helicoidal capillaries; neurochaetae acicular spines on first three chaetigers, subsequent neuropodia with uncini; 19 to 37 chaetigers; achaetous prepygidial segments may be present; pygidium funnel-shaped, bordered by cirri; pygidial plate with distal margin in lateral view straight; with well-developed edge dorsally and ventrally.

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References

Arwidsson, I. (1906): *Studien über die skandinavischen und arktischen Maldaniden nebst Zusammenstellung der übrigen bisher bekannten Arten dieser Familie.* Inaugural-Dissertation zur Erlangung der Doktorwürde der Mathematisch-Naturwissenschaftlichen Sektion der Philosophischen Fakultät zu Upsala, Upsala Universitet, Uppsala.

Bartolomaeus, T. & Meyer, K. (1997): Development and phylogenetic significance of hooked setae in Arenicolidae (Polychaeta, Annelida). *Invertebrate Biology* 116: 227–242.

Bartolomaeus, T., Purschke, G. & Hausen, H. (2005): Polychaete phylogeny based on morphological data: A comparison of current attempts. *Hydrobiologia* 535/536: 341–356.

Blainville, H. de. (1828): *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différens étres de la nature, considérés soit eux-mêmes, d'aprés l'état actuel de nos connaissance, soit relativement et l'utilité qu'en peuvent retirer*

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la médicine, l'agriculture, le commerce et les arts. Suive d'une biographie des plus célèbres naturalistes. Vol. 5. FG Levrault, Strasbourg.

Blake, J.A. & Hilbig, B. (1990): Polychaeta from the vicinity of deep-sea hydrothermal vents in the eastern Pacific. II. New species and records from the Juan de Fuca and Explorer Ridge systems. *Pacific Science* 44: 219–253.

Bleidorn, C. & Hausen, H. (2007): *Axiothella isocirra*, a new species of Maldanidae (Annelida; Polychaeta) from Belize. *Proceedings of the Biological Society of Washington* 120: 49–55.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2005): Molecular phylogeny of lugworms (Annelida, Arenicolidae) inferred from three genes. *Molecular Phylogenetics and Evolution* 34: 673–679.

Bleidorn, C., Kruse, I., Albrecht, S. & Bartolomaeus, T. (2006): Mitochondrial sequence data expose the putative cosmopolitan polychaete *Scoloplos armiger* (Annelida, Orbiniidae) as a species complex. *BMC Evolutionary Biology* 6: 47.

Bookhout, C.G. & Horn, E.C. (1949): The development of *Axiothella mucosa* (Andrews). *Journal of Morphology* 84: 145–183.

Brinkmann, N. & Wanninger, A. (2010): Capitellid connections: Contributions from neuromuscular development of the maldanid polychaete *Axiothella rubrocincta* (Annelida). *BMC Evolutionary Biology* 10: 168.

Carr, C.M., Hardy, S.M., Brown, T.M., Macdonald, T.A. & Hebert, P.D.N. (2011): A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS ONE* 6: e22232.

Chamberlin, R.V. (1919): Pacific coast Polychaeta collected by Alexander Agassiz. *Bulletin of the Museum of Comparative Zoology at Harvard University* 63: 251–270.

Clavier, J. (1984): Production due to regeneration by *Euclymene oerstedi* (Claparede) (Polychaeta: Maldanidae) in the maritime basin of the Rance (northern Brittany). *Journal of Experimental Marine Biology and Ecology* 75: 97–106.

Day, J.H. (1967): *A monograph on the Polychaeta of southern Africa. Part 2 Sedentaria*. Publication from the Trustees of the British Museum Natural History, London: 656–878.

Detinova, N.N. (1985): *Taksonomiya, sostav i rasprostenenie Mnogosche tinkovykh thervei polsemeistave Lumbriclymeninae (Maldanidae). pp. 25–29. In Mnogoshchetinkovye tchervei: Morfologiiya, Sistematika, Ekologyia*. Akademiya Nauk. SSSR, Zoologisk Institut, Leningrad: 147 pp. [in Russian]

De Assis, J.E. & Christoffersen, M.L. (2010): *Lumbriclymene interstricta* comb. nov. with a taxonomic key and a catalogue for all species of *Lumbriclymene* (Maldanidae, Polychaeta). *Zoologia* 27: 1008–1013.

De Assis, J.E. & Christoffersen, M.L. (2011): Phylogenetic relationships within Maldanidae (Capitellida: Annelida), based on morphological characters. *Systematics and Biodiversity* 9: 41–55.

De Assis, J.E., Alonso Samiguel, C. & Christoffersen, M.L. (2007a): Two new species of *Nicomache* (Polychaeta: Maldanidae) from the Southwest Atlantic. *Zootaxa* 1454: 27–37.

De Assis, J.E., Alonso Samiguel, C. & Christoffersen, M.L. (2007b): A catalogue and taxonomic keys of the subfamily Nicomachinae (Polychaeta: Maldanidade) of the world. *Zootaxa* 1657: 41–55.

De Assis, J.E., C. Christoffersen, M.L. & Lana, P.C. (2010): Phylogenetic analysis of *Petaloproctus* (Maldanidae, Polychaeta), with description of a new species from southeastern Brazil. *Scientia Marina* 74: 111–120.

Dufour, S.C., White, C., Desrosiers, G. & Juniper, S.K. (2008): Structure and composition of the consolidated mud tube of *Maldane sarsi* (Polychaeta: Maldanidae). *Estuarine Coastal and Shelf Science* 78: 360–368.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–188.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biological Annual Reviews* 17: 193–284.

Fauchald, K. & Rouse, G.W. (1997): Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71–138.

Fauvel, P. (1927). Polychètes sédentaires. Addenda aux errantes, Arachiannélides, Myzostomaires. Faune de France Volume 16. Paul Lechevalier. Paris. 1–494.

Green, K.D. (1994): The head of the Maldanidae polychaetes of the subfamily Maldaninae. *Mémories du Museum National d'Histoire Naturelle Zoology Paris* 162: 101–109.

Green, K.D. (2000): Septa and nephridia of maldanid polychaetes of the subfamily Maldaninae. *Bulletin of Marine Science* 67: 373–389.

Grube, A.E. (1850): Die Familien der Anneliden. *Archiv für Naturgeschichte* 16: 249–364.

Hartline, D.K. & Kong, J.H. (2009): Axonal sheaths in two reportedly myelinated polychaete nervous systems: *Asychis elongata* and *Capitella* sp. I. *Bulletin of the Mount Desert Island Biological Laboratory* 48: 86–87.

Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. *Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* Vol. 58. Gustav Fischer, Jena: 594 pp.

Hausen, H. & Bleidorn, C. (2006): Significance of chaetal arrangements for maldanid systematics (Annelida: Maldanidae). *Scientia Marina* 70: 75–79.

Imajima, M. & Shiraki, Y. (1982a): Maldanidae (Annelida: Polychaeta) from Japan. Part 1. *Bulletin of the National Science Museum of Tokyo, A Zoology* 8: 7–46.

Imajima, M. & Shiraki, Y. (1982b): Maldanidae (Annelida: Polychaeta) from Japan. Part 2. *Bulletin of the National Science Museum of Tokyo, A Zoology* 8: 48–88.

Jennings, R.M. & Halanych, K.M. (2005): Mitochondrial genomes of *Clymenella torquata* (Maldanidae) and *Riftia pachyptila* (Siboglinidae): Evidence for conserved gene order in Annelida. *Molecular Biology and Evolution* 22: 210–222.

Jennings, R.M., Shank, T.M., Mullineaux, L.S. & Halanych, K.M. (2009): Assessment of the Cape Cod phylogeographic break using the bamboo worm *Clymenella torquata* reveals the role of regional water masses in dispersal. *Journal of Heredity* 100: 86–96.

Jiménez-Cueto, M.S. & Salazar-Vallejo, S.I. (1997): Madánidos (Polychaeta) del Caribe Mexicano con una clave para las especies del Gran Caribe. *Revista de Biologia Tropical* 45: 1459–1480.

Johnson, G. (1865): *A Catalogue of the British Non-parasitical Worms in the Collection of the British Museum*. British Museum, London: 365 pp.

Kongsrud, J.A. & Rapp, H.T. (2012): *Nicomache* (*Loxochona*) *lokii* sp. nov. (Annelida: Polychaeta: Maldanidae) from the Loki's Castle vent field: An important structure builder in an Arctic vent system. *Polar Biology* 35: 161–170.

Kudenov, J.D. (1978): Feeding ecology of *Axiothella rubrocincta* (Johnson) (Polychaeta Maldanidae). *Journal of Experimental and Marine Biology and Ecology* 31: 209–221.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Lamarck, J.-B. de. (1818): *Histoire naturelle des Animaux sans Vertèbres, préséntant les caractéres générales et particuliers de ces animaux, leur distributìon, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractéres essentiels de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie*. Vol. 5. Déterville and Verdière, Paris: 612 pp.

Lee, J.H., & Paik, E.I. (1986a): Polychaetous annelids from the Yellow Sea: III. Family Maldanidae (Part 1). *Ocean Research* 8: 13–25.

Lee, J.H., & Paik, E.I. (1986b): Polychaetous annelids from the Yellow Sea: III. Family Maldanidae (Part 2). *Ocean Research* 8: 27–40.

Levin, L., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C. & Thomas, C. (1997): Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *Journal of Marine Research* 55: 595–611.

Light, W.H.J. (1991): Systematic revision of the genera of the Polychaeta subfamily Maldanidae Arwidsson. *Ophelia, Supplement* 5: 133–146.

Mach, M.E., Levings, C.D., McDonald, P.S. & Chan, K.M.A. (2012): An Atlantic infaunal engineer is established in the Northeast Pacific: *Clymenella torquata* (Polychaeta: Maldanidae) on the British Columbia and Washington Coasts. *Biological Invasions* 14: 503–507.

Malmgren, A.J. (1867): Annulata Polychaeta Spitsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. *Öfversigt af Koniglich Vetenskapsakademiens Forhandlingar* 24: 127–235.

Mangum, C.P. (1964): Studies on speciation in maldanid polychaetes of the North American Atlantic coast. II. Distribution and comparative interaction of five sympatric species. *Limnology and Oceanography* 9: 12–26.

McDaniel, J.K. & Banse, K. (1979): A novel method of suspension feeding by the maldanid polychaete *Praxillura maculata*. *Marine Biology* 55: 129–132.

Mesnil, F. (1897): Études de morphologie externe chez les annélides. II. Remarques complémentaires sur les spionidens. *Bulletin des Sciences de France et de Belgique* 30: 83–100.

Newell, G.E. (1951): The life history of *Clymenella torquata* (Leidy) (Polychaeta). *Proceedings of the Zoological Society of London* 121: 561–586.

Nicol, J.A.C. (1948): The giant axons of annelids. *Quarterly Reviews of Biology* 23: 291–323.

Pettibone, M.H. (1954): Marine polychaete worms from Point Barrow, Alaska, with additional records from the North Atlantic and North Pacific. *Proceedings of the United States National Museum* 103: 203–356.

Pilgrim, M. (1966a): The morphology of the head, thorax, proboscis apparatus and pygidium of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*. *Journal of Zoology* 148: 453–475.

Pilgrim, M. (1966b): The anatomy and histology of the blood system of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi Journal of Zoology* 149: 242–261.

Pilgrim, M. (1977): The functional morphology and possible taxonomic significance of the parapodia of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*. *Journal of Morphology* 152: 281–302.

Pilgrim, M. (1978): The anatomy and histology of the nervous system and excretory system of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*. *Journal of Morphology* 155: 311–326.

Purschke, G. (2005): Sense organs in polychaetes. *Hydrobiologia* 535/536: 53–78.

Purschke, G. & Hausen, H. (2007): Lateral organs in sedentary polychaetes (Annelida) — Ultrastructure and phylogenetic significance of an insufficiently known sense organ. *Acta Zoologica (Stockholm)* 88: 23–39.

Ratnasingham, S. & Hebert, P.D.N. (2007): BOLD: The Barcode of Life data system (www.barcodinglife.org). *Molecular Ecology Notes* 7: 355–364.

Read, G.B. (2011): A new *Clymenura* (Polychaeta: Maldanidae) from the intertidal of Banks Peninsula, New Zealand, with a reassessment of *Leiochone* Grube, 1868 and *Clymenura* Verrill, 1900. *Zootaxa* 2934: 39–52.

Rioja, E. (1925): Observaciones sobre *Micromaldane ornithochaeta* Mesnil. *Boletín de la Real Sociedad Española* 25: 22–30.

Rouse, G.W. (1990): Four new species of *Micromaldane* (Polychaeta: Maldanidae) from Eastern Australia. *Records of the Australian Museum* 42: 209–219.

Rouse, G.W. (1992): Oogenesis and larval development in *Micromaldane* spp. (Polychaeta: Capitellida: Maldanidae). *Invertebrate Reproduction and Development* 21: 215–230.

Rouse, G.W. (2001): Maldanidae Malmgren, 1867. In: Rouse G.W. & Pleijel F. (eds.), *Polychaetes*. Oxford University Press, Oxford: 49–52.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Savigny, J.C. (1822): *Système des annélides, principalement de celles des côtes de l'Égypte et de la Syrie, offran les caractéres tant distinctifs que naturels des Ordres, families et Genres, avec la Description des Espéces. Description de l'Égypte Histoire Naturalle*. l'Imprimerie Impériale, Paris: 128 pp.

Tzetlin, A.B. (1991): Evolution of feeding apparatus in the polychaetes of the order Capitellida. *Zoologicheskii Zhurnal* 70: 10–22. [in Russian]

Tzetlin, A.B. & Markelova, N.P. (1986): Asexual reproduction in the maldanid worm *Maldane sarsi* (Annelida, Polychaeta). *Doklady Akademii Nauk SSSR* 288: 763–765. [in Russian]

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535/536: 199–255.

Ullman, A. & Bookhout, C.G. (1949): The histology of the digestive tract of *Clymenella torquata* (Leidy). *Journal of Morphology* 84: 31–55.

Wilson, W.H. (1983): Life-history evidence for sibling species in *Axiothella rubrocincta* (Polychaeta, Maldanidae). *Marine Biology* 76: 279–300.

Wolf, P.S. (1983): A revision of the Bogueidae Hartman & Fauchald, 1971, and its reduction to Bogueinae, a new subfamily of Madanidae (Polychaeta). *Proceedings of the Biological Society of Washington* 96: 238–249.

Wolf, P.S. (1984): Family Maldanidae Malmgren 1867. In: Uebelacker, M. & Johnson, P.G. (eds.), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, Vol 2. Final Reports to the Minerals Management Service, Contract 14-12-00129091*. Barry A. Vitor & Ass. Mobile, Alabama: 15–21.

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Katrine Worsaae and Reinhardt M. Kristensen

7.8 Sedentaria incertae sedis: Diurodrilidae Kristensen & Niilonen, 1982

Introduction

Diurodrilidae is an exclusively meiofaunal annelid family, the members of which all exhibit a relatively conserved morphology, being 250 to 500 µm long and 50 to 80 µm wide, comprising an elongated head and a short, seemingly unsegmented, hyaline, dorsoventrally flattened body with two to four terminal toes (Figs. 7.8.1–7.8.5). They have no appendages, chaetae, parapodia, or nuchal organs but dorsally and laterally possess compound and single sensory cilia and ventrally carry dense multiciliated cells (ciliophores) on both head and trunk. The elongated anterior part of the head (prostomium) holds the brain and ventrally exhibits a dense species-specific pattern of large ovoid ciliophores with long internal rootlets, lined by two long-necked glands opening on the anterior ventral side. The posterior head (presumed peristomium) carries the pharynx with ciliophores found along each lateral side of the ventral mouth opening and fusing midventrally along the trunk. The number of trunk segments is debated but may range from two to five segments, some or all of which carry midventral rows of trunk ciliophores, followed by a posterior ciliated area anterior to the ventroterminal anus (sometimes on a protruding anal

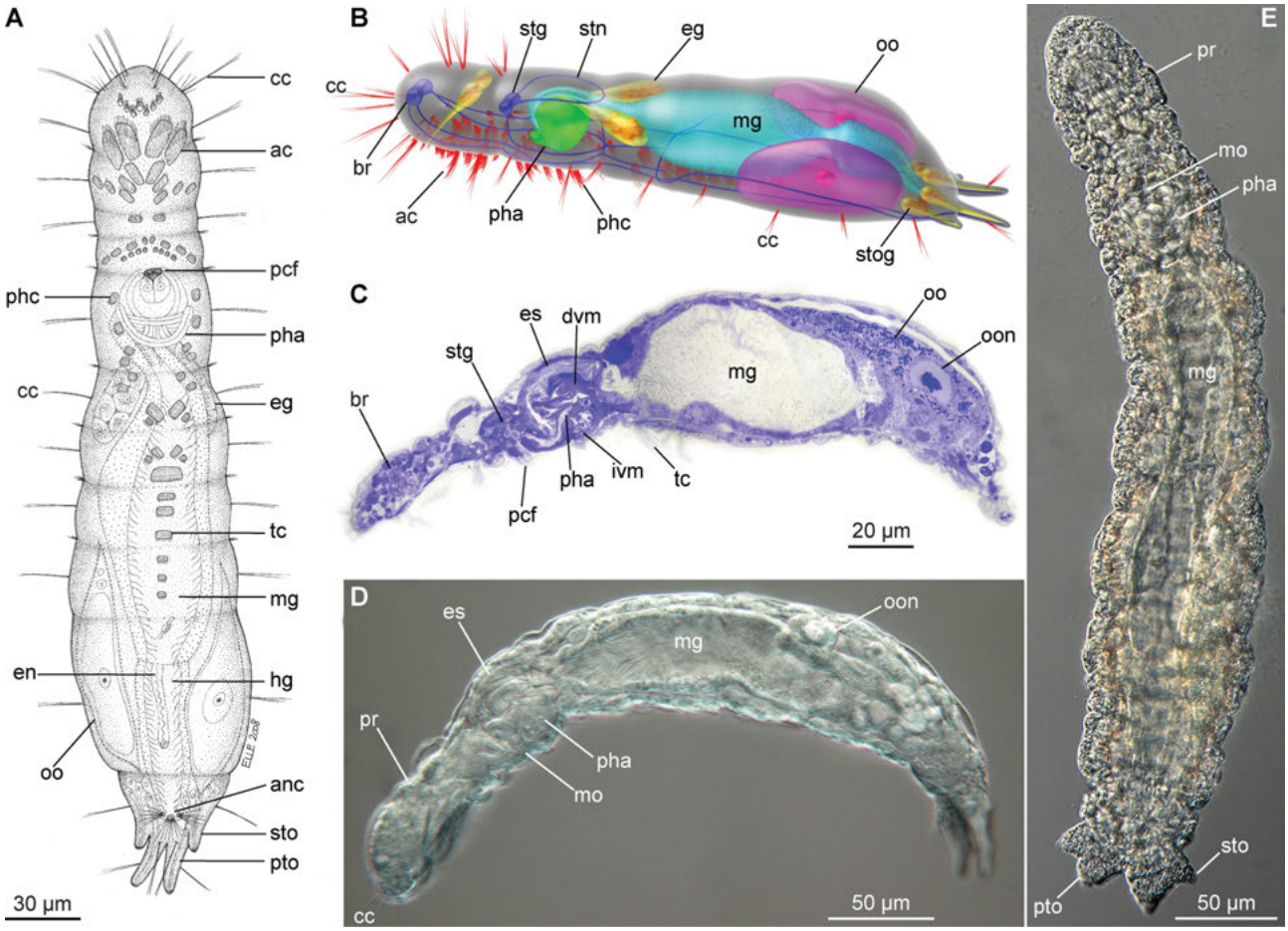


Fig. 7.8.1: A, Drawing of *Diurodrilus* sp. (Queensland, Australia), ventral side; B, Schematic illustration of *Diurodrilus* sp. (South Australia, Australia); C, Light microscopy (LM) micrograph of toluidine blue-stained semithick (~0.5-µm-thick) sagittal section of *Diurodrilus* sp. (Queensland, Australia); D, LM micrographs of *Diurodrilus* cf. *dohrni* (Lanzarote, Spain), lateral view; E, *Diurodrilus subterraneus* (Ystad, Sweden), dorsal view. ac, anterior head ciliophore; anc, anal ciliary field; br, brain; cc, compound cilia; dvm, dorsoventrally directed investing pharynx muscles; eg, esophageal gland; en, enteronephridium; es, esophagus; hg, hindgut; ivm, inner ventral ring extensions of investing muscles; mg, midgut; mo, mouth opening; pcf, prepharyngeal ciliary field; pha, pharynx; phc, peripharyngeal ciliophore; pr, prostomium; pto, primary toe; ptog, primary toe gland; oo, oocyte; oon, oocyte nucleus; stn, stomatogastric nerve ring; sto, secondary toe; stog, secondary toe gland; tc, trunk ciliophore; tgn, toe gland neck.

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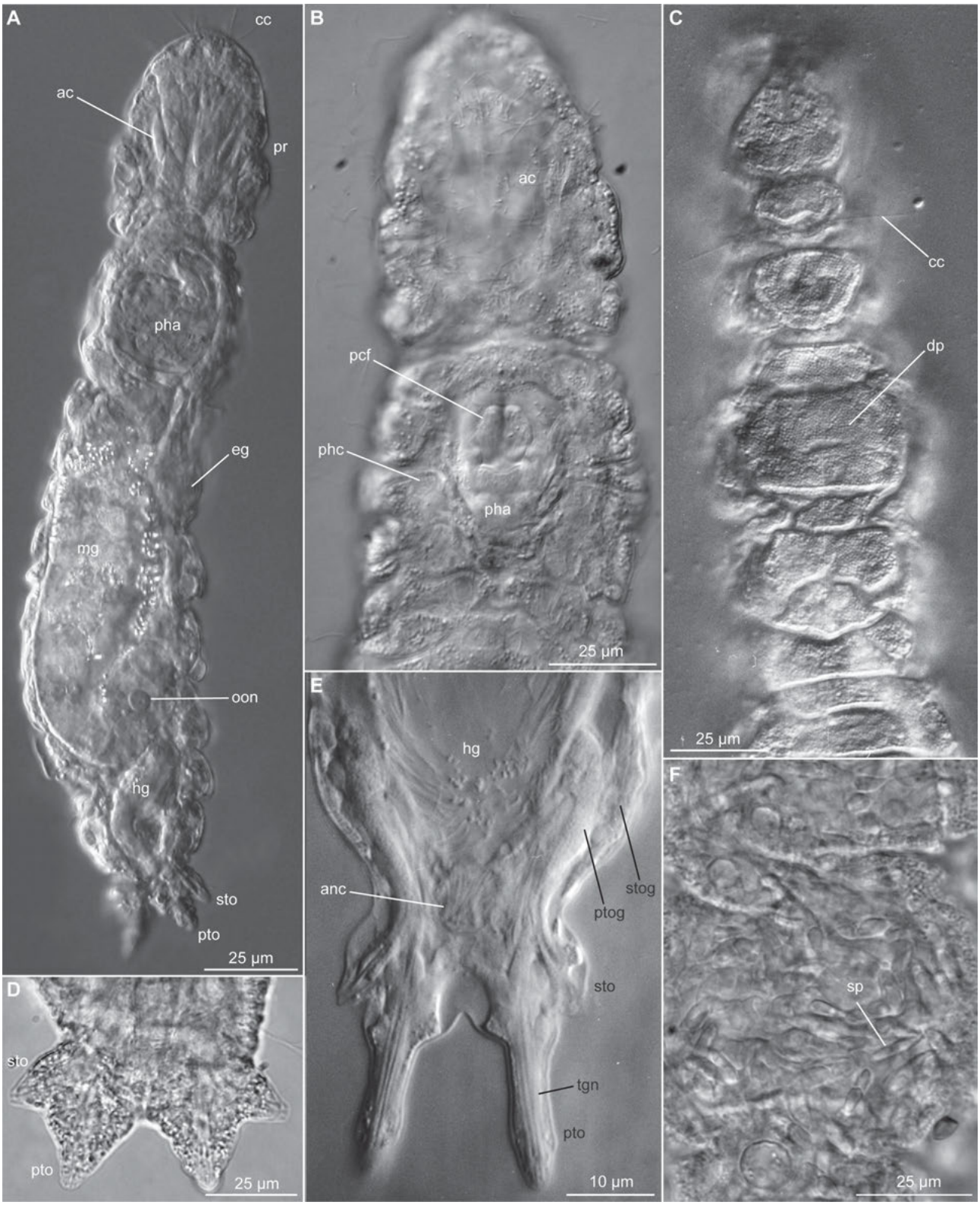


Fig. 7.8.2: LM micrographs. A, *Diurodrilus* sp. (Asamushi, Aomori, Japan); B, D, F, *D. subterraneus* (Ystad, Sweden); C, E, *Diurodrilus* sp. (Queensland, Australia); A, Overview, ventral side; B, Anterior end, ventral side; C, Anterior end, dorsal view of dorsal plates; D, Pygidial toes; E, Posterior end with toe glands; F, Sperm. ac, anterior head ciliophore; anc, anal ciliary field; cc, compound cilia; dp, dorsal plate; eg, esophageal gland; hg, hindgut; mg, midgut; pcf, prepharyngeal ciliary field; pha, pharynx; phc, peripharyngeal ciliophore; oon, oocyte nucleus; pr, prostomium; pto, primary toe; ptog, primary toe gland; sp, sperm cell; sto, secondary toe; stog, secondary toe gland; tgn, toe gland neck.

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cone). The mouth opening is anteriorly demarcated by two dense ciliary tufts and ventrolaterally enclosed by nonciliated, cuticular enforcements. The mouth cavity contains a muscular bowl-shaped pharynx and continues dorsally into the heavily ciliated esophagus, posteriorly lined by two esophageal glands, before entering the ciliated gut. All species are gonochoristic; males with two posterior gonopores and female openings not yet described.

The family contains one genus, *Diurodrilus*, with 7 described species and potentially more than 10 undescribed species. The different species are highly similar in morphology but can be distinguished by a combination of relative length of primary and secondary toes, configuration of toe glands, absence/presence of an anal cone, pattern of head and trunk ciliophores, and sperm morphology. Based on these characteristics, the following seven species are described: *D. minimus* Remane, 1925, *D. subterraneus* Remane, 1934, *D. dohrni* Gerlach, 1952, *Diurodrilus benazzii* Gerlach, 1953, *Diurodrilus ankeli* Ax, 1967, *Diurodrilus westheidei* Kristensen & Niilonen, 1982, and *Diurodrilus kunii* Kajihari, Ikoma, Yamasaki & Hiruta, 2019 (Remane 1925, 1934, Gerlach 1952, 1953, Ax 1967, Kristensen and Niilonen 1982, Kajihari et al. 2019).

All species are exclusively meiofaunal and interstitial, living in the interstices of medium to coarse sand substrate. They are reported from intertidal and shallow subtidal marine waters down to 60 m depth (Rieger and Rieger 1976, Villora-Moreno 1996 and references herein). Whereas *D. minimus*, *D. westheidei*, *D. ankeli*, and *D. dohrni* are reported from the lower tidal zone and subtidal waters, *D. benazzii*, *D. subterraneus*, and *D. kunii* are all restricted to the moist parts of the littoral zone and often found in the subterranean phreatic system, where fresh groundwater may mix with saline coastal waters (e.g., Remane 1934, Delamare-Deboutteville 1960, Fize 1963, Schmidt 1969, 1972b, Villora-Moreno 1996). The family seemingly has a worldwide distribution across tropic, temperate, and polar regions with reports from the East and West Atlantic Ocean, Mediterranean Sea, Indian Ocean, and East and West Pacific Ocean (see Taxonomy section).

Due to a poorly segmented, ventral nervous system (demonstrated by Worsaae and Rouse 2008) and lack of other significant annelid characteristics such as chaetae, head appendages, parapodia, and nuchal organs, the annelid affinity of Diurodrilidae has been debated (e.g., Rieger and Rieger 1976, Worsaae and Kristensen 2005, Worsaae and Rouse 2008). Furthermore, the first phylogenetic study based on SSU and LSU rDNA data alone did not position *Diurodrilus* among annelids but next to Micrognathozoa (Gnathifera) (Worsaae and Rouse 2008). However, now, both a mitochondrial genomic study (Golombek et al. 2013) and two comprehensive phylogenomic studies (Laumer et al. 2015, Struck et al. 2015) have clearly established its annelid status, with the family possibly nesting within Orbinida next to *Apharyngtus* (Struck et al. 2015, Martin-Duran et al. unpublished observations). The conclusion hereof is that the morphology of *Diurodrilus* most likely represents an intriguing and extreme case of paedomorphosis (see Systematics section).

Morphology

Integument

Cuticle and dorsal plates. The epidermal cells of diurodrilids are nonciliated, except for ciliophores and compound cilia (treated below). The epidermal cells secrete a thin cuticle lacking collagen and consisting only of a loose fibrous matrix composed of a thin outer layer with a trilaminar structure and a thicker, less electron-dense, inner layer of densely packed fibers (Fig. 7.8.5B, D). This matrix is occasionally penetrated by thin microvillus-like projections of the epidermal cell processes, which may also secrete the outer layer of electron-dense membrane-bounded bodies covered by small granules with interconnecting fine threadlike fibers (Fig. 7.8.5D) (and sometimes creating a regular hexagonal pattern) (Rieger and Rieger 1976, Kristensen and Niilonen 1982, Worsaae and Rouse 2008).

In a few species, a striking pattern of dorsal cuticular plates on the head and trunk has been observed on live animals in LM (Fig. 7.8.2C) (Ax 1967, Mock 1981, Paxton 2000), which, however, seems to disappear during fixation for TEM and is not present in all species observed alive. The dorsal plates do not follow a clear pattern of five segments as sometimes proposed.

Ciliophores and sensory structures. The external ciliation in diurodrilids encompasses ventral multiciliated cells (ciliophores) and ventral, lateral, and dorsal compound sensory cilia (Figs. 7.8.1A–D, 7.8.2A, B, 7.8.3, 7.8.4, 7.8.5A). Each epidermal ciliophore has cilia regularly arranged in multiple rows, all with very long ciliary rootlets and beating in unison as a brush in an anteroposterior direction. The ciliophores are innervated and may, in some cases, have fine muscles inserting onto them (Ax 1967, Kristensen and Niilonen 1982, Worsaae and Rouse 2008). The distinct pattern of ciliophores is species specific but follows an overall configuration (e.g., Worsaae and Rouse 2008): (1) small round and large ovoid-shaped ciliophores on the ventral anterior head; (2) two round ciliophores anterior to the mouth opening (beating asynchronously and continuously, strongly innervated by neurons of the prebuccal/stomatogastric ganglion and overlooked in earlier species descriptions); (3) several smaller, round

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or rectangular ciliophores laterally lining the mouth opening, which in the anterior trunk fuse to form a (4) locomotory discontinuous midventral band of ciliophore rows (each with two to four ciliophores) extending along the trunk to various degrees in different species. Lastly, a preanal ciliary field is found in all species.

Nuchal organs have never been found in Diurodrilidae, but it cannot be ruled out that some of the presumed head ciliophores may instead represent nuchal organs, although these are so far all reported to beat in unison and hence unlikely to represent nuchal organs.

The pattern of long, presumably sensory, cilia (compound cilia) varies slightly between the species, but tufts are always found on the lateral and dorsal surfaces of the head and toes and along the lateral surfaces of the trunk (Figs. 7.8.1A, B, 7.8.4A, C, 7.8.5A). The prostomium carries up to three lateral, four frontal/dorsal, and one to two dorsoposterior pairs of compound cilia. The peristomium carries one pair of lateral tufts, the trunk carries five pairs, and the pygidial toes each carry a few tufts. Each tuft is connected at their base with neurites leading either directly or via peripheral nerves to the main ganglia (Worsaae and Rouse 2008).

Adhesive glands. Large prostomial and pygidial adhesive glands are found consistently in all investigated diurodrilids (e.g., Kristensen and Niilonen 1982, Worsaae and Rouse 2008).

The prostomial adhesive glands are located dorsoposteriorly in the prostomium and comprise two cell types with long gland necks extending anteriorly (on each side of the brain) to open at the laterofrontal margin of the head (Figs. 7.8.1B, 7.8.5A). The posteriormost of these are large gland cells (30–40 μm) with small secretory granules, the gland necks of which are proximally lined by the cell bodies of the anteriormost and smaller gland cells (15–20 μm), containing few and large secretory granules (Kristensen and Niilonen 1982, Worsaae and Rouse 2008).

The cell bodies of the adhesive toe glands are positioned in the posteriormost trunk and via long necks open distally at the tip of the toes (Figs. 7.8.1A, B, 7.8.2E, 7.8.3C, D, 7.8.4E). Both primary and secondary glands (if existing) consist of each three to four cells, but the primary toe glands contain few and small secretory granules, whereas the secondary toe glands are densely packed with large granules (Kristensen and Niilonen 1982, Worsaae and Rouse 2008), indicating a combined duo-gland function (adhesion and release) of the two glandular types.

Body wall and pharyngeal musculature

The organization and ultrastructural details of the muscle system of the four species of *Diurodrilus* so far studied with CLSM or TEM are remarkably similar, with identical numbers and configuration of both longitudinal and circular muscles as well as the pharyngeal musculature (Fig. 7.8.4A, C). All body wall muscles are obliquely striated and the organization of circular muscles shows no pattern of segmentation (Worsaae and Rouse 2008).

The longitudinal musculature comprises two main ventral, two paramedian, two minor median, and two main dorsal muscle bundles. The two main ventral muscle strands extend from the anterior margin of the head to the tip of the anal toes. Anterior to the pharynx, they split into several lateral and ventral bundles, each of which again branches into multiple finer muscles inserting at the lateral and frontal margins of the head. The two paramedian ventral muscles may be regarded as a part of the paired main ventral bundles, running alongside these in the trunk, but insert posteriorly at the anal sphincter muscle and originate midventrally, ventroanterior to the pharynx, here possibly creating anchor points for the two groups of large ovoid head ciliophores. The two minor median muscles originate anteriorly next to the paramedian muscles but continue along the trunk median to the paramedian pair. Two large muscle strands are found middorsally, extending from the frontal head margin to the anus, but along the posterior trunk branch out dorsolaterally into four to eight muscles and anterior to the pharynx likewise separate into several thinner fibers, projecting laterally and anteriorly toward the frontal margin of the head (Worsaae and Rouse 2008).

About 20 thin, outer circular muscles are found distributed along the entire body (2–6 μm apart), each making a full transverse circle around the body, except for a small midventral gap. A seemingly similar number of muscles are found in species of differing sizes (3 in the head and 17 in the trunk) but never showing a distinct serial arrangement that could indicate segment borders (Worsaae and Rouse 2008).

The anteriorly directed, semicircular, bowl-shaped muscular organ of the pharynx (Fig. 7.8.4A, C) is composed of investing muscles and a few transverse muscles, forming a layer of obliquely striated musculature around at least two pairs of large glands (Worsaae and Rouse 2008).

A pair of closely adjoined, flattened muscle bundles extend dorsoventrally along the posterior pharyngeal lumen to form a semicircular bowl structure with an anteriorly directed opening (Fig. 7.8.4A, C). The lateralmost fibers extend in an anteroposterior direction rather than dorsoventrally, thereby crossing the dorsoventrally directed muscles on the posteriormost side of the pharyngeal bowl. Some additional transverse muscles connect the inner lateral sides of the bowl ventrally. Two thin

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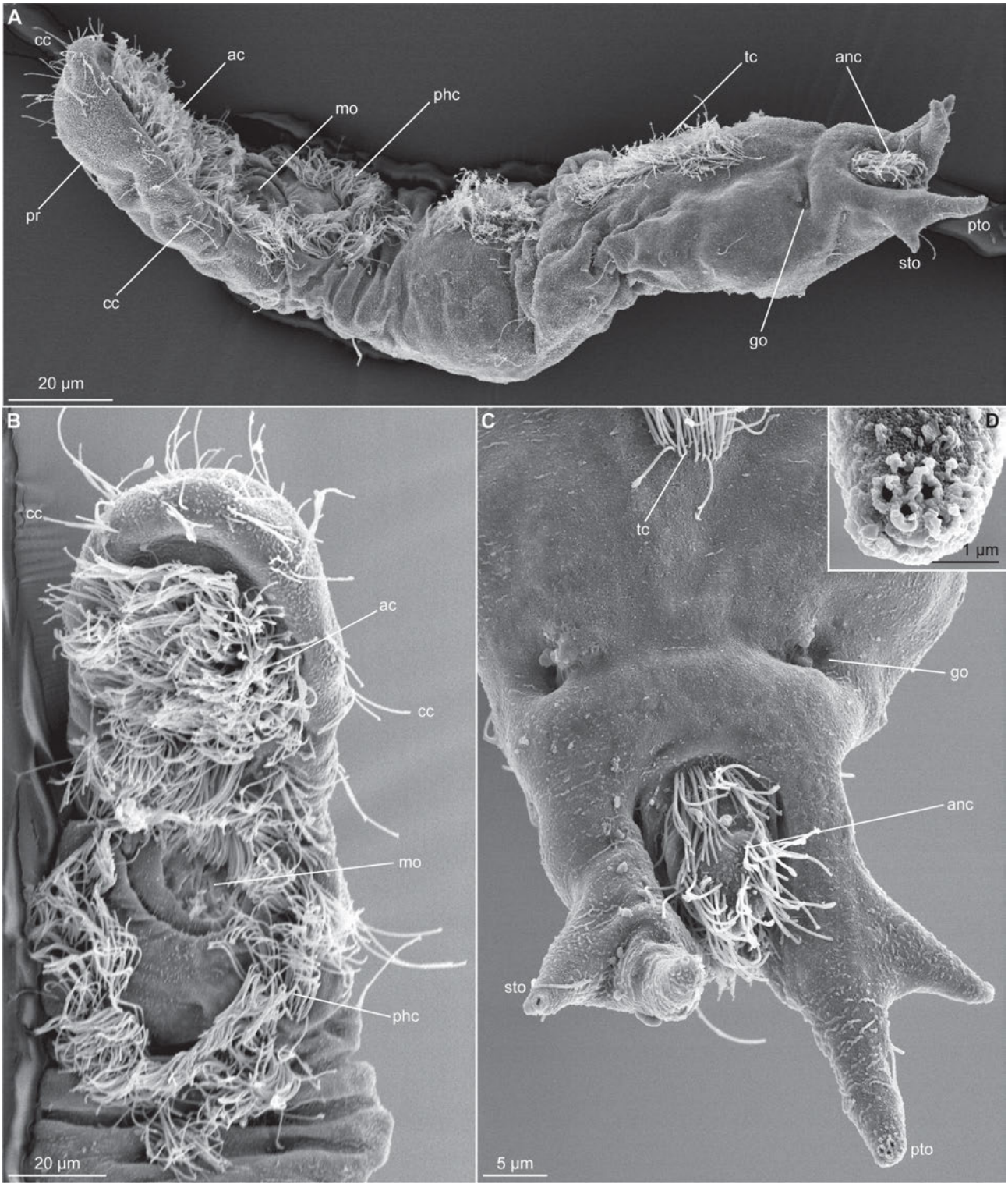


Fig. 7.8.3: Scanning electron microscopy (SEM) micrographs of *Diurodrilus minimus* (Ærø, Denmark). A, Lateroventral view; B, Anterior end, ventral view; C, Posterior end, ventral view; D, Primary toe, gland openings. ac, anterior head ciliophore; anc, anal ciliary field; cc, compound cilia; go, gonopore opening; mo, mouth opening; phc, peripharyngeal ciliophore; pr, prostomium; pto, primary toe; sto, secondary toe; tc, trunk ciliophore.

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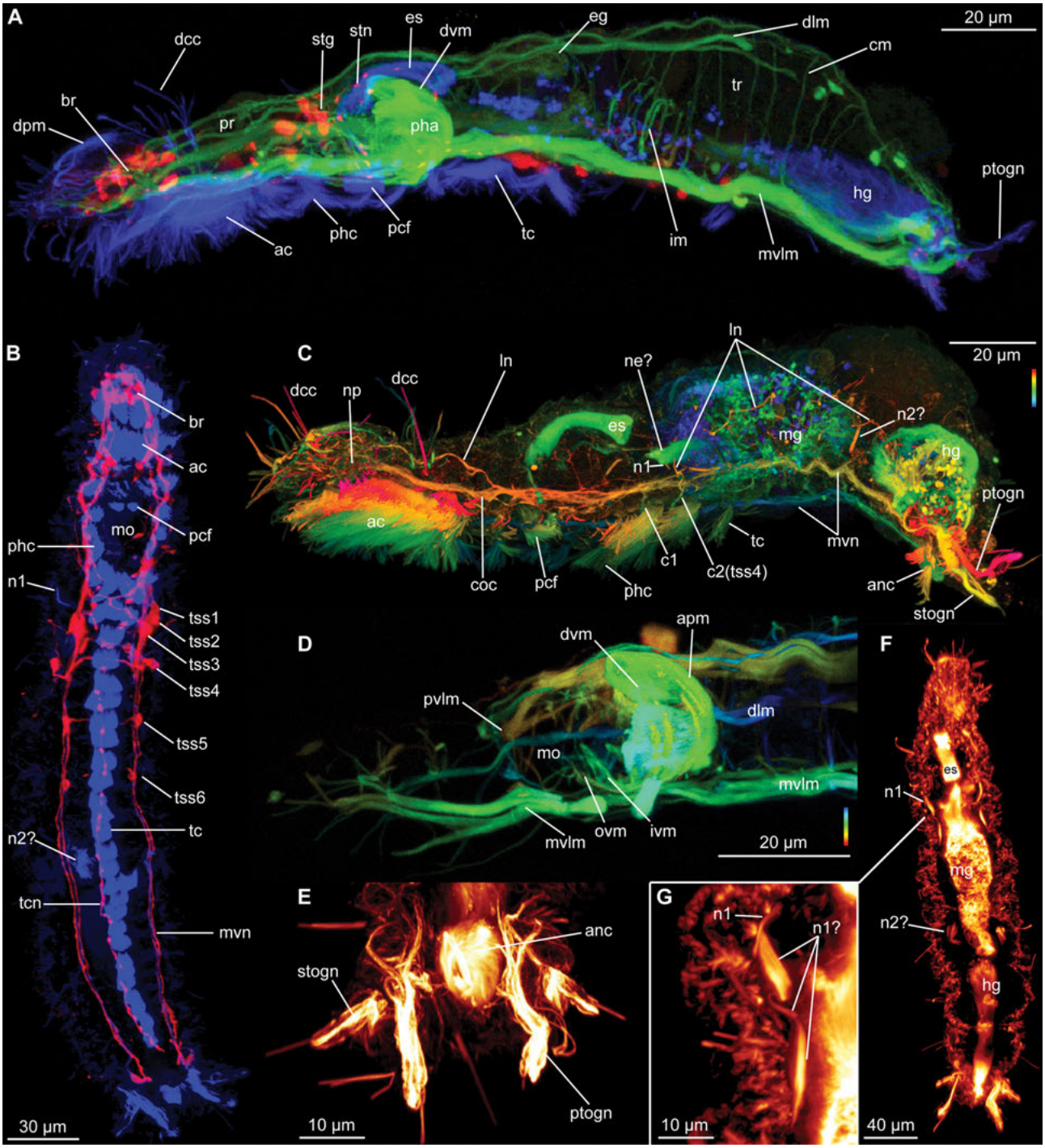


Fig. 7.8.4: Confocal laser scanning microscopy (CLSM), maximum intensity or depth-coded projection of Z-stack images. A, *Diurodrilus* sp. (South Australia, Australia), lateral view showing F-actin labeling (green), anti-acetylated α-tubulin-like immunoreactivity (LIR) (blue), and anti-serotonin LIR (red); B, *D. subterraneus* anti-acetylated α-tubulin LIR (blue) and anti-serotonin LIR (red); C, *D. dohrni* anti-tyrosinated tubulin LIR, depth scale through Z-stack follows the colors of the spectral light; D, *Diurodrilus* sp. (Queensland, Australia), F-actin labeling, depth scale through Z-stack follows the colors of the spectral light; E–G, *D. subterraneus*, anti-α-tubulin LIR. ac, anterior head ciliophore; anc, anal ciliary field; apm, anteroposteriorly directed investing pharynx muscles; br, brain; c1, c2, commissure 1, 2; cm, outer circular musculature; coc, circumesophageal connective; dcc, dorsal compound cilia; dlm, dorsal longitudinal muscle strand; dpn, dorsal posterior nerve loop; dvm, dorsoventrally directed investing pharynx muscles; eg, esophageal gland; es, esophagus; hg, hindgut; im, intestinal ring musculature; ivm, inner ventral ring extensions of investing muscles; ln, lateral nerve; mg, midgut; mo, mouth opening; mvn, longitudinal main ventral nerve; mvlm, main ventral longitudinal muscle strand; n1, n2, nephridium 1, 2; np, neuropil; ovm, outer ventral ring extensions of investing muscles; pcf, prepharyngeal ciliary field; pha, pharynx; phc, peripharyngeal ciliophore; pr, prostomium; ptogn, primary toe gland neck; stg, stomatogastric "ganglion"; stogn, secondary toe gland neck; stn, stomatogastric nerve ring; tc, trunk ciliophore; tcn, trunk ciliophore nerve; tss1–6, first to sixth pairs of trunk anti-serotonin LIR somata.

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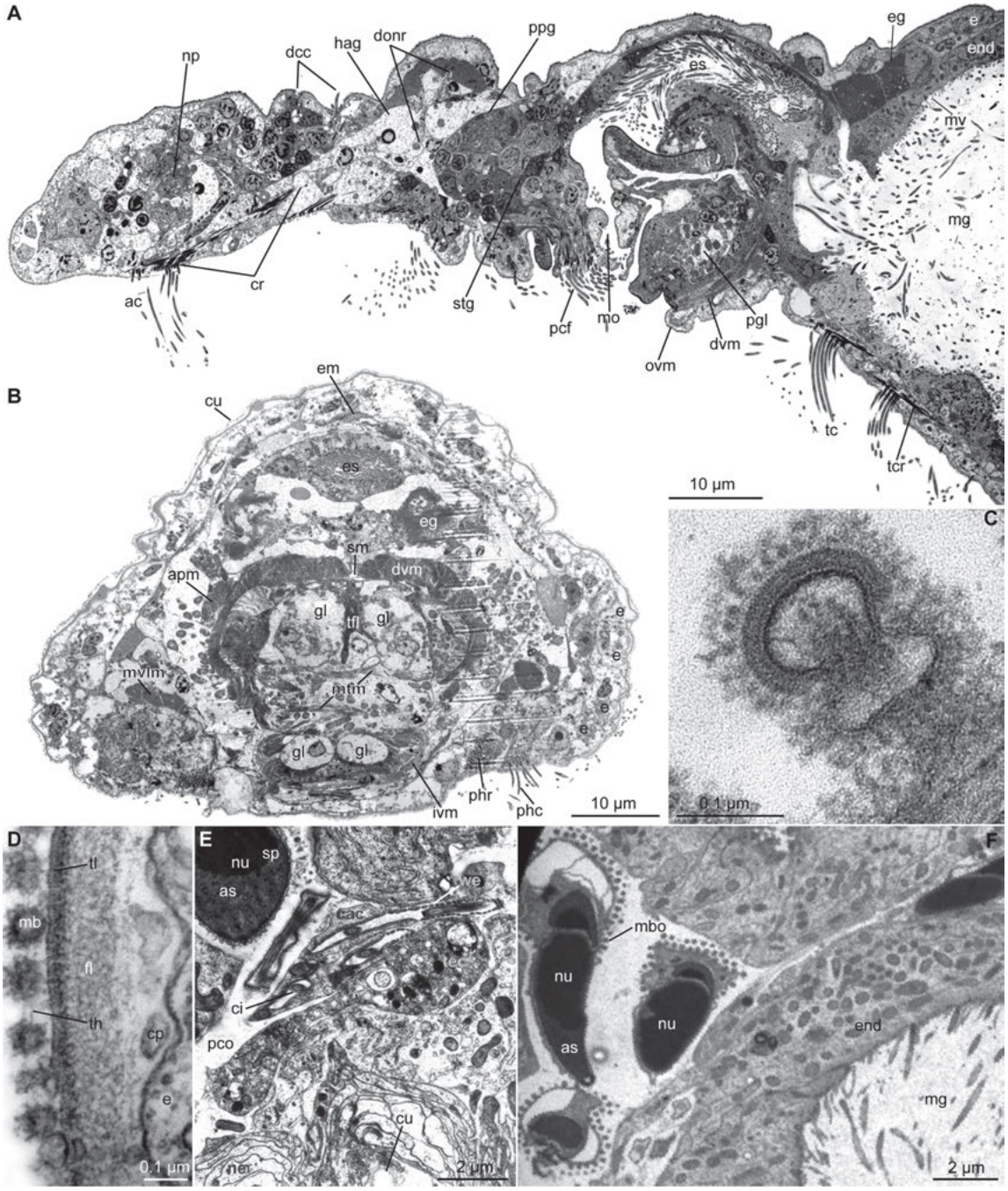


Fig. 7.8.5: Transmission electron microscopy (TEM) micrographs. A, *Diurodrilus* sp. (Queensland, Australia), median sagittal section, anterior end; B, *D. minimus* (Roscoff, France), transverse sections in posterior part of pharyngeal organ, overview; C, *D. subterraneus* (Ystad, Sweden); C, Mushroom body of sperm cuticle; D, *Diurodrilus* sp. (South Australia, Australia), cuticle in transverse section; E, F, *D. subterraneus*, cross-sections of the second protonephridium, sperm and gut in the middle trunk. ac, anterior head ciliophore; apm, anteroposteriorly directed investing pharynx muscles; as, acrosome; cac, canal cell; ci, cilium; cr, anterior head ciliophore rootlet; cu, cuticle; cp, epidermal cell processes; dcc, dorsal compound cilia; donr, neurite innervating dorsal organ; dvm, dorsoventrally directed investing pharynx muscles; e, epidermis cell; eg, esophageal gland; em, extracellular matrix; end, endoderm; es, esophagus; fl, fibrous inner matrix layer; gl, gland cell; hag, head adhesive glands; ivm, inner ventral ring extensions of investing muscles; mb, membrane-bounded bodies; mbo, mushroom body; mg, midgut; ml, median cuticularized lobe; mo, mouth opening; mtm, medial transverse pharynx muscles; mv, microvilli; mvlm, main ventral longitudinal muscle; ne, ventral cord nerve; np, neuropil; nu, nucleus; ovm, outer ventral ring extensions of investing muscles; pcf, prepharyngeal ciliary field; pco, pseudocoel; pgl, pharyngeal gland; phc, peripharyngeal ciliophore; phr, peripharyngeal ciliophore rootlet; ppg, prepharyngeal gland; sm, sagittal midline; sp, sperm cell; stg, stomatogastric "ganglion"; tc, trunk ciliophore; tcr, trunk ciliophore ciliary rootlet; tec, terminal cell; tfl, tonofilament-like structure; th, threadlike connections of epicuticular projections; tl, trilaminar outer matrix layer; we, weir.

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muscles extend anteriorly from the ventralmost side of the dorsoventrally directed bowl muscles, creating an inner ventral ring surrounding the labial lobes and central mouth opening. External to these, some of the anteroposteriorly directed muscle fibers extend to form an additional second outer ventral ring, meeting the inner ring in front of the mouth. The lateral lobes are further supported by many transverse muscle fibers, indicating the ability of the lobes to move and retract laterally.

The muscular pharynx is noneversible and does not represent a dense muscle bulbus such as found in Dinophilidae and several other annelids (Tzetlin and Purschke 2005), but intriguingly, a muscular pharynx is completely lacking in the proposed sister taxon of Diurodrilidae, *Apharyngtus* (see Westheide 2019), questioning the origin of the specialized pharyngeal musculature in Diurodrilidae. Food particles (detritus and algae) are instead brushed into the mouth by the cilia of the prepharyngeal ciliary field. The muscularized nonciliated inner labial lobes and inner circular muscles of the ventral pharynx contract and expand the mouth opening, possibly aiding to the suction of particles into the mouth cavity.

Alimentary tract

The alimentary tract extends from a ventral oval mouth opening in the peristomium (posterior to the elongated prostomium) to the terminal anus. The mouth cavity is nonciliated followed by a densely ciliated esophagus, which opens into the foregut. The gut is ciliated throughout but more densely in the hindgut part. Inner circular muscles are serially repeated along the gut (most obviously in the middle part), with the distinct anteriormost and posteriormost ones representing the mouth and anus sphincter muscles, respectively. Some of the circular muscles around the gut may likewise act as sphincter muscles, constricting the transition between the esophagus and the gut as well as between the midgut and the hindgut (Worsaae and Rouse 2008). Kajihari et al. (2019) suggested that the foregut may furthermore be delineated from a midgut region.

Diurodrilids possess an oval nonciliated mouth opening with paired inner lateral labial lobes and an unpaired median lobe, all surrounded by two cuticular rings. The inner cuticular ring and the dorsal and frontal surfaces of the pharyngeal organ are covered by a thick cuticle composed of a smooth supramicrovillous electron-dense coating and a thick less dense fibrous inner layer, overlaying a palisade of microvilli with dense tips that do not penetrate the surface layer.

At least four glandular complexes open into the mouth cavity and esophagus: (1) A central, unpaired, peristomial gland is found dorsoanterior to the mouth opening, consisting of peripheral gland cell bodies surrounding central gland ducts, which may open dorsoanteriorly in the mouth cavity and here secrete fine granular material; (2) two small lip glands, each consisting of three cells with openings next to and possibly associated with the two multiciliated cells, constitute the anterior ciliary field of the mouth opening; (3) two to four adjoined pharyngeal glands located in the middle of the bowl-shaped pharyngeal musculature and opening into the pharynx; and (4) paired, large, sac-shaped esophageal glands positioned anterolaterally to the anterior gut, with ducts extending anteriorly along the esophagus and opening into the anterior of this (Kristensen and Niilonen 1982, Worsaae and Rouse 2008).

Nephridia, blood vascular system, and body cavity

Two pairs of protonephridia have been reported from *D. subterraneus*, *D. kunii*, *D. westheidei*, and *Diurodrilus* sp. (South Australia, Australia) (Kristensen and Niilonen 1982, Worsaae and Kristensen 2005, Worsaae and Rouse 2008, Kajihari et al. 2019).

The first short pair of nephridia is positioned in the anteriormost trunk, lateral to the first trunk ciliophores and the first pair of somata of the ventral nerve cords (Fig. 7.8.4B, C, F, G). Their lateral trunk openings have been documented using SEM in *D. kunii* (Kajihari et al. 2019), and TEM investigations of *D. subterraneus* showed that these possess a single monociliated terminal cell with a weir lacking a basal lamina (Worsaae and Kristensen 2005). The terminal cell cilium spirals several times within the canal cell, the laminae of which proximally are weakly developed or totally lacking between this and the germinal cells lying freely in the presumed coelomic cavity (Worsaae and Kristensen 2005). These nephridia are difficult to document with anti-tubulin staining and CLSM, and previous experiments (Worsaae and Rouse 2008) only illustrated one to two cilia in these nephridia, whereas some recent scans of *D. subterraneus* seem to show a denser multiciliary signal in this region (ne, n1?) (Fig. 7.8.4C, G). The second pair of nephridia has been reported from the same investigated species and found halfway along the trunk, before the midgut-hindgut constriction, with lateral openings documented using SEM (Kajihari et al. 2019). These are from LM observations and TEM found to contain multiple beating cilia (Fig. 7.8.5E) (Worsaae and Kristensen 2005). A recent staining against α-tubulin in *D. subterraneus* revealed paired thick bundles of internal cilia in this middle region of the trunk, possibly representing the second pair of nephridia (Fig. 7.8.4B, E, F). The putative second pair of nephridia in *D. dohrni* (Fig. 7.8.4C)

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is more prominent than the first pair but less conspicuous than in *D. subterraneus*, which may reflect differences in immunoreactivity across the various experiments or possibly species-specific differences of the nephridial configuration. The presence of a third pair of nephridia in the posteriormost trunk has been discussed for *D. westheidei* (see Kristensen and Niilonen 1982); however, these signs of ciliation may also represent the yet undocumented gonoducts (Fig. 7.8.4A, B, E–G). A single blind-ending enteronephridium opening dorsally from the posteriormost midgut and lining the hindgut has been detected in *Diurodrilus* sp. from Brisbane, Australia (Fig. 7.8.1A).

Due to their small size and compact anatomy, the presence of a coelomic cavity was only proposed after TEM investigations and found to be most prominent dorsally of the gonads in the posterior trunk (Kristensen and Niilonen 1982, Kristensen and Eibye-Jacobsen 1995, Worsaae and Kristensen 2005, Worsaae and Rouse 2008). The cavity lacks an obvious peritoneal lining, which is fairly common for meiofaunal annelids with reduced coelomic space (Fransen 1980, Kerbl et al. 2015).

Nervous system

The nervous systems of diurodrilids have only been investigated in a few studies (mainly Worsaae and Rouse 2008), and further detailed studies are warranted to uncover more details and corrections to the current interpretation of the architecture. It comprises an anterior brain, a prebuccal or stomatogastric ganglion, a terminal ganglion, and two (or three) anterior trunk commissures connecting the two main ventral, two paramedian ventral, and two lateral longitudinal nerves. Dorsal nerves are so far only distinguishable as fine peripheral offshoots of the lateral nerves.

An anti-alpha-tubulin staining of *D. dohrni* (Fig. 7.8.4C) revealed a central neuropil of the brain, which is surrounded by somata, eight to nine of which show serotonin LIR (Worsaae and Rouse 2008). The brain contains multiple commissures, which laterally seem to form the dorsal and ventral roots of the circumesophageal connectives, continuing posteriorly into the paired main ventral nerves. Both anterior and dorsal compound cilia cells project axons into the brain; however, the axons of the posterior middorsal compound cilia cell instead seem to insert in the stomatogastric "ganglion", also innervating and receiving axons of the prepharyngeal ciliated field (Worsaae and Rouse 2008). This separate dense cluster of somata (three to six pairs showing serotonin LIR) is found at the posterior border of the prostomium and surrounds a large central gland. With its many central neurites (and a possible commissure), it seems to represent stomatogastric "paired ganglia", possibly controlling the stomatogastric nervous system and coordinating some of the head cilia and ciliophores involved in feeding or food sensing. Nerves project anteriorly from these, underlining the head ciliophores and connecting with the brain. Other nerves project posteriorly forming a dorsal ring along the esophagus, possibly connecting with indistinct nerves innervating the gut musculature (Worsaae and Rouse 2008). In all species investigated by Worsaae and Rouse (2008), a paired terminal ganglion is found lateral to the anus, surrounded by a terminal commissural ring.

Paired main ventral nerves extend posteriorly from the circumesophageal connectives along the entire ventral side of the trunk into the primary toes (Fig. 7.8.4B, C). Posterior to the mouth, neurites branch off from the circumesophageal connectives to form the paired ventral paramedian longitudinal nerves, which may fuse into one median nerve in the anterior trunk or run separately along the trunk, innervating and extending as long as the midventral trunk ciliophores. Lateral longitudinal nerves that may belong to the peripheral nervous system projects laterally from the brain, continuing around the pharyngeal region and along the lateral trunk to the terminal ganglion, innervating the lateral compound sensory cilia of the head and trunk. Fine neurite processes of the lateral nerves extend over the lateral and dorsal surfaces possibly innervating the dorsal and circular musculature.

Six pairs of somata showing serotonin LIR are found in the anterior part of the trunk (tss1–6) (Fig. 7.8.4B), but how many of these form true commissural projections is debatable (Worsaae and Rouse 2008). Only two commissures show distinct α-tubulin or tyrosinated tubulin LIR (Fig. 7.8.4B, C).

Segmentation

Diurodrilids have been interpreted to have five evenly distributed trunk segments based on the folded appearance of the cuticle, the position of the lateral compound cilia (e.g., Ax 1967, Kajihari et al. 2019), and the numbers of midventral trunk ciliophores (e.g., Mock 1981). However, this interpretation does not follow the configuration of the nervous system, presenting only two distinct anterior commissures, or the distribution of two pairs of nephridia in the anterior and middle trunk, respectively (see above). The muscle system shows no sign of serial repetition. However, now knowing that diurodrilids are annelids (Laumer et al. 2015, Struck et al. 2015), the presence of two pairs of nephridia does support that the trunk consists of a minimum of two segments but likely not five segments. The commissural pattern in the anterior trunk of Diurodrilidae may further

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aid to elucidate the segment borders of the first trunk segment also containing the anterior pair of nephridia, as the two commissures and two crossing neurites in the anterior trunk show great resemblance to the neural pattern of the anteriormost segments in the meiofaunal family Dinophilidae (Kerbl et al. 2015). In *Dimorphilus gyrociliatus*, the two first segments each possess three commissures with multiple somata, whereas in *Dinophilus vorticoides* each segment only contains one commissure in the adult stage (Kerbl et al. 2015), and depending on the comparison to one or the other species, the total of two to three commissures and six pairs of somata in *Diurodrilus* may reflect it to possess either one or two anterior and one posterior segments in the trunk (Fig. 7.8.4B, C) (but see also Worsaae and Rouse 2008). Depending on the number of commissures and somata contained in the first segment, the second pair of nephridia in *Diurodrilus* may then belong to either the second or third trunk segment. The lack of both commissures, somata, and nephridia in the posterior half of the trunk indicates that *Diurodrilus* may not possess more than these one or two short anterior segments as well as one elongated posterior segment. According to this interpretation, yielding a total of maximum three trunk segments, the external cuticular folds and paired sensory cilia previously interpreted to indicate five evenly distributed segments may not hold true. However, further developmental studies of nerves (and their possible fusion or addition during development) as well as other organ systems are necessary to finally resolve the segmentation pattern and total number of segments in adult Diurodrilidae.

Reproduction, gametes, and development

All species of *Diurodrilus* are dioecious (although males are not described for *D. westheidei*).

Females carry paired ovaries containing one to two large oocytes and additional undeveloped small oocytes, but oviducts have not been observed, however, see discussion above on oviducts possibly misinterpreted as nephridia. The ovaries could not be located in TEM studies of females (Kristensen and Niilonen 1982, Worsaae and Rouse 2008), and these may disappear during development, with the eggs consequently lying freely in the body cavity.

Males possess paired testes, but for the mature females the reproductive products of the mature males (spermatids or spermatozoa) lie freely in the single large cavity of the trunk (Figs. 7.8.2F, 7.8.5E, F) (Kristensen and Niilonen 1982). The spermatozoa can vary in shape between the species and during development, but for *D. subterraneus*, where spermatogenesis is described in detail with TEM (Kristensen and Eibye-Jacobsen 1995), the fully developed spermatozoa have been found to possess a giant acrosome (e.g., much smaller in *D. kunii* Kajihari, Ikoma, Yamasaki & Hiruta, 2019) followed by a middle region containing the nucleus and mitochondria and then a terminal flagellum enclosed by a helically coiled mucous coat. TEM investigations of male *D. westheidei* and *D. subterraneus* revealed that, at least in these species, the plasma membrane of the middle region bears mushroom-shaped cytoplasmic processes each including filaments (Fig. 7.8.5C, E, F) (Kristensen and Niilonen 1982, Kristensen and Eibye-Jacobsen 1995, Worsaae and Rouse 2008). A pair of ventral gonopores are found ventrally on the posterior trunk of male *D. minimus* (Fig. 7.8.3A, C).

Internal fertilization is likely to occur at least in *D. westheidei*, as its females have been found to possess clusters of sperm (Kristensen and Niilonen 1982). However, the speculated intromittent function in sperm transfer of the anal cone (Kristensen and Niilonen 1982) is not very likely with the anal cone being (1) highly ciliated, (2) females also having an anal cone, and (3) males of *D. minimus* having paired gonopores anterior to the ciliated anal cone (Worsaae and Rouse 2008).

Similar to many other interstitial annelids, diurodrilids probably all have direct development. Although the life cycle has never been possible to study in detail, an indirect support for direct development has been found in the fact that their females develop only one to two oocytes at a time (Figs. 7.8.1A–E, 7.8.2A) and the smallest juveniles observed are smaller than a mature oocyte but have similar shape and morphology as the adults (Worsaae and Rouse 2008, Worsaae unpublished observations).

Motility, feeding, and habitat preferences

Diurodrilids glide over surfaces by the beating of the ventral ciliophores, but the temporary adhesion (and release) of the anterior head and posterior toe glands make their movement stop and start abruptly, somewhat resembling the movement patterns of Gastrotricha, also possessing ventral cilia and adhesive duo-glands. Diurodrilids are found in medium to coarse sand of shallow marine waters, with several species restricted to the phreatic systems of the littoral zone. Although it has been proposed that a shorter toe length may reflect an adaptation to the subterranean environment more protected from waves and currents (Villora-Moreno 1996), the finding of the subterranean *D. kunii* with longer toes indicates that the adhesive force of the toe glands may not be directly linked to the length of the toes (Kajihari et al. 2019). *D. minimus* is often found in brackish waters, which often also characterizes the habitat of the stygobiotic species of the littoral zone, and the latter species may even prefer

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areas of the beach where there is an adequate freshwater influx from groundwater or rivers. Not much is known about the feeding habits of Diurodrilidae, but LM examinations indicate that they feed on detritus and microalgae (Worsaae, Kristensen unpublished observations).

Systematics

Phylogeny

D. minimus was first assigned to Dinophilida Remane, 1925 as part of the now-abandoned taxon Archiannelida, grouping several meiofaunal annelid families previously thought to present ancestral annelid traits (see Westheide 1985, Worsaae and Kristensen 2005). The genus was thereafter moved to the family Diurodrilidae Kristensen & Niilonen, 1982; later, the order Diurodrilida Westheide, 1985 was erected (Westheide 1985). Although *Diurodrilus* was consistently regarded as an annelid group, there was little morphological evidence to support its annelid affinity. Diurodrilids lack significant annelid characteristics such as chaetae, head appendages, parapodia, nuchal organs, or obvious segmentation. They also lack the characteristic midventral ciliary band found in many interstitial annelids, such as Dinophilidae, but do possess a ventral muscular pharynx and a cuticle, showing some resemblance to other interstitial and juvenile annelids. The first detailed study of the nervous system likewise showed only a few anterior ganglia along the widely separated two main and four minor ventral nerves (Worsaae and Rouse 2008), hereby defying the previous externally assessed interpretation of the trunk consisting of five segments. Moreover, diurodrilids have several traits in common with other micrometazoans, such as Gnathifera, e.g., their trunk ciliophores with long ciliary rootlets, adhesive head and toe glands, spermatozoa with mushroom bodies, dorsal plates, and a ventral muscular pharynx with large central glands (Worsaae and Rouse 2008). However, annelids are now known to also contain taxa such as Echiura, Sipuncula, or some siboglinids, which adult nervous systems are more or less nonsegmented. The very small size, aberrant morphology, and poorly segmented nervous system of *Diurodrilus* have therefore been discussed to possibly reflect an extreme case of pedomorphosis within Annelida (Worsaae and Kristensen 2005, Worsaae and Rouse 2008, Struck et al. 2015).

The first phylogenetic study based on SSU and LSU rDNA data did not position *Diurodrilus* among annelids but together with Micrognathozoa. However, later on, both a mitochondrial genome study (Golombek et al. 2013) and two comprehensive phylogenomic studies (Laumer et al. 2015, Struck et al. 2015) found the family to group with annelids, although none of them with certainty identifying its exact position within Annelida. Yet intriguingly, both Struck et al. (2015) and an ongoing phylogenomic study (Martin-Duran et al. unpublished observations) find *Diurodrilus* to group with another meiofaunal, annelid taxon *Apharyngtus* (within Orbinida), to which *Diurodrilus* shows at least some superficial morphological resemblance (Westheide 2008).

Recently, a phylogenetic study of the family, including three gene fragments from three species (Kajihari et al. 2019), showed no geographic pattern with the two Pacific species not being sister to each other. Instead, the two upper littoral species *D. kunii* and *D. subterraneus* were shown to be closer related, although Kajihari et al. (2019) pointed out that subterranean species with a more restricted dispersal potential than subtidal species might be more likely to resemble isolated, endemic entities of separate origin and that inclusion of further taxa might prove that. An ongoing phylogenetic study of the family, including multiple species (Worsaae et al. unpublished observations), aim to test the degree of endemism among the European populations and whether the habitat preference and adaptations may be reflected in the phylogenetic relationships among the different subtidal and littoral species of Diurodrilidae.

Taxonomy

Diurodrilidae Kristensen & Niilonen, 1982

Diurodrilus Remane, 1925

Diagnosis: Microscopic, dorsoventrally flattened, seemingly unsegmented annelids with enlarged head region, short trunk, and two to four pygidial lobes (toes) each provided with adhesive glands and muscles. Ventral surface carrying large multiciliated cells with long ciliary rootlets (ciliophores), large and ovoid on the prostomium, rectangular on the peristomium and trunk. Ciliophores surround the mouth opening and continue along the trunk as transverse rows of rectangular ciliophores, forming a midventral, discontinuous band. Prostomium flat and elongated, dorsally bearing long sensory compound cilia and internally bearing the brain laterally lined by two elongated head glands with anteroventral gland-neck openings. Peristomium with ventral mouth opening and a bowl-shaped muscular pharynx with central paired glands, whereas two, large salivary (esophageal) glands extend posterior to the muscle bulb. Direct developers, gonochoristic, males producing specialized spermatozoa with large acrosomes and mushroom bodies.

Type species: *Diurodrilus minimus* Remane, 1925.

Diurodrilus minimus Remane, 1925. Type locality: Kiel Bay, Baltic Sea and Helgoland, North Sea, subtidal fine-coarse sand (Remane 1925). Multiple additional

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records from Northeast Atlantic and Mediterranean waters (e.g., Boaden 1963, Fize 1963, Renaud-Debyser and Salvat 1963, Swedmark 1964, Schmidt 1969, 1972b, Wolff et al. 1980, von Nordheim 1984, Villora-Moreno 1996, Worsaae and Rouse 2008) as well as the Indian Ocean (Rao and Ganapati 1968a).

Diurodrilus subterraneus Remane, 1934. Type locality: Kiel Bay, Baltic Sea, Germany. Intertidal, groundwater mark, medium-sized sand (Remane 1934, Schmidt 1972a). Multiple additional records from Northeast Atlantic and Mediterranean waters (e.g., Schulz 1940, Boaden 1963, Fize 1963, Schmidt 1969, Mock 1981, Kristensen and Niilonen 1982, von Nordheim 1984, Wolff et al. 1980, Villora-Moreno 1996, Worsaae and Rouse 2008) and the Davis Strait, North Atlantic Ocean (Kristensen and Niilonen 1982).

Diurodrilus benazzii Gerlach, 1952. Type locality: San Rossore, Thyrrenian Sea. Intertidal, groundwater mark, medium-sized sand (Gerlach 1952). Additional records from East Atlantic and Mediterranean waters (Delamare-Deboutteville 1953, 1960, Fize 1963, Ax 1969, Westheide 1972, Villora-Moreno 1996) as well as the Indian Ocean (Rao and Ganapati 1968a, b, Rao 1969).

Diurodrilus dohrni Gerlach, 1953. Type locality: Gulf of Napoli, Italy, 15 to 16 m depth, mixed medium-coarse sand and shell gravel (Gerlach 1953). Additional records from Northeast Atlantic and Mediterranean waters (Westheide 1972, Wolff et al. 1980, Villora-Moreno 1996).

Diurodrilus ankeli Ax, 1967. Type locality: False Bay, San Juan Island, Washington, USA. Intertidal, groundwater mark, coarse sand (Ax 1967).

Diurodrilus westheidei Kristensen & Niilonen, 1982. Type locality: Flakkerhuk, Disko Island, Greenland, 2 to 5 m depth, coarse sand (Kristensen and Niilonen 1982, Worsaae and Rouse 2008).

Diurodrilus kunii Kajihari, Ikoma, Yamasaki & Hiruta, 2019. Type locality: Ishikari Beach, Hokkaido, Japan. Intertidal, groundwater mark, sand (Kajihari et al. 2019). Also found at Otobe, Hokkaido, Japan (Kajihari et al. 2019).

In addition, six unidentified species of *Diurodrilus* have been reported from the Atlantic coast of the United States (Rieger and Rieger 1976), Galapagos Islands (Schmidt and Westheide 1977), New Zealand (Riser 1984, two species), and northeast and southern Australia (Paxton 2000, Worsaae and Rouse 2008; two species), respectively. Four additional and potentially new species of *Diurodrilus* were furthermore sampled in Trinidad and Tobago by R.M. Kristensen, in Brazil by Didomenico, and in northern Cuba and Aomori, northern Kyushu, Japan by K. Worsaae (K. Worsaae, M. Didomenico, and R.M. Kristensen unpublished observations). Moreover, some of the multiple sampled populations of *D.* cf. *minimus* and *D.* cf. *subterraneus* in the North Atlantic and *D.* cf. *dohrni* in the Canary Islands waters and Mediterranean Sea by K. Worsaae may represent new cryptic species (Worsaae unpublished observations).

Key to the species of *Diurodrilus*

1. Two pairs of toes	*2*
—One pair of toes	*Diurodrilus benazzii*
2. Primary and secondary toes of equal size	*3*
—Primary and secondary toes of unequal size	*4*
3. Long toes (Fig. 7.8.17), small anal cone	*Diurodrilus minimus*
—Short toes (Fig. 7.8.17), without an anal cone	*Diurodrilus subterraneus*
4. Secondary toes tube-like, large anal cone	*Diurodrilus westheidei*
—Secondary toes cone-like, without an anal cone	*5*
5. Proximal part of primary toes breeches-like	*Diurodrilus dohrni*
—Primary toes tube-like in whole length	*6*
6. Three pairs of anterior head ciliophores	*Diurodrilus kunii*
—Four pairs (and one median) anterior head ciliophores	*Diurodrilus ankeli*

References

Ax, P. (1967): *Diurodrilus ankeli* nov.spec. (Archiannelida) von der Nordamerikanischen Pazifikküste. *Zeitschrift für Morphologie und Ökologie der Tiere*: 5–16.

Ax, P. (1969): Populationsdynamik, Lebenszyklen und Fortplanzungsbiologie der Mikrofauna des Meeressandes. *Zoologischer Anzeiger, Suppl*. 32: 66–113.

Boaden, P.J.S. (1963): The interstitial fauna of some North Wales beaches. *Journal of the Marine Biological Association UK* 43: 79–96.

Delamare-Deboutteville, C. (1953): *Diurodrilus benazzii* Gerlach dan les eaux souterraines littorales de Canet-Plage. *Vie Milieu* 4: 747.

Delamare-Deboutteville, C. (1960): *Biologie des eaux souterraines littorales et continentales*. Hermann, Paris.

Fize, A. (1963): Contribution à l'étude de la microfaune des sables littoraux du golfe d'Aigues Mortes. *Vie Milieu* 14: 669–774.

Fransen, M.E. (1980): Ultrastructure of colomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphology* 95: 235–249.

Gerlach, S.A. (1952): *Diurodrilus benazzii*, ein neuer Archiannelide aus dem Küstengrundwasser des Mittelmeeres. *Zoologischer Anzeiger* 149: 185–188.

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Gerlach, S.A. (1953): Zur Kenntnis der Archianneliden des Mittelmeeres. *Kieler Meeresforschung* 9: 248–251.

Golombek, A., Tobergte, S., Nesnidal, M.P., Purschke, G. & Struck, T.H. (2013): Mitochondrial genomes to the rescue — Diurodrilidae in the myzostomid trap. *Molecular Phylogenetics and Evolution* 68: 312–326.

Kajihari, H., Ikoma, M., Yamasaki, H. & Hiruta, S.F. (2019): *Diurodrilus kunii* sp. nov. (Annelida: Diurodrilidae) and a molecular phylogeny of the genus. *Zoological Science* 36: 250–258.

Kerbl, A., Bekkouche, N., Sterrer, W. & Worsaae, K. (2015): Detailed reconstruction of the nervous and muscular system of Lobatocerebridae with an evaluation of its annelid affinity. *BMC Evolutionary Biology* 15: 277.

Kristensen, R.M. & Eibye-Jacobsen, D. (1995): Ultrastructure of spermiogenesis and spermatozoa in *Diurodrilus subterraneus* (Polychaeta, Diurodrilidae). *Zoomorphology* 115: 117–132.

Kristensen, R.M. & Niilonen, T. (1982): Structural studies on *Diurodrilus* Remane (Diurodrilidae fam.n.), with description of *Diurodrilus westheidei* sp.n. from the Arctic interstitial fauna of Disko Island, W. Greenland. *Zoologica Scripta* 11: 1–12.

Laumer, C.E., Bekkouche, N., Kerbl, A., Goetz, F., Neves, R.C., Sørensen, M.V., Kristensen, R.M., Hejnol, A., Dunn, C.W., Giribet, G. & Worsaae, K. (2015): Spiralian phylogeny informs the evolution of microscopic lineages. *Current Biology* 25: 2000–2006.

Mock, H. (1981): Zur Kenntnis von *Diurodrilus subterraneus* (Polychaeta, Dinophilidae) aus dem Sandhang der Nordseeinsel Sylt. *Helgoländer Meeresuntersuchungen* 34: 329–335.

Paxton, H. (2000): Family Diurodrilidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula, Vol. 4A*. CSIRO Publishing, Melbourne: 104–105.

Rao, G.C. (1969): The marine interstitial fauna inhabiting the beach sands of Orissa Coast. *Journal of the Zoological Society India* 21: 89–103.

Rao, G.C. & Ganapati, P.N. (1968a): The interstitial fauna inhabiting the beach sands of Waltair Coast. *Proceedings of the National Institute of Science India* 31: 82–122.

Rao, G.C. & Ganapati, P.N. (1968b): On some archiannelids from the beach sands of Waltair Coast. *Proceedings of the Indian Academy of Science* 67: 24–30.

Remane, A. (1925): Diagnosen neuer Archianneliden. *Zoologischer Anzeiger* 65: 15–17.

Remane, A. (1934): *Diurodrilus subterraneus* nov. spec., ein Archiannelide aus dem Küstengrundwasser. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* 20: 479.

Renaud-Debyser, J. & Salvat, B. (1963): Éléments de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. *Vie Milieu* 14: 463–550.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the Spiralia. *Acta Zoologica* 57: 53–68.

Riser, N.W. (1984): General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239–250.

Schmidt, P. (1969): Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordsee-Insel Sylt. II. Quantitative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobioligie* 54: 95–174.

Schmidt, P. (1972a): Zonierung und jahreszeitliche Fluktuationen des Mesopsammons im Strand von Schilksee (Kieler Bucht). *Mikrofauna des Meeresbodens* 10: 353–410.

Schmidt, P. (1972b): Zonierung und jahreszeitliche Fluktuationen der interstitiellen Fauna in Sandstränden des Gebiets von Tromsø (Norwegen). *Mikrofauna des Meeresbodens* 12: 1–164.

Schmidt, P. & Westheide, W. (1977): Interstitielle Fauna von Galàpagos. XVII. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). *Mikrofauna des Meeresbodens* 62: 1–38.

Schulz, E. (1940): Über eine Mikrofauna im oberen Eulitoral auf Amrum. *Kieler Meeresforschungen* 3: 158–164.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Swedmark, B. (1964): Interstitial fauna of marine sand. *Biological Reviews* 39: 1–42.

Villora-Moreno, S. (1996): Ecology and distribution of the Diurodrilidae (Polychaeta), with redescription of *Diurodrilus benazzii*. *Cahiers de Biologie Marine* 37: 99–108.

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. In: Bartolomaeus, T. & Purschke, G. (eds.), *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa. Hydrobiologia* 535/536: 199–225.

von Nordheim, H. (1984): Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae, and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchungen* 38: 1–20.

Westheide, W. (1972): La faune des polychètes et des archiannélides dans les plages sableuses à ressac de la côte Mediterranéene de la Tunisie. *Bulletin de l'Institut National Scientifique et Technique d´Océanographie et de Pêche, Salammbô* 2: 449–468.

Westheide, W. (1985): The systematic position of the Dinophilidae and the archiannelid problem. In: Conway Morris, S., George, J.S., Gibson, R. & Platt, H.M. (eds.), *The Origin and Relationships of Lower Invertebrates*. Clarendon Press, Oxford: 310–326.

Westheide, W. (2008): *Polychaetes: Interstitial Families*, Vol. 44. The Linnean Society of London, Shrewsbury.

Westheide, W. (2019): Apharyngtidae. In: Purschke, G. Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology Annelida: Volume 1: Annelida Basal Groups and Pleistoannelida: Sedentaria I*. DeGruyter, Berlin: 234–237.

Wolff, J.W., Sandee, A.J.J. & Stegenga, H. (1980): The Archiannelida of the estuarine area of the rivers Rhine, Meuse and Scheldt, with some remarks on their ecology. *Netherlands Journal of Sea Research* 14: 94–101.

Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). In: Bartolomaeus, T. & Purschke, G. (eds.), *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa*. Hydrobiologia 535/536: 319–340.

Worsaae, K. & Rouse, G.W. (2008): Is *Diurodrilus* an annelid? *Journal of Morphology* 269: 1426–1455.

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Errantia

Katrine Worsaae

7.9 Errantia incertae sedis: Nerillidae Levinsen, 1883

Introduction

The family Nerillidae is exclusively meiofaunal, with the body ranging in size from 0.3 to 2.1 mm, comprising a prostomium, a limited peristomium, seven to nine body segments, and a pygidium. The family contains 59 described species in 15 genera: *Nerilla* Schmidt, 1848 as the type genus, *Afronerilla* Faubel, 1978, *Aristonerilla* Müller, 2002, *Leptonerilla* Westheide & Purschke, 1996, *Speleonerilla* Worsaae, Sterrer & Iliffe, 2018, *Meganerilla* Boaden, 1961, *Mesonerilla* Remane, 1949, *Micronerilla* Jouin, 1970, *Nerillidium* Remane, 1925, *Nerillidopsis* Jouin, 1966, *Paranerilla* Jouin & Swedmark, 1965, *Psammoriedlia* Kirsteuer, 1966, *Thalassochaetus* Ax, 1954, *Trochonerilla* Tzetlin & Saphonov, 1992, and *Troglochaetus* Delachaux, 1921 (for review, see Worsaae 2005a).

Nerillidae shares characteristics with Aciculata families (Rouse and Pleijel 2001) such as compound chaetae, one pair of pygidial cirri, a muscular ventral buccal organ, prostomial antennae, and short, nongrooved, sensory, ventrolateral palps. Levinsen (1883) defined the family based on *Nerilla antennata* Schmidt, 1848 with annulated antennae and cirri and placed it in the suborder "Syllidiformia vera". Due to their minute size, some resemblances to Protodrilidae, and paedomorphic appearance in ciliary patterns (midventral ciliary band and transverse patterns of cilia), Nerillidae were later classified as part of "Archiannelida" (Hatschek 1878, Beauchamp 1910, Goodrich 1912, Worsaae and Kristensen 2005). However, their resemblance to juvenile stages of various aciculate families such as Onuphidae and Syllidae is striking (Westheide 1990, Worsaae et al. 2005), which led Westheide and Purschke (1996) to suggest a progenetic origin of the family rejecting the "archiannelid" hypothesis.

A combined phylogenetic analysis positioned Nerillidae among macrofaunal eunicidan taxa (Worsaae et al. 2005). The analyses hereby supported an evolutionary pathway of secondary miniaturization (Worsaae et al. 2005), most likely facilitated by maturation in a juvenile stage of a macrofaunal ancestor (progenesis) (Westheide 1987). However, the branch support was not high (Worsaae et al. 2005), and later studies have not been able to resolve its position with certainty (Struck et al. 2008, 2015, Zrzavý et al. 2009). Therefore, despite Goodrich (1912) calling Nerillidae the most "polychaete-like" archiannelid family due to its many morphological characteristics, its position is still debated and calls for phylogenomic analyses with larger data sets. As described below, the wide distribution patterns, several apomorphies of the family, and the huge morphological diversity within all indicate a long evolutionary history of the family.

Morphology

Nerillidae possess a prostomium, a pygidium, and seven to nine body segments, consistent in number within genera. All nerillids possess a pair of prostomial palps (Figs. 7.9.1A, 7.9.2, 7.9.3F, H, I), except for *Paranerilla* instead having lateral extensions of the prostomium (so-called horns) (Fig. 7.9.3A), the probable homology of which with palps warrants further examinations. The palps are generally relatively short, club- or spoon-shaped, with various ciliary patterns and of sensory function. However, in the aberrant anchialine and facultative pelagic species *Speleonerilla saltatrix* (Worsaae, Sterrer & Iliffe, 2004), the palps exceed the body length and function in particle collecting. The prostomium can further carry zero to three anterior antennae ("tentacular cirri"), and the pygidium carries two, usually long, thread-shaped cirri, all being annulated in *Nerilla*.

The prostomium is delineated dorsally from the body segments by a groove and ventrally by the anterior border of the mouth opening (Figs. 7.9.1, 7.9.3I, J), which is located on the first body segment, in all genera. Paired nuchal organs in the form of heavily ciliated pits are found on the posterior border of the prostomium in all species (Figs. 7.9.1A, 7.9.3C, H, I, 7.9.4D, J) (Müller 1999). The nuchal organs have been investigated by transmission electron microscopy in a few species and comprise a few ciliated cells with a specific microvillar cover, a few receptor cells, and a retractor muscle (Purschke 1997). Paired pigmented or unpigmented eyes are found in only a few species; in *Nerilla* (Fig. 7.9.2C, G), they are unpigmented and consist of six cells, two rhabdomeric sensory cells, two corneal cells, and two supportive cells with flat platelets causing the silvery appearance when reflecting light (Eakin et al. 1977). Nonpigmented ciliary receptors resembling photoreceptor-like sensory organs are observed in the anterior prostomium of *Mesonerilla* n. sp. (Fig. 7.9.4J) and *Mesonerilla intermedia* Wilke, 1953 as well as *Nerillidium mediterraneum* Remane, 1928 (Müller 1999).

The first conspicuous body segment, generally termed segment 1 or the buccal segment, contains the ventral pharyngeal organ with a muscular bulb, investing muscle, a muscular dorsal tongue, intracellular skeletal elements, and a heavily ciliated lower lip (Fig. 7.9.1B)

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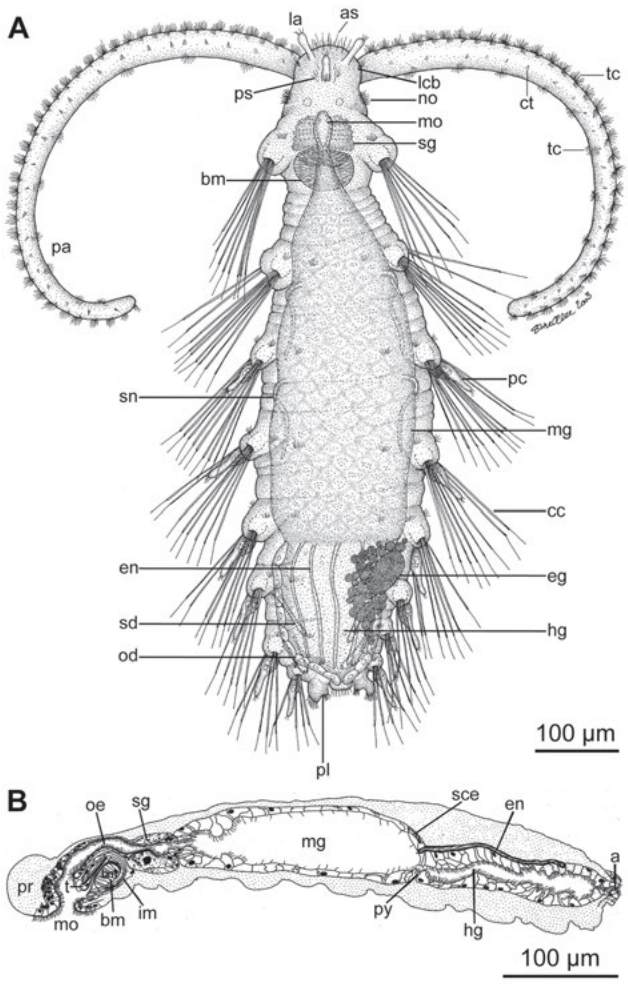


Fig. 7.9.1: Nerillidae. A, Habitus drawing of *Speleonerilla saltatrix*, dorsal view (from Worsaae et al. 2004); B, Semischematic drawing of sagittal section of *Nerillidium troglochaetoides* (from Tzetlin et al. 1992), showing alimentary canal with pharyngeal apparatus, gut, and enteronephridia. a, anus; as, anterior field of sensory cilia; bm, bulbus muscle; cc, compound chaetae; ct, ciliary small tuft; eg, eggs; en, enteronephridium; hg, hindgut; im, investing muscles; la, lateral antenna; lcb, lateral ciliary band; mg, midgut; mo, mouth opening; no, nuchal organ; oe, esophagus; ov, oviduct; pa, palp; pc, parapodial (interramal) cirrus; pl, pygidial lobe; pr, prostomium; ps, posterior field of sensory cilia; py, pylorus; sce, secretory cell; sd, spermioduct; sg, salivary glands; sn, segmental nephridium; t, tongue-like organ; tc, tuft of cilia.

(Jouin 1967b, Purschke 1985, Tzetlin et al. 1992). This segment may further differ from the following segments in different length or shape of parapodial cirri, uniramous parapodia, and occasional absence of cirri, chaetae, and nephridia (Figs. 7.9.1A, 7.9.2, 7.9.3, 7.9.4F). The overall presence of nephridia (e.g., in *Nerilla*) (Worsaae and Müller 2004), parapodia, and compound chaetae in this segment indicates its origin from a posterior growth zone and that it is a true body segment rather than a peristomium of presegmental larval ancestry (Rouse and Pleijel 2001). The peristomium may instead be reduced to the area around the mouth opening (and fused with the first segment) as predicted for many aciculates (e.g., Rouse and Pleijel 2001, Worsaae et al. 2005). Nonetheless, the early development, cell lineage, or hox genes have not been studied for any Nerillidae — that is why it is not possible to establish an exact fusion zone or clearly define this region.

The seven to nine body segments carry parapodia, each with two bundles of chaetae (except for segment 1) and zero, one, or two interramal parapodial cirri (Figs. 7.9.1A, 7.9.2A–F, 7.9.3G). The presence of interramal cirri is an apomorphic feature for Nerillidae. The cirri are often lacking on the first and last segments and may have various lengths and shapes, which may also vary along the body. In *Nerilla*, the first pair is annulated and the rest is generally simple and cirriform; in *Leptonerilla* (occasionally *Micronerilla*), the cirri are long, cylindrical, and double. In others, they are bottle shaped (e.g., *Speleonerilla saltatrix* and *Mesonerilla intermedia*), tapering toward the tip (e.g., *Mesonerilla fagei* Swedmark, 1959), or leaf-shaped (*Meganerilla* spp.), whereas in some they are short (e.g., *Nerillidium gracile* Remane, 1925) or completely rudimentary throughout (*Paranerilla* spp., *Troglochaetus simplex* Lévi, 1953, and *Troglochaetus beranecki* Delachaux, 1921). In species of *Meganerilla*, the parapodia possess an additional small ventral lobe (Fig. 7.9.3G).

The biramous parapodia are outgrowths of the body wall, comprising dorsal and ventral muscular chaetal sacs with numerous chaetae (Levi 1953, Jouin and Swedmark 1965, Müller and Worsaae 2006). The chaetal sacs and parapodia can be moved in several directions by the muscles attached, but the chaetae hang loosely along the body during gliding. Nerillidae lack aciculae; the chaetae are longer than body width and very fine, sometimes serrated, and either capillary or compound with heterogomph shafts (Fig. 7.9.3G).

The cuticle is weakly developed and the partly ciliated epidermis is often glandular, with particular glandular regions sometimes found near the nuchal organs (Fig. 7.9.2G) and at the base of the parapodia. Nerillids all possess a midventral ciliary band, which extends from the heavily ciliated mouth area to the pygidium (Fig. 7.9.3J, K) and serves as the main locomotory organ. Transverse dorsal and ventral ciliation is present on each segment in the form of tufts of cilia (Figs. 7.9.1A, 7.9.3C, I, K, 7.9.4D), continuous bands, or shields of cilia (Fig. 7.9.3A). Lateral ciliary tufts or bands may also be present (*Meganerilla* and *Nerilla*). The prostomium always possesses three possibly apomorphic groups of cilia: a pair of dense dorsolateral bands, a ventroanterior area of sensory cilia, and

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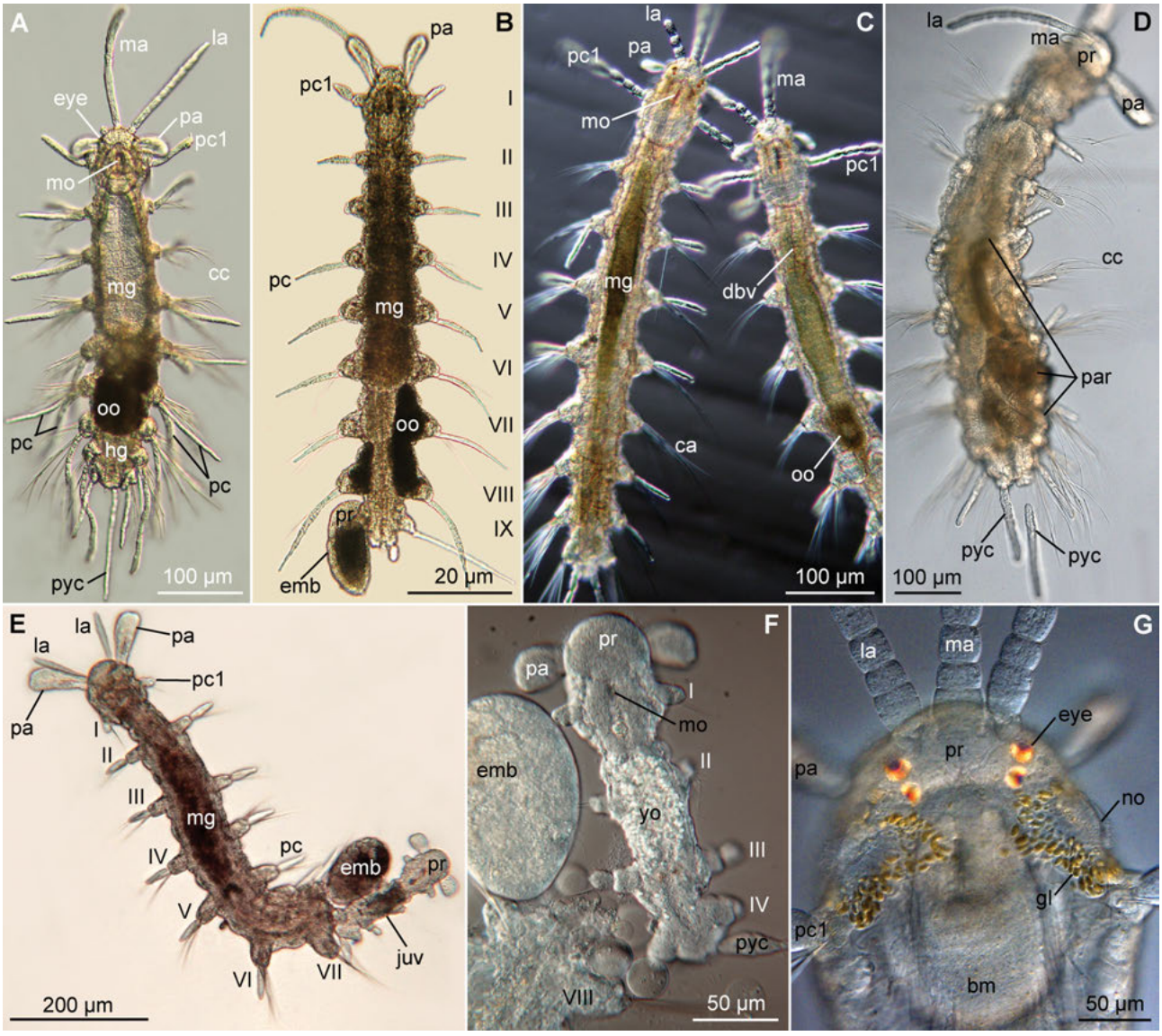
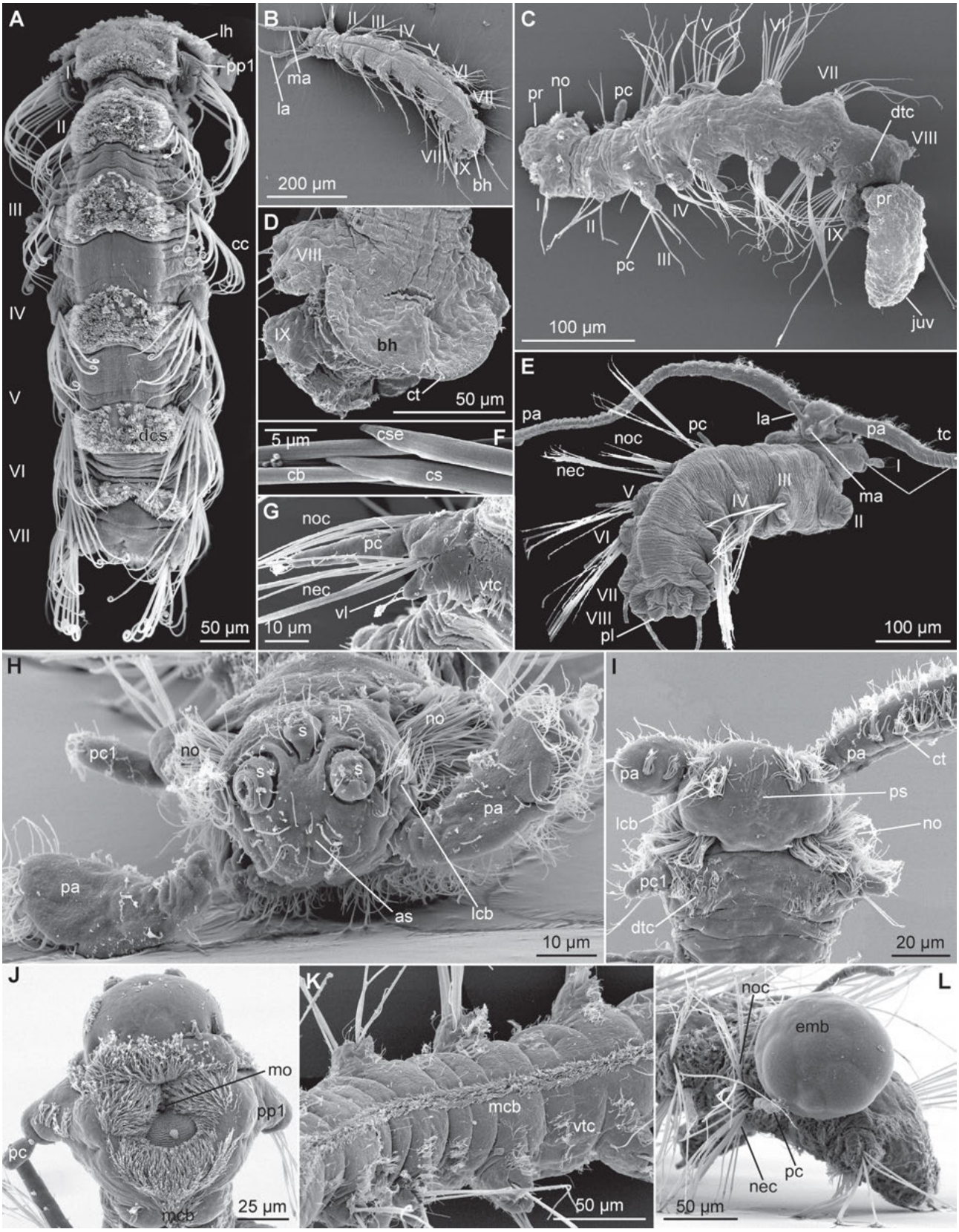


Fig. 7.9.2: Morphology of Nerillidae. Light micrographs. A, *Leptonerilla* sp. (California, USA) with double parapodial cirri, left antenna lost; B, *Mesonerilla* sp. (Lanzarote, Spain) brooding embryo, median and right antenna lost; C, *Nerilla* sp. (California, USA), male left and female right; D, *Mesonerilla roscovita* (Roscoff, France) parasitized by a large nematode; E, *Nerillidium* sp. (Lanzarote, Spain) brooding embryo and juvenile; F, Close up of four-segmented juvenile from E, showing yolk content; G, *Nerilla antennata* (Roscoff, France), prostomium and buccal segment. bm, bulbous muscle; ca, capillary chaetae; cc, compound chaetae; dbv, dorsal blood vessel; emb, embryo; gl, glands; hg, hindgut; juv, juvenile; la, lateral antenna; ma, median antenna; mg, midgut; mo, mouth opening; no, nuchal organ; oo, oocyte; pa, palp; par, parasite; pc, parapodial (interramal) cirrus; pc1, parapodial cirrus segment 1; pr, prostomium; pyc, pygidial cirrus; yo, yolk; I–IX, segment number.

a dorsoposterior area of sensory cilia, possibly positioned in species specific patterns (Fig. 7.9.3H, I). The palps may also possess various longitudinal bands and tufts of cilia (Figs. 7.9.1A, 7.9.3F, H, I) (e.g., Jouin 1967b).

The coelom lacks an epithelial lining according to Fransen (1980), and a blood vascular system composed of dorsal and ventral vessels (and a female lateral vessel) has only been described briefly for *Nerilla* (see Beauchamp 1910, Goodrich 1912) and may not exist in the other genera. *Nerilla* possess metanephridia with a blood vascular system, therefore being a prerequisite in this genus, as opposed to all other nerillid genera reportedly having protonephridia (Jouin 1967b, Worsaae and Müller 2004). In *Nerilla*, Goodrich (1912) mentioned a peri-intestinal blood sinus from which springs a median dorsal vessel, which runs forward above the esophagus to the head, where it divides in two branches. Those are presumably the vessels distinguishable in Fig. 7.9.2C underlying the epidermis of a *Nerilla* sp. The body wall musculature consists of two major ventral and two major dorsal longitudinal bands,

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dorsoventral muscles, oblique parapodial muscles, and transverse ventral muscles but no true circular fibers (Fig. 7.9.4A, C) (Müller and Worsaae 2006).

The nervous system comprises the bilobed brain with nerves innervating the prostomial appendages and nuchal organs, the esophageal connectives continuing into the two main lateral and one median nerve cords, extending to the pygidium (Müller et al. 2001, Worsaae and Müller 2004). Paired ventral ganglia exist as ganglionic swelling of the cords in each segment (except the first) at the level of the parapodia, from where also the main lateral nerves progress (Fig. 7.9.4C, E, H–J).

The digestive system consists of the mouth, pharyngeal organ, esophagus, foregut (or stomach), hindgut, and anus, with great details provided by Purschke (1985), Tzetlin et al. (1992), and Müller et al. (2001). Except for the buccal cavity, the entire canal is ciliated, often more conspicuously in the esophagus and hindgut (Fig. 7.9.4D, E, G–I). Salivary glands are positioned along the esophagus, with first and second segments open anteriorly through canals into the buccal cavity. Secretory cells are also found in the stomach epithelium (Tzetlin et al. 1992).

Paired protonephridia have been documented for most nerillid genera (e.g., Jouin 1970b, Worsaae and Müller 2004), whereas *Nerilla* has been found to possess metanephridia (Goodrich 1912). The possible basal position of *Nerilla* in Nerillidae (Worsaae 2005a) having metanephridia similar to the presumed related "Aciculata" families hereby indicates a secondary reduction to protonephridia within the family. Segmental nephridia are found in several segments, although not all, and replaced by gonoducts in fertile animals (except for the mixonephridia reported for *Paranerilla limicola* Jouin & Swedmark, 1965) (see Jouin and Swedmark 1965, reviewed by Worsaae and Müller 2004). Special blind-ending ciliated tubes, called enteronephridia, extend posteriorly from the stomach along the hindgut (Fig. 7.9.4G) (Jouin 1967b, Tzetlin et al. 1992, Worsaae and Müller 2004, Worsaae et al. 2004). The numbers and position can vary among genera.

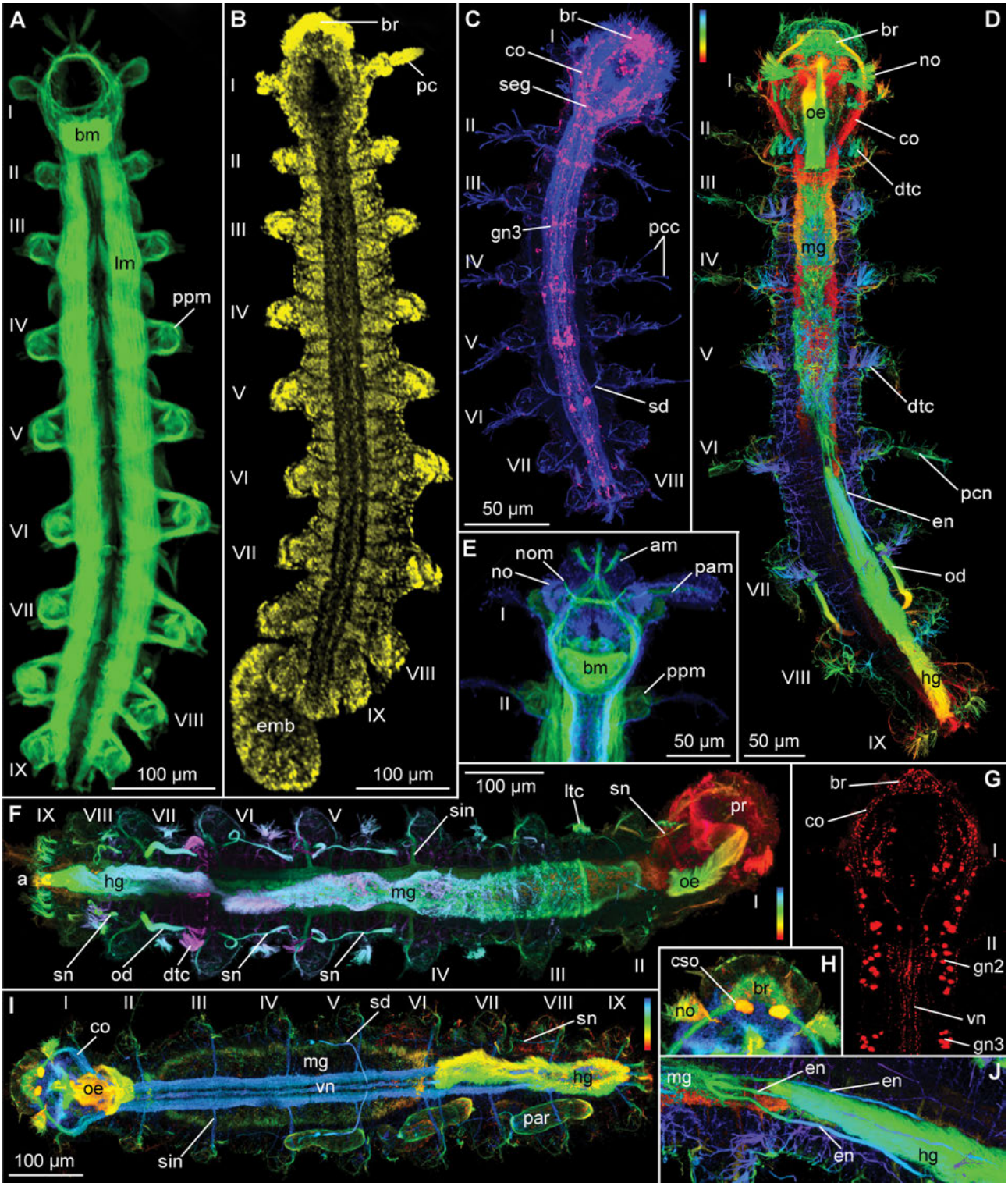
Most nerillids are gonochoristic, whereas others are protandric hermaphrodites (Jouin 1966, 1967a, 1968, 1973, Worsaae and Müller 2004). Asexual reproduction has never been reported. The course and position of gonoducts vary, although with consistency within most genera, showing one pair of oviducts and up to three pairs of spermioducts with separate or fused midventral openings (Fig. 7.9.4C, H, I) (Jouin 1966, 1967b, 1968, 1973, Worsaae and Müller 2004, Worsaae 2005a). Sperm show a variety of shapes in the few species studied so far (e.g., Jouin 1970a, Franzén and Sensenbaugh 1984, Purschke 2006).

Reproduction, development, and life cycles

Eggs or cocoons are fertilized externally either by random spawning of sperm or spermatophores or by pseudocopulation where the sperm are shed in the vicinity of spawning females (Jouin 1968, 1970b, 1971, Magagnini 1982). In *Nerilla*, females have been found only to release eggs in the presence of spermatophores, which open when eggs are laid nearby (Magagnini 1982). All nerillids have direct development, except *Paranerilla* with a benthic, free, lecithotrophic, trochophore larvae (Jouin and Swedmark 1965). In *Nerilla*, juveniles hatch directly from the eggs after 6 days (19°C) and become sexually mature in 1 month (Magagnini 1964). The genera *Mesonerilla*, *Nerillidium*, and *Nerillidopsis* have external brooding with the released eggs becoming attached to the posterior dorsal surface by the sticky egg membrane or secretions forming a single thin strap attachment per egg (Jouin 1968). If the female carries several eggs, they can be at different developmental stages and adhere by either the anterior end (all species of *Mesonerilla* except *Mesonerilla biantennata* Jouin, 1963) (Fig. 7.9.2B) or the posterior end (*Nerillidium* and *Nerillidopsis*) (Fig. 7.9.2E, F). *Mesonerilla intermedia* has a

◂ **Fig. 7.9.3:** External Morphology. Scanning electron micrographs. A, *Paranerilla cilioscutata* (northeast Greenland) with dorsal shields of cilia; B, *Mesonerilla intermedia* (Ischia, Italy), dorsal view; C, *Mesonerilla peteri* (Trinidad and Tobago) brooding juvenile, dorsal view, antennae lost; D, Close-up of brooding hood of *M. intermedia*, dorsal view; E, *Speleonerilla calypso* (Abaco, Bahamas), dorsoposterior view; F, Compound chaetae of *Mesonerilla neridae* (hydrothermal vent, West Pacific); G, Parapodial interramal cirrus of *Meganerilla cesari*; H, *Mesonerilla xurxoi* (Lanzarote, Spain), anterior end, anterior view, antennae lost; I, *M. cesari* (Lanzarote, Spain) anterior end, dorsal view; J, *Mesonerilla* sp. (Sardinia, Italy), anterior end, ventral view, antennae lost; K, *M. intermedia* (Mallorca, Spain), ventral view of middle segments; L, *M. xurxoi* sp. (Lanzarote, Spain), posterior segments with embryo, lateral view. as, anterior field of sensory cilia; bh, brooding hood; cb, chaetal blade; cc, compound chaetae; cs, chaetal shaft; cse, chaetal shaft extension; dtc, dorsal tufts of cilia; emb, embryo; juv, juvenile; la, lateral antenna; lcb, lateral ciliary band; lh, lateral horn; ma, median antenna; mcb, midventral ciliary band; mo, mouth opening; nec, neurochaetae; no, nuchal organ; noc, notochaetae; pa, palp; pc, parapodial (interramal) cirrus (pc1 - of segment 1); pl, pygidial lobe; pp1, parapodium segment 1; pr, prostomium; ps, posterior field of sensory cilia; s, scar from antennae; tc, tuft of cilia; vtc, ventral tuft of cilia; I–IX, segment number.

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brooding hood covering the eggs during the early development (Jouin 1968) and the embryo may receive maternal nutrition through the attachment string (Fransen 1983). *Nerillidium troglochaetoides* Remane, 1925 and *Nerillidium gracile* Remane, 1925 are reported to be semicontinuous breeder with a life span of approximately 6 months, whereas for many other species the reproductive period is limited to the summer period (von Nordheim 1984, Westheide 1990).

Biology and ecology

Distribution

All species of Nerillidae are marine or brackish, except for the limnic *Troglochaetus beranecki* found in both hyporheic and subterranean localities. The highest diversity of nerillids is found subtidally in the interstitial environment of coarse, oxygenated, well-sorted sand or shell gravel in high-saline oceanic waters (Swedmark 1964, Renaud-Mornant and Jouin 1965, Cabioch et al. 1968, Gelder 1974, Westheide 2008). However, members of the family are found worldwide (except Antarctica) from the intertidal to the deep sea and inhabiting a range of different habitats including mud, anchialine caves (mix of fresh and isolated marine water), subterranean freshwater, hydrothermal vents, algae, and bacterial mats (for review, see Worsaae 2005a, Westheide 2008, Worsaae and Rouse 2009, Worsaae et al. 2009). Whereas the seven monotypic genera so far each have very limited geographical distributions, five of the eight polytypic genera, *Nerilla*, *Nerillidium*, *Meganerilla*, *Mesonerilla*, and *Leptonerilla*, all span the East and West Atlantic as well as the Pacific Ocean. Even genera with a preference for anchialine caves, such as *Speleonerilla* (so far exclusively recorded from caves), *Leptonerilla*, and *Mesonerilla*, all have a disjunct distribution, occupying cave systems of the East Atlantic (Canary Islands) as well as the West Atlantic (Bahamas, Bermuda, Cuba, and Mexico) (Sterrer and Iliffe 1982, Westheide and Purschke 1996, Núñez et al. 1997, Worsaae et al. 2004, 2009, 2018, 2019, Worsaae 2005a).

A few species, such as *Nerilla antennata* and *Mesonerilla intermedia*, have been reported widely, but detailed morphological studies and especially molecular tools indicate that most of these cosmopolitans actually include several sibling species (Schmidt and Westheide 1998, Worsaae et al. 2019, Worsaae unpublished observations). The limnic species *Troglochaetus beranecki* is surprisingly reported from both European and North American continents (e.g., Delachaux 1921, Pennak 1971, Jouin 1973, Pennak and Ward 1986, Morselli et al. 1995, Särkkä and Mäkelä 1998), but molecular studies may prove otherwise. Molecular studies of Nerillidae indicate much higher species diversity than previously reported, unfortunately often not morphologically identifiable, especially within *Mesonerilla*, *Nerilla*, and *Nerillidium* (Schmidt and Westheide 1998, Worsaae et al. 2018, 2019).

Most nerillids have direct development (see Reproduction, development, and life cycles section), which may limit their dispersal abilities. The geographical distribution of a species is likely also limited by physiological adaptations to water temperature and salinity, but this is poorly studied (Magagnini 1968). However, it could be an indication that a few widely distributed genera are only found in either warmer waters (*Leptonerilla* and *Trochonerilla*) or colder waters (*Paranerilla*) (Worsaae et al. 2009, Curini-Galletti et al. 2012). Likewise, for the two most species-rich genera *Mesonerilla* and *Nerilla*, the former, although very diverse, is never found in brackish waters and mainly subtidally (with stabile high salinity), whereas

◂ **Fig. 7.9.4:** Musculature and nervous system. Confocal laser microscopy, Z-stack maximum intensity or depth-coded projections. A, *Mesonerilla intermedia* (Budelli Island off Sardinia, Italy), female, ventral view, F-actin staining showing musculature; B, Same specimen as A, DAPI staining showing embryo; C, *Nerillidium* sp. (Hawaii, USA), male, ventral view, blue signal is anti-α-tubulin immunoreactivity (IR) showing cilia, ciliated spermioducts, and nerves, pink signal is anti-serotonin IR of brain, paired ventral ganglia, and nerves; D, *Meganerilla* sp. (Bermuda, Great Britain), female, dorsal view, depth-coded Z-stack projection of anti-α-tubulin IR, showing cilia, ciliated oviducts, nerves; E, *Mesonerilla* sp. (Tenerife, Spain), male, anterior end, ventral view, blue signal is anti-α-tubulin IR showing cilia, ciliated spermioducts, and nerves, green is F-actin staining showing musculature; F, *Nerilla* sp. (Mono Island, Solomon Islands), female, dorsal view, depth-coded Z-stack projection of anti-α-tubulin IR, showing cilia, ciliated oviducts, and nephridia, nerves; G, Specimen from D, anti-serotonin IR of brain, paired ventral ganglia, and nerves; H, Close-up of prostomium of specimen I showing ciliated sense organs and nuchal organs; I, *Mesonerillia xurxoi* (Lanzarote, Spain), male, ventral view, depth-coded Z-stack projection of anti-α-tubulin IR, showing cilia, ciliated oviducts, and nephridia, nerves, as well as ciliated parasites; J, Close-up of D, showing ciliated enteronephridia around hindgut. a, anus; am, antenna muscle; bm, bulbus muscle; br, brain; co, circumesophageal connectives; cso, ciliated sense organ; dtc, dorsal tufts of cilia; emb, embryo; en, enteronephridium; gn2-3, ganglia of segments 2 and 3; hg, hindgut; la, lateral antenna; lcb, lateral ciliary band; lct, lateral tufts of cilia; lm, longitudinal muscle strands; mg, midgut; mo, mouth opening; no, nuchal organ; nom, nuchal organ muscle; oe, esophagus; ov, oviduct; pa, palp; pam, palp muscle; pc, parapodial (interramal) cirrus; pcc, parapodial cirrus cilium; pcn, parapodial cirrus nerve; ppm, parapodial muscles; pr, prostomium; sd, spermioduct; seg, subesophageal ganglia; sin, side nerves from ventral cord; sn, segmental nephridium; tc, tuft of cilia; I–IX, segment number.

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the latter seems to have overcome the osmotic problems of changing salinity and is one of the few nerillid genera with several species found intertidally and in brackish waters, above the halocline (Gelder 1974). Intriguingly, the cave obligate species of *Speleonerilla* are likewise highly tolerant to changing salinities, which allow them to swim and suspension feed around the brackish halocline of anchialine caves (Worsaae et al. 2018).

Whereas most polytypic genera show the highest diversity in the interstitial, sandy habitats, some genera such as *Nerilla* and *Meganerilla* contain several larger species seemingly adapted to more silty, spacious environments, such as algae, silty shell gravel, and mud. The genus *Paranerilla* is even restricted and highly adapted to muddy habitats. Several species are adapted to very specific environments such as anchialine caves (*Speleonerilla* and *Leptonerilla* spp.) or sulfur-rich, hypoxic sediments (*Meganerilla bactericola* (Müller, Bernhard & Jouin-Toulmond, 2001) and *Mesonerilla neridae* Worsaae & Rouse, 2009). Finally, several species seem to thrive in aquarium systems (e.g., *Aristonerilla brevis* Saphonov & Tzetlin, 1997, *Nerilla antennata*, and *Trochonerilla mobilis* Tzetlin & Saphonov, 1992, the latter even being described from an aquarium) (Tzetlin and Saphonov 1992, Müller 2002).

Nerillids generally move by ciliary gliding, primarily by the help of the midventral ciliary band, transporting them through the interstices among sand grains or over the surface of flocculent mud. A fast undulatory escape reaction caused by contractions of the longitudinal muscle bands is found in all nerillids observed alive. In several species, this reaction has been observed accompanied by the release of a thin mucus thread linking and securing them to the sediment surface during the escape to the above waters (e.g., *Meganerilla swedmarki* Boaden, 1961 and *Nerilla antennata*). Some species have pronounced transverse ciliary bands that can aid to the gliding motion or even be used for swimming above the sediment in still waters (e.g., *Trochonerilla mobilis*) (see Tzetlin and Saphonov 1992, Müller and Worsaae 2006). In the mud-dwelling species of *Paranerilla*, the ciliary bands are so well developed that the animals can burrow into the flocculent mud by moving particles above the dorsum by the aid of the transverse bands of dorsal cilia (Jouin and Swedmark 1965, Worsaae and Kristensen 2003). *Speleonerilla* spp. living in the still waters of anchialine caves are found to swim high into the water column, performing loops and propelling forward by the help of the unique densely ciliated pygidial lobes, as well as sideways bending by muscle action, and circling, dancing movements aided by the very long muscular and ciliated palps (Worsaae et al. 2004, 2018). Contrary to most annelids, actively moving their parapodia and chaetae by muscular action when swimming or crawling, nerillids during forward gliding have their parapodia and chaetae inactively resting along the body or even firmly compressed along the body when swimming.

Few studies have been made on the feeding mode and food sources of nerillids. Most nerillids browse detritus, bacteria, and algae by the help of their ventral pharyngeal organ, sometimes involving a "tongue" and/or ciliated ventral oral shield; thereafter, the food particles are conveyed to the esophagus by a combination of cilia and mucus (Tzetlin et al. 1987, 1992, Westheide 1990). The mud-dwelling *Paranerilla* spp. and *Meganerilla swedmarki* have been observed to feed directly on detritus and mud particles, seemingly unselectively (Worsaae 2003). However, more detailed studies of *Nerilla antennata* showed that this species browses selectively on organic debris and microorganisms (Gelder and Uglow 1973). Diatoms fill the gut of *Leptonerilla diatomeophaga* (Núñez, Ocaña & Brito, 1997), which also lives in bacterial and diatom mats (Núñez et al. 1997, Müller et al. 2001, Worsaae et al. 2009). Symbiosis with bacteria is found in *Trochonerilla mobilis* and *Aristonerilla brevis* Saphonov and Tzetlin, 1997, which have endosymbiotic bacteria located in epidermal bacteriocytes (Tzetlin and Saphonov 1995), and possibly also in *Meganerilla bactericola* with epibiotic bacteria and living in bacterial mats.

Parasites have been found associated with nerillids in a few species. A very high percentage of the *Paranerilla* spp. from both Sweden and west Greenland waters contains parasites of the group Orthonectida (personal observations, Jouin and Swedmark 1965, Worsaae and Müller 2004). *M. roscovita* Lévi, 1953 has been observed being infested by a very large nematode (several times the length of the nerillid) (Fig. 7.9.2D) (Worsaae unpublished observations).

Phylogeny and taxonomy

Two phylogenetic studies of Nerillidae have been conducted: combined analyses of 14 species only (morphology + 18S rRNA) (Worsaae 2005b) as well as morphological analyses of 49 species (Worsaae 2005a). The latter analysis (Worsaae 2005a) resulted in the synonymization of three genera (*Bathychaetus* with *Psammoriedlia*, *Akessoniella* with *Nerillidium*, and *Xenonerilla* with *Meganerilla*) and two reassignments of species to different genera (*Nerillidium simplex* to *Troglochaetus simplex* and *Mesonerilla diatomeophaga* to *Leptonerilla diatomeophaga*). The

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species-rich genus *Mesonerilla* with high intrageneric variation in key characters such as antennae and genital organs was paraphyletic in the analyses of Worsaae (2005a) and warrants a revision. The genus *Nerilla* was not included in the combined analyses (Worsaae 2005b) yet branches off most basally in the morphological analyses (Worsaae 2005a).

Both analyses showed that reductions or losses have ocurrred throughout the evolutionary history of the family, and not only once in the possibly progenetic origin of the family. In all analyses, the nine-segmented genera branch off first, with segments 8 and 9 being lost secondarily in the more terminal positioned seven- or eight-segmented genera, through several independent evolutionary events (Worsaae 2005a, b). Segment number is one of the diagnostic generic characters and seems to be consistent in the phylogenetic analyses yet shows several independent losses. Although the pattern of character evolution seems more complex than first expected, with several independent losses and occasional gains, the character reconstructions (Worsaae 2005a, b) support the overall suggestion of Westheide and Purschke (1996) on regressive evolution having taken place within Nerillidae possibly through progenesis. It would be highly interesting to investigate whether annelid families such as Nerillidae, Dorvilleidae, and Syllidae may be genetically predisposed to progenesis, explaining the many losses as possibly repeated paedomorphic processes within these groups during their evolution.

The high species diversity found in the temperate waters of Europe and the U.S. East Coast compared to Asia, Africa, or South America just reflects the higher sampling and research effort in the former areas. In general, the majority of nerillids found in new sampling areas are new to science (especially when using molecular tools). However, the morphological differences may be minor or indistinct, and new genera is a rare phenomenon and more likely to be found in isolated or aberrant environments than in shallow sandy substrates.

Genera diagnoses

Afronerilla Faubel, 1978 (Fig. 7.9.5A)

Type species: *Afronerilla hartwigi* Faubel, 1978
Monotypic.
Diagnosis: Eight segments, no palps described (possibly artifact), no antennae, no pygidial cirri, short cirriform interramal cirri on segments 2 to 7, capillary chaetae on segments 2 to 8, eyes absent, buccal pieces and reproductive mode not studied.

Aristonerilla Müller, 2002 (Fig. 7.9.5B)

Type species: *Aristonerilla brevis* (Saphonov & Tzetlin, 1997) as *Micronerilla brevis*
Monotypic.
Diagnosis: Seven segments, two club-shaped palps, one median and two lateral wrinkled antennae and two wrinkled pygidial cirri, long cirriform interramal cirri on segments 2 to 7, compound chaetae in all segments, two red or black eyes, not examined for buccal pieces, and gonochoristic with one pair of spermioducts or oviducts opening in segment 7.

Leptonerilla Westheide & Purschke, 1996 (Fig. 7.9.5C)

Type species: *Leptonerilla diplocirrata* Westheide & Purschke, 1996
3 species.
Diagnosis: Nine segments, two club-shaped palps, one median and two lateral cirriform antennae, two cirriform pygidial cirri, single cirrus in segment 1 and double, long, cirriform interramal cirri in segments 2 to 9, compound chaetae in all segments, eyes absent, and buccal pieces unknown. Gonochoristic with one pair of spermioducts or oviducts opening in segment 8.

Speleonerilla Worsaae, Sterrer & Iliffe, 2018 (Fig. 7.9.5D)

Type species: *Speleonerilla saltatrix* (Worsaae, Sterrer & Iliffe, 2004)
4 species.
Diagnosis: Eight or nine segments, two very long cirriform palps (equal to body length), one short median and two short lateral cirriform antennae. Pygidium with two dorsal ciliated lobes and two terminal cirri. Bottle-shaped interramal cirri in segments 3 to 8 or 2 to 9, compound chaetae in all segments, eyes absent, buccal pieces unknown (cuticular plates observed), hermaphroditic with one pair of spermioducts in segment 7 or segments 6 and 7 and one pair of oviducts in segment 8.

Meganerilla Boaden, 1961 (Fig. 7.9.5E, F)

Type species: *Meganerilla swedmarki* Boaden, 1961 (including *Xenonerilla* Müller, Bernhard & Jouin-Toulmond, 2001)
5 species.
Diagnosis: Nine segments, two large palps with crenulate margin, one or no short median and no lateral antennae, two leaf-shaped or cirriform pygidial cirri, leaf-shaped interramal cirri in segments 1 to 9 or 2 to 9, capillary chaetae in segments 1 to 9 (only in segments 5–7 in *M. bactericola*), eyes absent, and buccal pieces in ventral tongue. Gonochoristic with one pair of spermioducts or one pair of oviducts opening in segments 7 and 8, respectively.

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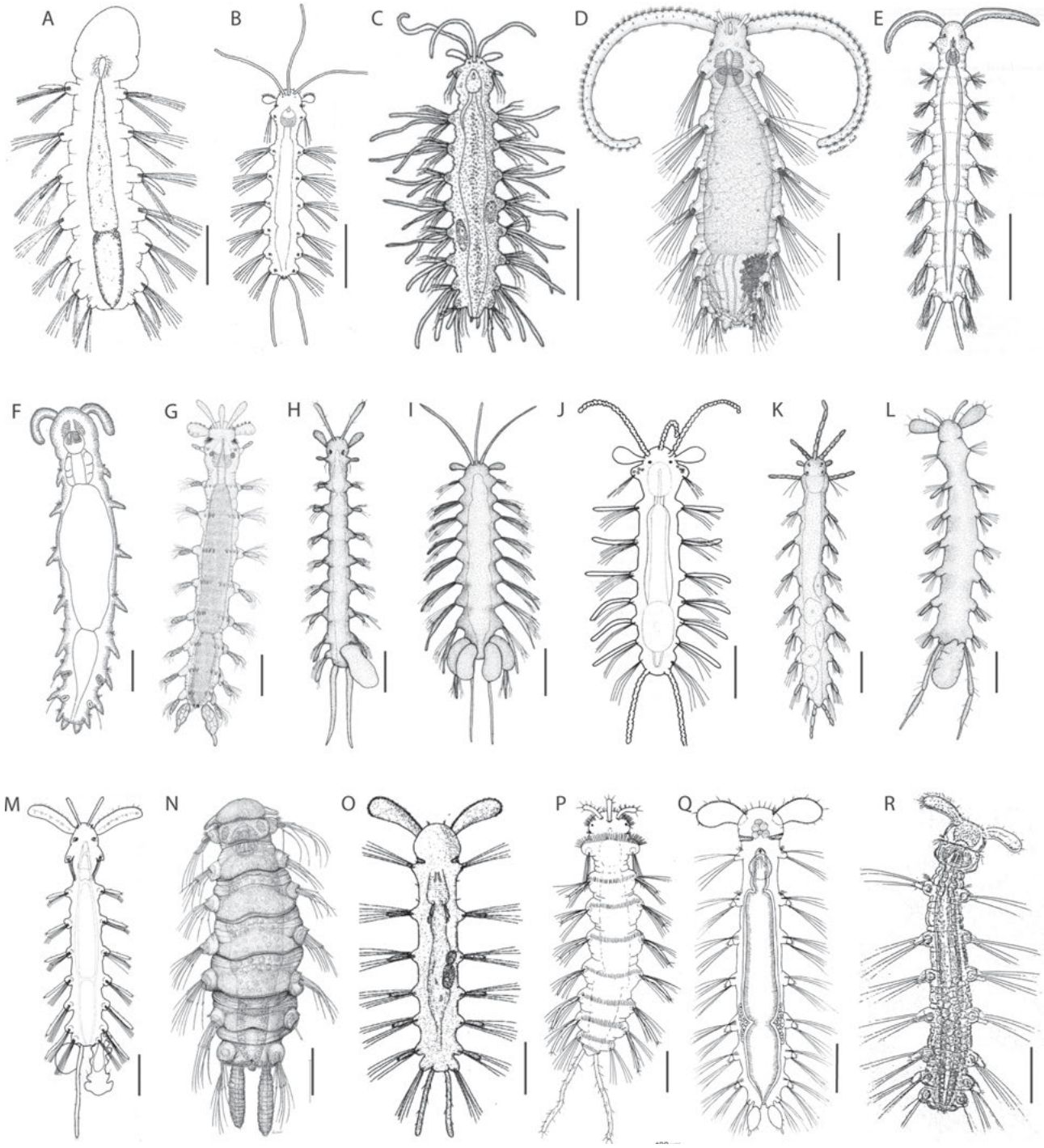


Fig. 7.9.5: Schematic drawings of Nerillidae genera. A, *Afronerilla hartwigi* from Faubel (1978), scale bar 50 µm; B, *Aristonerilla brevis* from Müller (2002), scale bar 100 µm; C, *Leptonerilla prospera* from Sterrer & Illife (1982), scale bar 500 µm; D, *Speleonerilla saltatrix* from Worsaae et al. (2004), scale bar 100 µm; E, *Meganerilla swedmarki* from Westheide (2008), scale bar 500 µm; F, *Meganerilla bactericola* from Müller, Bernhard & Jouin-Toulmond (2001), scale bar 100 µm; G, *Mesonerilla armoricana* from Worsaae et al. (2009), scale bar 100 µm; H, *Mesonerilla biantennata* from Besteiro et al. (2012), scale bar 100 µm; I, *Mesonerilla intermedia* from Besteiro et al. (2012), scale bar 250 µm; J, *Micronerilla minuta* from Westheide (2009), scale bar 100 µm; K, *Nerilla antennata* from Besteiro et al. (2012), scale bar 200 µm; L, *Nerillidium mediterraneum* from Besteiro et al. (2012), scale bar 100 µm; M, *Nerillidopsis hyalina* from Westheide (2009), scale bar 100 µm; N, *Paranerilla cilioscutata* from Worsaae and Kristensen (2003), scale bar 100 µm; O, *Psammoriedlia ruperti* from Kirsteuer (1966), scale bar 100 µm; P, *Trochonerilla mobilis* from Tzetlin and Saphonov (1997), scale bar 100 µm; Q, *Thalassochaetus palpifoliaceus* from Ax (1954), scale bar 100 µm; R, *Troglochaetus beranecki* from Delachaux (1921), scale bar 100 µm.

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***Mesonerilla* Remane, 1949 (Fig. 7.9.5G–I)**
Type species: *Mesonerilla luederitzi* Remane, 1949
15 species.
Diagnosis: Nine segments, two club-shaped palps, no or one short/long median and two long lateral cirriform antennae, two cirriform or bottle-shaped pygidial cirri, cirriform or bottle-shaped interramal cirri in all segments, compound chaetae in segments 1 to 9 or 2 to 9, eyes absent, and buccal pieces unknown. Gonochoristic with one pair (opening in segment 5) or two pairs (opening in segments 5 and 6) of spermioducts or hermaphroditic with two pairs of spermioducts opening in segments 6 and 7. One pair of oviducts opening in segment 8.

***Micronerilla* Jouin, 1970 (Fig. 7.9.5J)**
Type species: *Micronerilla minuta* (Swedmark, 1959) as *Mesonerilla minuta*
Monotypic.
Diagnosis: Eight segments, two club-shaped palps, one median and two lateral wrinkled antennae and two wrinkled pygidial cirri, long cirriform interramal cirri in segments 2 to 7, compound chaetae in all segments, two red eyes, two buccal pieces. Gonochoristic with two pairs of spermioducts opening in segments 7 and 8 or one pair of oviducts opening in segment 8.

***Nerilla* Schmidt, 1848 (Fig. 7.9.5K)**
Type species: *Nerilla antennata* Schmidt, 1848 (includes *Dujardinia* Quatrefages, 1866)
11 species.
Diagnosis: Nine segments, two short bulb-shaped palps, one median and two lateral annulated long antennae, two annulated pygidial cirri, long annulated interramal cirri on segment 1, cirriform interramal cirri in segments 2 to 8, capillary chaetae in all segments, eyes absent or two pairs present, 16 dorsal buccal pieces. Gonochoristic with three pairs of spermioducts, in segments 6 to 8 with a joint midventral opening, or oviducts opening in segment 7.

***Nerillidium* Remane, 1925 (Fig. 7.9.5L)**
Type species: *Nerillidium gracile* Remane, 1925 (includes *Akessoniella* Tzetlin & Larionov, 1988 and *Bathynerilla* Faubel, 1978)
9 species.
Diagnosis: Eight segments, two club-shaped palps, two lateral cirriform antennae, two cirriform or bottle-shaped pygidial cirri, cirriform interramal cirri in segments 1 to 7 or 2 to 7, capillary chaetae in all segments, eyes absent, and 4 to 12 dorsal buccal pieces. Hermaphroditic with one pair of spermioducts and one pair of oviducts opening in segments 6 and 8, respectively.

***Nerillidopsis* Jouin, 1966 (Fig. 7.9.5M)**
Type species: *Nerillidopsis hyalina* Jouin, 1966
Monotypic.
Diagnosis: Eight segments, two straight palps of medium length, two lateral cirriform antennae, two cirriform pygidial cirri, cirriform interramal cirri in segments 2 to 7, capillary chaetae in segments 1 and 4 to 8, compound chaetae in segments 2 to 4, eyes absent, and 8 to 14 dorsal buccal pieces. Hermaphroditic with one pair of spermioducts and one pair of oviducts opening in segments 6 and 8, respectively.

***Paranerilla* Jouin & Swedmark, 1965 (Fig. 7.9.5N)**
Type species: *Paranerilla limicola* Jouin & Swedmark, 1965
2 species.
Diagnosis: Seven segments, no palps, lateral prostomial horns, no antennae, two cirriform pygidial cirri, rudimentary interramal cirri in all segments, compound chaetae in all segments, eyes absent, buccal pieces not studied. Gonochoristic with one pair of spermioducts opening in segment 5, no oviducts observed.

***Psammoriedlia* Kirsteuer, 1966 (Fig. 7.9.5O)**
Type species: *Psammoriedlia ruperti* Kirsteuer, 1966 (includes *Bathychaetus* Faubel, 1978)
2 species.
Diagnosis: Seven segments, two club-shaped palps, no antennae, two cirriform pygidial cirri, cirriform interramal cirri in segments 1 to 6 or 1 to 7, capillary chaetae in all segments, eyes absent, two to four buccal pieces, reproductive mode unknown.

***Thalassochaetus* Ax, 1954 (Fig. 7.9.5P)**
Type species: *Thalassochaetus palpifoliaceus* Ax, 1954
Monotypic.
Diagnosis: Eight segments, two club-shaped palps, no antennae, two short bottle-shaped pygidial cirri, cirriform interramal cirri in segments 2 to 7, compound chaetae in all segments, eyes absent, and buccal pieces not studied (cuticular plates observed). Reproductive mode unknown.

***Trochonerilla* Tzetlin & Saphonov, 1992 (Fig. 7.9.5Q)**
Type species: *Trochonerilla mobilis* Tzetlin & Saphonov, 1992
Monotypic.
Diagnosis: Eight segments, two short club-shaped palps (see Müller and Worsaae 2006), one median and two lateral short antennae and two cirriform pygidial cirri, long cirriform interramal cirri in segments 2 to 7, capillary chaetae in all segments, two pigmented eyes, and 4 dorsal

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buccal pieces. Gonochoristic with two pairs of spermioducts opening in segments 7 and 8, respectively, or one pair of oviducts opening in segment 8.

***Troglochaetus* Delachaux, 1921 (Fig. 7.9.5R)**

Type species: *Troglochaetus beranecki* Delachaux, 1921

2 species.

Diagnosis: Eight segments, two club-shaped palps, no antennae, two pygidial lobes or bulbs, rudimentary interramal cirri in segments 2 to 7 or 2 to 8, capillary chaetae in segments 1 to 8 or 2 to 8, eyes absent, and four dorsal buccal pieces. Hermaphroditic with one pair of spermioducts and one pair of oviducts opening in segments 6 and 8, respectively.

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References

Ax, P. (1954): *Thalassochaetus palpifoliaceus* nov. gen., nov. spec. (Archiannelida, Nerillidae), in marinen Verwandter von *Troglochaetus beranecki* Delachaux. *Zoologischer Anzeiger* 153: 64–75.

Beauchamp, P. de (1910): Sur l'organisation de la *Nerilla*. *Bulletin Biologique de la France et de la Belgique* 44: 11–12.

Besteiro, C., Núñez, J., & Martínez, A. (2012): Nerillidae Levinsen 1883. In: Parapar, J., Alós, C., Núñez, J., Moreira, J., López, E., Aguirrezabalaga, F., Besteiro, C., & A. Martínez (eds.), *Fauna Ibérica. Annelida, Polychaeta III*. Museo Nacional de Ciencias Naturales, CSIC, Madrid: 335–345.

Boaden, P.J.S. (1961): *Meganerilla swedmarki*, nov. gen., nov. spec., an archiannelid of the family Nerillidae. *Arkiv för Zoologi* 13: 553–559.

Cabioch, L., Hardy, J.P.L. & Rullier, F. (1968): *Inventaire de la faune marine de Roscoff. Annélides*. Station Biologique de Roscoff: 81 pp.

Curini-Galletti, M., Artois, T., Delogu, V., De Smet, W.H., Fontaneto, D., Jondelius, U., Leasi, F., Martínez, A., Meyer-Wachsmuth, I., Nilsson, K.S., Tongiorgi, P., Worsaae, K. & Todaro, A.M. (2012): Patterns of diversity in soft-bodied meiofauna: Dispersal ability and body size matter. *PLoS ONE* 7: e33801.

Delachaux, T. (1921): Un polychète d'eau douce cavernicole *Troglochaetus beranecki* nov. gen. nov. spec. *Bulletin de la Société des Sciences naturelles de Neuchatel* 45: 1–11.

Eakin, R.M., Martin, G.G. & Reed, C.T.R. (1977): Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphology* 88: 1–18.

Faubel, A. (1978): Neue Nerillidae (Archiannelida) aus dem sublitoral der Nordsee und des Mittelatlantik (Nordwest Afrika). *Zoologica Scripta* 7: 257–262.

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphology* 95: 235–249.

Fransen, M.E. (1983): Fine structure of the brooding apparatus of the archiannelid *Mesonerilla intermedia*: Maternal connections to brooded eggs. *Transactions of the American Microscopical Society* 102: 25–37.

Franzén, Å. & Sensenbaugh, T. (1984): Fine structure of spermiogenesis in the archiannelid *Nerilla antennata* Schmidt. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening (København)* 145: 23–36.

Gelder, S.R. (1974): A review of the zoogeography and habitat data of the genus *Nerilla* Schmidt, 1848 (Annelida: Archiannelida). *Journal of Natural History* 8: 631–643.

Gelder, S.R. & Uglow, R.F. (1973): Feeding and gut structure in *Nerilla antennata* (Annelida: Archiannelida). *Journal of Zoology (London)* 171: 225–237.

Goodrich, E.S. (1912): *Nerilla* an archiannelid. *Quarterly Journal of Microscopical Science* 57: 397–425, 4 pls.

Hatschek, B. (1878): Studien über Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilaterien. *Arbeiten aus dem Zoologischen Institut der Universität Wien* 1: 277–404.

Jouin, C. (1963): *Mesonerilla biantennata* n. sp. nouvelle Archiannélide Nerillidae de la region de Roscoff. *Comptes Rendus de l'Académie de Sciences (Paris)* D 257: 4057-4060.

Jouin, C. (1966): Hermaphrodisme chez *Nerillidopsis hyalina* n. g., n. sp. et chez *Nerillidium* Remane, Archiannélides. *Comptes Rendus de l'Académie de Sciences (Paris)* D 263: 412–415.

Jouin, C. (1967a): Sexualité chez *Meganerilla* Boaden et *Mesonerilla* Remane (Archiannélide Nerillidae) et modalités de reproduction chez ce dernier genre. *Comptes Rendus de l'Académie de Sciences (Paris)* D 265: 150–153.

Jouin, C. (1967b): Étude morphologique et anatomique de *Nerillidopsis hyalina* Jouin et de quelques *Nerillidium* Remane (Archiannélides Nerillidae). *Archives de Zoologie Expérimentale et Générale* 108: 97–110.

Jouin, C. (1968): Sexualité et biologie de la reproduction chez *Mesonerilla* Remane et *Meganerilla* Boaden. *Cahiers de Biologie Marine* 9: 31–52.

Jouin, C. (1970a): Archiannélides interstitielles de Nouvelle-Calédonie. *Editions de la Fondation Singer-Polignac* 4: 149–167.

Jouin, C. (1970b): Recherches sur les Archiannélides interstitielles: Systématique, anatomie et développement des Protodrilidae et des Nerillidae. Thèse Doctorat, Faculté des Sciences des Paris: 204 pp.

Jouin, C. (1971): Status on the knowledge of the systematics and ecology of Archiannelida. In: Hulings, N.C. (ed.), Proceedings of the First International Conference on Meiofauna. *Smithsonian Contributions to Zoology* 76: 47–56.

Jouin, C. (1973): Nouvelles données sur *Troglochaetus beranecki* Delachaux (Archiannelida Nerillidae). *Annales de Spéléologie* 28: 575–579.

Jouin, C. & Swedmark, B. (1965): *Paranerilla limicola* n. g., n. sp., Archiannélide Nerillidae du benthos vaseux marin. *Cahiers de Biologie Marine* 6: 201–218.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Kirsteuer, E. (1966): Zur Kenntnis der Archiannelida des Roten Meeres. *Zoologischer Anzeiger* 177: 288–296.

Lévi, C. (1953): Archiannélides Nerillidae de la région de Roscoff. *Archives de Zoologie Expérimentale et Générale* 90: 64–70.

Levinsen, G.M.R. (1883): Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening (København)*: 1–354.

Magagnini, G. (1964): Elevage au laboratoires d'une espèce mésopsammique: *Nerilla antennata* O. Schmidt (Archiannélida Nerillidae). *Cahiers de Biologie Marine* 5: 405–409.

Magagnini, G. (1968): Influenza della temperature e della salinita sulla biologia riproduttiva di una popolazione atlantica di *Nerilla antennata* Schmidt (Archiannelida: Nerillidae). *Atti della Societa dei Naturalisti e Matematici* 99: 1–15.

Magagnini, G. (1982): Reproduction in *Nerilla antennata* O. Schmidt (Archiannelida Nerillidae): Induction of spawning. *Bolletino di Zoologia* 49: 283–286.

Morselli, I., Mari, M. & Sarto, M. (1995): First record of the stygobiont "archiannelid" *Troglochaetus beranecki* Delachaux from Italy. *Bolletino di Zoologia* 62: 287–290.

Müller, M.C.M. (1999): *Das Nervensystem der Polychaeten: Immunohistochemische Untersuchungen an ausgewählten Taxa.* Ph.D. thesis, University of Osnabrück: 402 pp.

Müller, M.C.M. (2002): *Aristonerilla*: a new nerillid genus (Annelida: Polychaeta) with description of *Aristonerilla (Micronerilla) brevis* comb. nov. from a seawater aquarium. *Cahiers de Biologie Marine* 43: 131–139.

Müller, M.C.M., Bernhard, J.M. & Jouin-Toulmond, C. (2001): A new member of Nerillidae (Annelida: Polychaeta), *Xenonerilla bactericola* gen. et sp. nov., collected off California, USA. *Cahiers de Biologie Marine* 42: 203–217.

Müller, M.C.M. & Worsaae, K. (2006): CLSM analysis of the phalloidin stained muscle system in *Nerilla antennata, Nerillidium* sp. and *Trochonerilla mobilis* (Polychaeta: Nerillidae). *Journal of Morphology* 267: 885–896.

Núñez, J., Ocaña, O. & Brito, M.C. (1997): Two new species (Polychaeta: Fauveliopsidae and Nerillidae) and other polychaetes from the marine lagoon cave of Jameos del Agua, Lanzarote. (Canary Islands). *Bulletin of Marine Science* 60: 252–260.

Pennak, R.W. (1971): A fresh-water archiannelid from the Colorado Rocky Mountains. *Transactions of the American Microscopical Society* 90: 372–375.

Pennak, R.W. & Ward, J.V. (1986): Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. *Archiv für Hydrobiologie, Supplement* 74: 356–396.

Purschke, G. (1985): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). II. The pharynx of the Nerillidae. *Microfauna Marina* 2: 23–60.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2006): Problematic annelid groups. In: Rouse, G., & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield: 639–667.

Remane, A. (1925): Diagnosen neuer Archianneliden (zugleich 3. Beitrag zur Fauna der Kieler Bucht). *Zoologischer Anzeiger* 65: 15–17.

Remane, A. (1928): *Nerillidium mediterraneum* n. sp. und seine tiergeographische Bedeutung. *Zoologischer Anzeiger* 77: 57–60.

Remane, A. (1949): Archianneliden der Familie Nerillidae aus Sudwest-Afrika. *Kieler Meeresforschung* 6: 45–50.

Renaud-Mornant, J. & Jouin, C. (1965): Note sur la microfaune du fond a *Amphioxus* de Graveyron et d'autres stations du Bassin d'Arcachon. *Actes de la Société linnéenne de Bordeaux* 102: 1–7.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes.* Oxford University Press, New York: 354 pp.

Saphonov, M.V. & Tzetlin, A.B. (1997): Nerillidae (Annelida, Polychaeta) from the White Sea, with description of a new species of *Micronerilla* Jouin. *Ophelia* 47: 215–226.

Särkkä, J. & Mäkelä, J. (1998): *Troglochaetus beranecki* Delachaux (Polychaeta, Archiannelida) in esker groundwaters of Finland: a new class of limnic animals for northern Europe. *Hydrobiologia* 379: 17–21.

Schmidt, E.O. (1848): *Neue Beiträge zur Naturgeschichte der Würmer gesammelt auf einer Reise nach dem Färör im Frühjahr 1848*. F. Manke, Jena: 44 pp.

Schmidt, H. & Westheide, W. (1998): RAPD-PCR experiments confirm the distinction between three morphologically similar species of *Nerilla* (Polychaeta: Nerillidae). *Zoologischer Anzeiger* 236: 277–285.

Sterrer, W. & Iliffe, T.M. (1982): *Mesonerilla prospera*, a new archiannelid from marine caves in Bermuda. *Proceedings of the Biological Society of Washington* 95: 509–514.

Swedmark, B. (1959): Archiannélides Nerillidae des côtes du Finistère. *Archives de Zoologie Expérimentale et Générale* 98: 26–42.

Swedmark, B. (1964): Interstitial fauna of marine sand. *Biological Reviews* 39: 1–42.

Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Tzetlin, A.B. & Saphonov, M.V. (1992): *Trochonerilla mobilis* gen. et sp. n., a meiofaunal nerillid (Annelida, Polychaeta) from a marine aquarium in Moscow. *Zoologica Scripta* 21: 251–254.

Tzetlin, A.B. & Saphonov, M.V. (1995): A new finding of intracellular bacterial symbionts in the Nerillidae (Annelida: Polychaeta). *Russian Journal of Aquatic Ecology* 4: 55–60.

Tzetlin, A.B., Zarvarzina, E.G., & Saphonov, M.V. (1987): Functional morphological analysis of the pharynx in some annelids. *Doklady Akademii Nauk SSSR* 294: 1008–1011. [in Russian]

Tzetlin, A.B., Purschke, G., Westheide, W. & Saphonov, M.V. (1992): Ultrastructure of enteronephridia and general description of the alimentary canal in *Trochonerilla mobilis* and *Nerillidium troglochaetoides* (Polychaeta, Nerillidae). *Acta Zoologica (Stockholm)* 73: 163–176.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

von Nordheim, H. (1984): Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae, and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchungen* 38: 1–20.
Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21: 843–854.
Westheide, W. (1990): *Polychaetes: Interstitial Families. Synopsis of the British Fauna (New Series)*. Universal Book Services/ Dr. W. Backhuys, Oegstgeest: 152 pp.
Westheide, W. (2008): *Polychaetes: Interstitial Families. Synopsis of the British Fauna (New Series), no. 44*. 2nd ed. The Linnean Society of London, London: 169 pp.
Westheide, W. & Purschke, G. (1996): *Leptonerilla diplocirrata*, a new genus and species of interstitial polychaetes from the island of Hainan, south China (Nerillidae). *Proceedings of the Biological Society of Washington* 109: 586–590.
Wilke, U. (1953): *Mesonerilla intermedia* nov. sp., ein neuer Archiannelide aus dem Golf von Neapel. *Zoologischer Anzeiger* 150: 211–215.
Worsaae, K. (2003): *Functional Morphology of Two Mud-Dwelling Meiofana Polychaetes of the Family Nerillidae (Annelida)*. Arctic Biology Field Course, Qeqertarsuaq, 2002. ISBN 87-87519-58-5: 119–128.
Worsaae, K. (2005a): Systematics of Nerillidae (Polychaeta, Annelida). *Meiofauna Marina* 14: 49–74.
Worsaae, K. (2005b): Phylogeny of Nerillidae (Polychaeta, Annelida) as inferred from combined 18S rDNA and morphological data. *Cladistics* 21: 143–162.
Worsaae, K. & Kristensen, R.M. (2003): A new species of *Paranerilla* (Polychaeta: Nerillidae) from northeast Greenland waters, Arctic Ocean. *Cahiers de Biologie Marine* 44: 23–39.
Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial polychaetes. *Hydrobiologia* 535/536: 310–340.
Worsaae, K. & Müller, M.C.M. (2004): Nephridial and gonoduct distribution patterns in Nerillidae (Annelida: Polychaeta) — Examined by tubulin staining and CLSM. *Journal of Morphology* 261: 259–269.
Worsaae, K. & Rouse, G.W. (2009): *Mesonerilla neridae*, n. sp. (Nerillidae): First meiofaunal annelid from deep-sea hydrothermal vents. *Zoosymposia* 2: 297–303.
Worsaae, K., Sterrer, W. & Iliffe, T.M. (2004): *Longipalpa saltatrix*, a new genus and species of the meiofaunal family Nerillidae (Annelida: Polychaeta) from an anchihaline cave in Bermuda. *Proceedings of the Biological Society of Washington* 117: 346–362.
Worsaae, K., Nygren, A., Rouse, G.W., Giribet, G., Persson, J., Sundberg, P. & Pleijel, F. (2005): Phylogenetic position of Nerillidae and *Aberranta* (Polychaeta, Annelida), analyzed by direct optimization of combined molecular and morphological data. *Zoologica Scripta* 34: 313–328.
Worsaae, K., Martínez, A. & Núñez, J. (2009): Nerillidae (Annelida) from the Corona lava tube, Lanzarote, with description of *Meganerilla cesari* n. sp. *Marine Biodiversity* 39: 195–207.
Worsaae, K., Gonzalez, B.C., Kerbl, A., Nielsen, S.H., Jørgensen, J.T., Armenteros, M., Iliffe, T.M. & Martínez, A. (2018): Diversity and evolution of the stygobitic *Speleonerilla* nom. nov. (Nerillidae, Annelida) with description of three new species from anchialine caves in the Caribbean and Lanzarote. *Marine Biodiversity* 49.
Worsaae, K., Mikkelsen, M.D. & Martínez, A. (2019): Description of six new species of *Mesonerilla* (Nerillidae, Annelida) and an emended description of *M. intermedia* Wilke, 1953, from marine and cave environments. *Marine Biodiversity*.
Zrzavý, J., Riha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189: 1–14.

Errantia

Igor Eeckhaut and Déborah Lanterbecq

7.10 Myzostomida

Introduction

Myzostomids, or myzostomes, are minute, soft-bodied, marine "worms" that are mainly associated with echinoderms. They are found in all oceans from subtidal to a depth of more than 3000 m. Most of them are ectocommensals of crinoids, but some species are parasites of crinoids, asteroids, or ophiuroids, and a few others infest black corals (Bo et al. 2013, Terrana and Eeckhaut 2017). When they are parasites, they live in the gonads, coelom, integument, or digestive system of their hosts. Due to their long history as host-specific symbionts, myzostomids have acquired a unique, highly derived anatomy that has obscured their phylogenetic affinities to other metazoans during decades (see Eeckhaut and Lanterbecq 2005), but recent advances in molecular phylogeny show that they are undoubtedly close to annelids (e.g., Bleidorn et al. 2007, 2009a, b, Helm et al. 2012, Hartmann et al. 2012). The body plan of most myzostomids is singular inasmuch as they are incompletely segmented, parenchymous, acoelomate organisms with chaetae (see Grygier 2000, Lanterbecq et al. 2009, and Helm et al. 2014 for reviews of myzostomid body plans).

Most myzostomids are ectocommensals and move freely on the surface of crinoids. For most of them, the body consists of an anterior cylindrical introvert (also called proboscis) and a flat, oval, or disk-like trunk (Fig. 7.10.1). The introvert is extended when the individuals feed; it is retracted into an anteroventral pouch of the trunk most of the time. The trunk ranges from a few millimeters to 3 cm long for the largest species. Five pairs of parapodia are located lateroventrally in two rows, each parapodium containing a protrusible hook, some replacement hooks, and a support rod (or acicula). Most species have four pairs of slit- or disk-like lateroventral sense organs, commonly named lateral organs, and the trunk margin often bears flexible needle-like cirri (more than 100 in some species). Hump-like or pointed cirri also occur at the base of each

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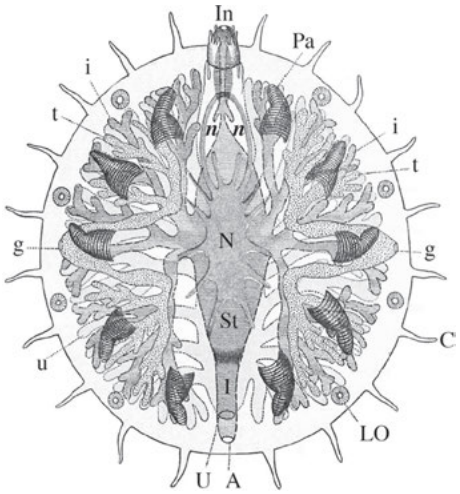


Fig. 7.10.1: General anatomy of Myzostomida. Redrawn from Graff (1884b). A, anogenital opening; C, marginal cirrus; g, the two male gonopores; i, intestinal diverticulum; I, intestine; In, introvert; LO, lateral organ; N, central nervous system; n, esopharyngeal ring; Pa, parapodium; St, stomach; t, testicular follicles; u, uterine diverticulum; U, opening of the uterus into the intestine.

parapodium of about 20 species. Two male gonopores are located at the level of the third pair of parapodia, and the female gonopore opens close to the anus, posteroventrally.

The body of parasitic myzostomids is often highly modified. The introvert, external appendages, and sensory organs are usually reduced or have disappeared. Parasitic myzostomids are known to infest the gonads, coelom, integument, or digestive system of their host (mainly crinoids but also ophiurids and asteroids), and according to their location, their trunk will be folded up dorsally (e.g., *Pulvinomyzostomum pulvinar*), very much longer than wide (e.g., Protomyzostomatidae and Mesomyzostomatidae), very much wider than long (e.g., *Contramyzostoma* species), mushroom-shaped (e.g., *Mycomyzostoma calcidicola*), or totally irregular (unnamed species described by Heinzeller et al. 1995). Parasitic myzostomids may induce changes in their host as, for example, forming swellings on crinoid stems or arms.

Myzostomids are hyponeural organisms with a ventral nerve chain, circumpharyngeal connectives, and cerebral ganglia. The species that live on crinoids feed on particles carried by the ciliated host's ambulacral grooves. The digestive system is complete and made of a pharynx included in the introvert, a stomach, an intestine, and two to three digestive caeca. There are six pairs of protonephridia. Most species are simultaneous hermaphrodites and reproduce in transferring spermatophores what is followed by hypodermic sperm penetration. Fertilization is internal, and eggs develop in the water column into trochophora larvae. There is no circulatory system.

The first writings on myzostomids were from Leuckart (1827, 1830, 1836). In 1827, he wrote "... a new genus that I found several times as parasites on the disk of *Comatula mediterranea* and that I named *Myzostoma parasiticum*". A few years later, Leuckart (1830) mentioned the existence of two myzostomid species: "... Finally, it seems that there is a new genus of parasites named *Myzostoma* and belonging to the Trematoda. There are already two species living on the disk of *Comatula* as parasites; 1) *Myz. Glabrum* on *Comat. Mediterranea* and 2) *Myz. Costatum* on a comatulid from the Red Sea". Unfortunately, there is no description of these two species that are thus *numina nuda*. The first diagnosis of the genus *Myzostoma* has been given by Leuckart (1836): "*M. Corpore molli, disciformi, supra glabro, infra organis motoriis, tam acetabulis suctoriis in utroque latere 4-5, quam hamulis duriusculis instructo; ore anteriore, simplice, prominente, retractili*." At present, about 97 species have been described in the literature (including possible synonym names) with about 31 parasites. Some other species exist in various collections (waiting for a description) or have been cited in the literature but without any description.

Graff (1885a) was the first to report the infestation of fossil crinoids by myzostomids. He had access to five specimens of fossilized crinoids showing presumed myzostomidan galls from the Late Jurassic in Germany and Switzerland. All specimens presented swellings on the stem that contained a chamber with one or two apertures. Since the description of Graff (1885a), two cases of similarly infested crinoid stem have been reported, one from the Late Jurassic of Ernstbrunn in Austria (Abel 1920, Bachmayer 1964) and one in Poland (Radwanska and Radwanski 2005). Yet, the structure of large cysts, of an irregular shape, embedded in tests of the Neogene echinoid *Clypeaster* from Morocco and Turkey was very close to the galls of present-day myzostomids (Roman 1952, 1953). Clarke (1921) introduced the term *Myzostomites* for deep pits in Carboniferous crinoid stems, this name being used afterward for various structures on crinoids of Paleozoic age (reviewed by Franzen 1974 and Brett 1978). There are reports of suggested myzostomidan infestation on Ordovician to Carboniferous crinoids stems in which one or several columnals are heavily swollen into gall-like structure provided with one large opening (Arendt 1961, Warn 1974). Except for the cyst-like, bulbous forms observed on Carboniferous crinoids of the Moscow region (Yakovlev 1939, Arendt 1961), the assignment of Paleozoic abnormalities to Myzostomida is not strongly supported.

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Morphology

Body structure and segmentation

The many unique features of Myzostomida have fueled debates about the phylogenetic position of the group. A major point of contention has been whether Myzostomida are segmented animals and, if so, whether their segmentation is homologous with that of annelids (e.g., Haszprunar 1996, Zrzavy et al. 2001). Usually, a distinction is made between "true" segmentation and iteration (serial repetition). Whereas iteration includes all kinds of repetition of structures (Seaver 2003), segmentation is often linked to coelom formation (Willmer 1990, Seaver 2003, Tautz 2004). Scholtz (2002) defined true segmentation as repeated units along an anteroposterior body axis, and each segment comprises a combination of structures with both ectodermal and mesodermal origins. Some structures in myzostomids are iterated, most obviously the parapodia-like structures. Pietsch and Westheide (1987) have shown that *Myzostoma cirriferum* also has serially arranged protonephridia, and a more recent study revealed the metameric nature of the nervous system (Müller and Westheide 2000). However, all these structures are of ectodermal origin. The occurrence of a coelom — which is of mesodermal origin — in myzostomids is questionable. Recent ultrastructural investigation revealed that the female genital cavities of myzostomids, which are scattered in the parenchyma, are lined by an epithelium and thus represent secondary body cavities (see Eeckhaut and Lanterbecq 2005); furthermore, the ontogeny of these structures seems to be different from that of annelid coelom. Thus, there is no evidence for internally repeated coelomic cavities within myzostomids. Even the sequence of emergence of parapodia in juvenile myzostomids differs from a strict addition facilitated by a posterior growth zone. The third pair of parapodial structures appears first, followed by the fourth, second, and fifth (both synchronously), with the first pair of parapodia last (Jägersten 1940a). A recent developmental investigation of segmentation in polychaetous annelids also indicates the plasticity of segment-generating mechanisms present in different annelid life histories (Seaver et al. 2005). However, using the strict definition presented above, Myzostomida can be regarded as possessing iterated organs but not as truly segmented organisms. Nevertheless, iteration as observed in myzostomids probably represents a derived state from true segmentation as found in many annelids.

Body wall

The ultrastructure of the regular (i.e., nonsensory) integument of myzostomids is known in four species: *Myzostoma cirriferum* (see Eeckhaut and Jangoux 1993a), *Contramyzostoma bialatum* (see Eeckhaut and Jangoux 1995), *Pulvinomyzostomum pulvinar* (see Kronenberg 1997), and *Myzostoma alatum* (see Kronenberg 1997). In all of them, the integument (Fig. 7.10.2) consists of an epidermis covered by a cuticle and an underlying parenchymomuscular layer that extends between the internal systems (i.e., digestive, nervous, excretory, and genital systems). The parenchymomuscular layer, also called dermis, includes a thick layer of collagen on the dorsal part of some myzostomids (Graff 1877, Rao and Sowbhagyavathi 1972). A mesothelium lining a coelomic cavity is not evident in myzostomids, although the female genital tract and ovaries are sometimes considered as coeloms in old works (Eeckhaut and Lanterbecq 2005). There is no mineralized skeleton, and the only hard parts are the chitinous hooks and acicula of parapodia (Lanterbecq et al. 2008).

Nonciliated and ciliated cells form most of the myzostomid epidermis (Fig. 7.10.3), maybe with the exception of *Protomyzostomum* and *Stelechopus* species, where a syncytial epidermis with nuclei sunken below the integumental muscle has been reported (Fedotov 1914, Nigmatullin 1970). They have been observed in the four species cited here above and in *Contramyzostoma sphaera*, *Myzostoma cuniculus*, *Myzostoma laingense*, *Myzostoma horologium*, and *Notopharyngoides aruense* (Eeckhaut and Lanterbecq

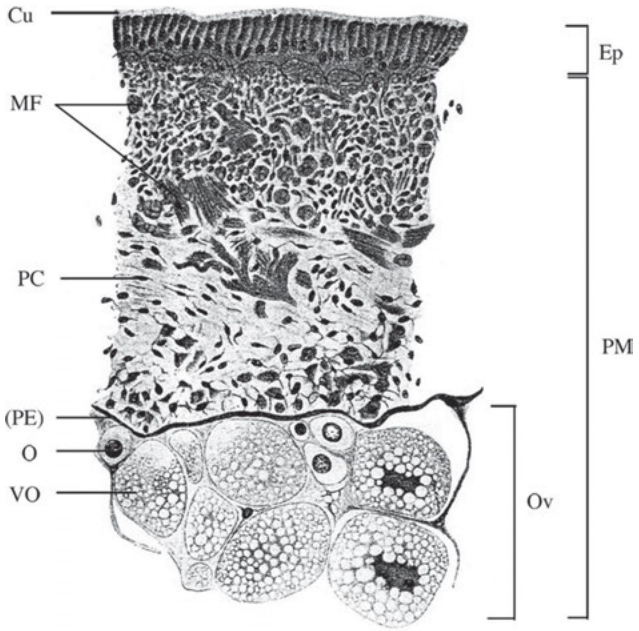


Fig. 7.10.2: Section of a dorsal portion of the integument in *Asteriomyzostomum asteriae* (Marenzeller, 1895). Redrawn from Stummer-Traunfels (1926). Cu, cuticle; Ep, epidermis; MF, muscular fibers; O, oogonia; Ov, ovary; PC, parenchymal cell; (PE), pseudoepithelium (according to Stummer-Traunfels 1926); PM, parenchymomuscular layer; VO, vitellogenic oocyte.

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2005). The cuticle of all these species is generally less than 1 µm thick and consists of several superposed fibrillar layers crossed by numerous microvilli (Fig. 7.10.3). Nonciliated cells, also called covering cells, are flattened to cylindrical and mainly characterized by having two types of vesicles (Fig. 7.10.3). Vesicles of the first type are spherical to ovoid in shape and contain electron-dense material that forms a dark margin. Vesicles of the second type are generally ovoid and located in the most apical part of the cytoplasm, just under the cuticle. They are either empty or full of a granular material and are thought to participate in the formation of the cuticle, whereas the role of the vesicles of the first type is unknown. Ciliated cells are of similar shape and size to covering cells and bear from 20 to 50 cilia (Fig. 7.10.3). The cilia are 10 to 20 µm long, have the classical microtubular arrangement (9 × 2 + 2 microtubules), and are each prolonged by a ciliary rootlet. Most species have usual, tube-like cilia, but paddle-like cilia have been observed in *Myzostoma jagersteni*, *Myzostoma fissum*, and *Myzostoma ambiguum* (see Eeckhaut et al. 1994). The proportions of covering and ciliated cells vary according to the myzostomid species considered, and this seems to be related to the type of association existing between the myzostomid and the host: in ectocommensals, ciliated cells are sparse with a ratio of ciliated cells to nonciliated cells of about 1:5. At the opposite extreme, the trunk of intradigestive myzostomids, such as *Pulvinomyzostomum pulvinar* and *Notopharyngoides aruense*, is almost totally covered by cilia (CC/NC ratio of about 1:1). Ciliary beating induces a water current on the surface of the individuals and surely facilitates the intake of both oxygen and dissolved nutrients through the integument. The overdevelopment of epidermal cilia in intradigestive myzostomids could be an adaptation to their symbiotic way of life.

Two types of gland cells have been observed in the myzostomid epidermis. The first type is mainly found in parapodia, cirri, and the folds that surround lateral organs. It has been observed in *Myzostoma cirriferum* (see Eeckhaut and Jangoux 1993), *Pulvinomyzostomum pulvinar* (see Kronenberg 1997), *Myzostoma alatum* (see Kronenberg 1997), and *Notopharyngoides aruense*, *Myzostoma laingense*, and *Myzostoma horologium* (see Eeckhaut and Lanterbecq 2005). These cells are cylindrical in shape, and their cytoplasm is full of ovoid vesicles, including Alcian blue-positive granular material. These gland cells most likely release mucous for protecting places where contact with the substratum or the host is frequent (Eeckhaut and Jangoux 1993). The second type of gland cells has been observed in the villous and ciliated central part of the lateral organs of *M. cirriferum*. This type has a large cell body resting under the other epidermal cells, and an elongated apical process running to the apex of the epidermis. The cytoplasm is full of spherical vesicles filled with a homogenous, finely granular, Alcian blue-positive material. The vesicle content has various electron densities, and some vesicles appear empty.

Muscle fiber cells, called myoepithelial cells by Eeckhaut and Jangoux (1993), were observed in the epidermis of *Myzostoma cirriferum* (see Eeckhaut and Jangoux 1993) and *Contramyzostoma bialatum* (see Eeckhaut and Jangoux 1995), but they were not found in *Myzostoma alatum* and *Pulvinomyzostomum pulvinar* nor in *Endomyzostoma* sp. (see Kronenberg 1997, Wautier 2009). They are thin,

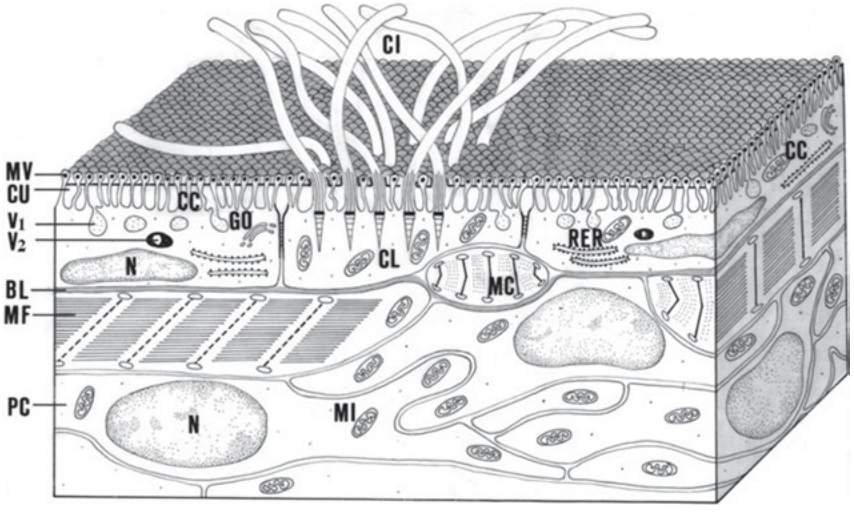


Fig. 7.10.3: Schematic drawing of a portion of a longitudinal section through a nonsensory area of the integument of *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Eeckhaut and Jangoux (1993). BL, basal lamina; CC, covering cell; CI, cilium; CL, ciliated cell; CU, cuticle; GO, Golgi apparatus; MC, myoepithelial cell; MI, mitochondrion; MF, muscular fiber; MV, microvillus; N, nucleus; PC, parenchymal cell; RER, rough endoplasmic reticulum; V1 and V2, vesicles of first and second types.

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elongated muscle cells lying under the covering and ciliated cells (they never contact the cuticle) in such a way that their longitudinal axis is perpendicular to the anteroposterior axis of the myzostomid (Fig. 7.10.3). They are particularly abundant at the level of the introvert (Eeckhaut and Jangoux 1993), where their main action is to reduce the introvert diameter and its length while inducing deep pleats when they contract.

The parenchymomuscular layer includes muscle cells and parenchymal cells (Fig. 7.10.3). Dermal muscles are conspicuous ventrally as well as in the introvert and parapodia; they are less developed dorsally. They consist of longitudinal, circular, and transverse muscle cells of the double-obliquely striated type. In addition, dorsoventral muscles, which form septa, occur in the trunk. Helm et al. (2013) analyzed the distribution of F-actin, a common component of muscle fibers, in specimens of *Myzostoma cirriferum* using phalloidin-rhodamine labeling in conjunction with confocal laser scanning microscopy. Their data reveal that the musculature of the myzostomid body comprises an outer circular layer, an inner longitudinal layer, numerous dorsoventral muscles, and prominent muscles of the parapodial complex. These features correspond well with the common organization of the muscular system in Annelida. In contrast to other annelids, however, several elements of the muscular system in *M. cirriferum*, including the musculature of the body wall and the parapodial flexor muscles, exhibit radial symmetry overlaying a bilateral body plan. These findings are in line with the annelid affinity of myzostomids and suggest that the apparent partial radial symmetry of *M. cirriferum* arose secondarily in this species (Helm et al. 2013). The thickness of the parenchyma varies according to the development of the gonads (it is the thinnest when gonads are mature). The parenchyma is particularly well developed on the dorsal part of the myzostomid trunk where parenchymal cells occur in contact with developing female gametes. On the dorsal side of the trunk of *Myzostoma gopalai*, the parenchyma is completed by a wall of collagen fibers that has only been analyzed by histochemical methods (Rao and Sowbhagyavathi 1972). Parenchymal cells have a highly variable size and shape. Their cytoplasm includes very few organelles. The external matrix that surrounds parenchymal cells is generally poorly developed and is made of a granular material.

Locomotion and locomotory organs

Ectocommensal myzostomids walk on the surface of their hosts. They do not crawl or swim, as it is the case for many polychaetes. Myzostomids have no true segments, and they consequently cannot use coelomic cavities to lengthen or shorten body parts to move (Eeckhaut and Lanterbecq 2005). Yet, they do not have a huge development of longitudinal muscles in their trunk that could have allowed them to swim as some polychaetes do. The locomotion of myzostomids is thus unique within polychaetes. In contrast, as typical for annelid chaetae, myzostomid chaetae are formed by chaetoblasts, which gives rise to microvilli where chaetal material is assembled on the outer surface.

A myzostomid parapodium is a conical structure of about 100 to 500 µm long. A hook protrudes from its apex, the length of the part of the hook visible externally being variable, depending on the state of protrusion (Fig. 7.10.4). Tissues that compose a parapodium are the epidermis, a parenchyma, muscles, nerves, and a chaetal apparatus. The epidermis and parenchyma are similar to those observed in the trunk (Eeckhaut and Jangoux 1993). The differences observed here are that (i) the epidermis is extremely flat where muscles anchor and (ii) the parenchyma is low developed as muscles fill the most parts of parapodia. Parapodial nerves have been described by Müller and Westheide (2000). The chaetal apparatus is a deep epidermal fold made of a few chaetal follicles where chaetae are located (Fig. 7.10.4). *Myzostoma cirriferum* possesses three chaeta: a hook that protrudes to the exterior, an internal replacement hook, and an internal acicula.

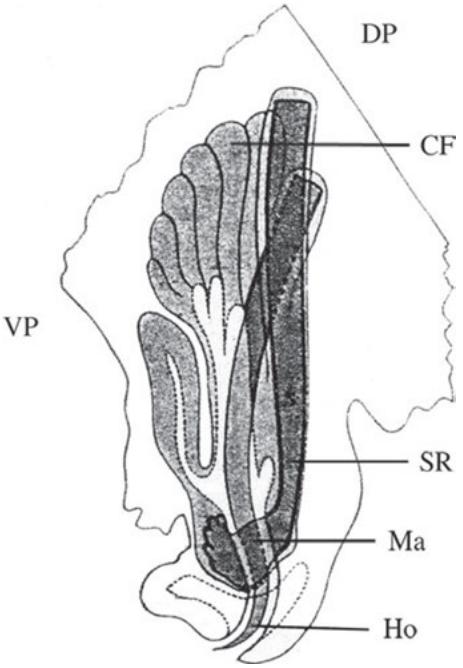


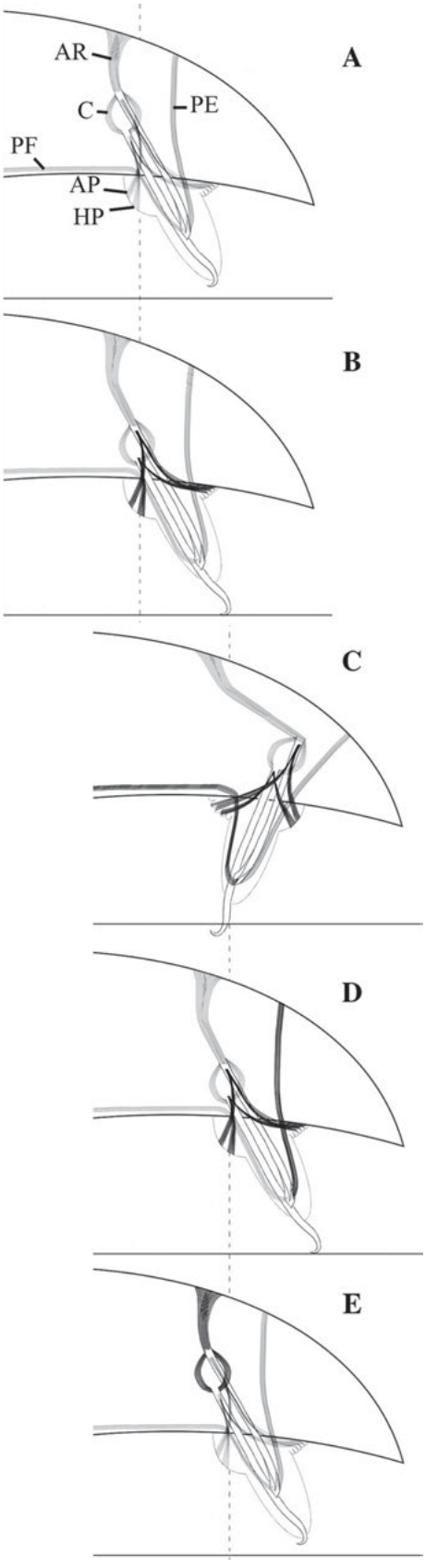
Fig. 7.10.4: Parapodial structure of *Myzostoma gigas* Lütken, 1875. Redrawn from Stummer-Traunfels (1926). CF, chaetal follicle; DP, dorsal part; Ho, hook; Ma, manubrium; SR, support rod; VP, ventral part.

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Observations made on living individuals put in evidence that (i) myzostomids move the anterior, posterior, or lateral parts forward; (ii) they are able to rotate 180° on themselves; (iii) their locomotion relies entirely on parapodial motions and not on trunk movements; (iv) the five pairs of parapodia do not work together at the same time; and (v) the main parapodial motion is directed to the myzostomid ventral midpoint and implies a flexion of the parapodial cone followed by its coming back to the normal position, the parapodial motions always occurring in planes located 30°, 60°, or 90° from the myzostomid sagittal plane. Myzostomids walk on their hosts thanks to the ventral position of the parapodia. The 10 parapodia are, however, located by pairs on two opposite lateroventral arcs — what implies that all parapodia cannot act all together at the same time. The two first pairs and the two last pairs act when the myzostomids move the anterior and posterior parts forward, respectively. The parapodia of the left and right sides (some or all) should be solicited when the myzostomids move right and left, respectively.

The nomenclature and proposed function for parapodial muscles of Stummer-Traunfels (1926) differ to some extent from the analysis of Lanterbecq et al. (2008). He proposed the following actions for parapodial movement: At first, the hook apparatus is protracted (using protractores uncini and protractores suffulcri), which also leads to the extension of the parapodium. Then, the direction of the hook is regulated through unilateral contraction of particular retractores laterales and protractores suffulcri. The hook will be then pushed forward and hooked with help of the retractor internus and musculus centralis. The hook and the complete hook apparatus will be retracted through the retraction of the parapodium through its own musculature, and together with the retraction of the musculus centralis, this results in the movement of the myzostomid body. The contraction of the retractor externus pulls the hook out of the substratum.

The analysis of Lanterbecq et al. (2008) suggests that three pairs of muscles are involved in parapodial motions: parapodium flexor and parapodium extensor, acicula protractor and chaeta retractor, and hook protractor with conjonctor (Fig. 7.10.5). When all these muscles are



▸ **Fig. 7.10.5:** Schematic representation of the parapodia during locomotion (from Lanterbecq et al. 2008). Drawing of one parapodium showing the various actions (A–E) of parapodial muscles during the parapodial motion. Muscles in gray and black are relaxed and contracted, respectively. AP, acicula protractor; AR, acicula retractor; C, conjunctor; HP, hook protractor; PE, parapodium extensor; I, parapodium flexor.

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relaxed, the hook is retracted into the parapodial cone with just its tip emerging from the parapodial opening (Fig. 7.10.5A). The first action should be the contraction of the acicula and hook protractors: they pull both chaetae toward the tip of the parapodial cone, the hook being projected toward the substratum (i.e., the host surface) (Fig. 7.10.5B). As both these muscles stay contracted, the parapodium flexor enters in action: its contraction results in the penetration of the hook into the substratum (Fig. 7.10.5C). The individual is consequently pushed forward along the axis joining the parapodium and the myzostomid midpoint. Then, with the protractors still contracted, the parapodium flexor relaxes and the parapodium extensor acts: the hook comes out of the substratum and the parapodium comes back at its initial position (Fig. 7.10.5D). Finally, the two protractors relax and the acicula retractor with the conjonctor contract pulling the two chaetae to their initial positions (Fig. 7.10.5E).

Sense, sense organs, and nervous system

The anatomy of the nervous system has been described most thoroughly for several species of *Myzostoma* (see Nansen 1887, Grygier 2000, Helm and Bleidorn 2016 for reviews). Its ultrastructure has been studied in *Myzostoma cirriferum* and *Mesomyzostoma* cf. *katoi* (see Müller and Westheide 2000, Helm et al. 2014, Helm and Bleidorn 2016) by means of confocal laser microscopy. In *M. cirriferum*, the nervous system consists of two small cerebral ganglia connected by a dorsal commissure, a ventral nerve mass, and a pair of circumpharyngeal connectives joining the former to the latter (Fig. 7.10.6). The two neuropil cords within the ventral nerve mass curve outward and are joined to one another anteriorly and posteriorly. They are connected by 12 commissures forming a ladder-like system (Fig. 7.10.6). A single median nerve runs along the midventral axis (Fig. 7.10.6). In addition to the circumpharyngeal connectives, 11 peripheral nerves arise from each cord (Fig. 7.10.6). The first innervates the anterior body region. The others form five groups of two nerves each, the first and thicker nerve of which is the parapodial nerve, innervating the parapodium and two corresponding cirri (Fig. 7.10.6). Except for those of the most posterior group, the second nerves innervate the lateral organs and the trunk margin. One pair of dorsolateral longitudinal nerves was visualized by tubulin staining. The arrangement of the peripheral nerves and commissures strongly suggests that the myzostomid body is made of six segments (Müller and Westheide 2000).

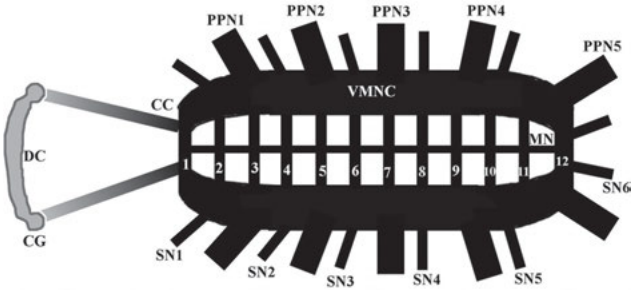


Fig. 7.10.6: Schematic drawing of the central nervous system observed in the trunk of *Myzostoma cirriferum* Leuckart, 1836 (from Eeckhaut and Lanterbecq 2005). CC, circumpharyngeal connective; CG, cerebral ganglia; DC, dorsal commissure; MN, median nerve; PPN 1 to 5, parapodial nerves 1 to 5; SN 1 to 6, side nerves 1 to 6; VMNC, ventral main nerve cord. Numbers 1 to 12 indicate the 12 commissures that connect the two ventral main nerve cords.

Sensory regions of the epidermis either show small structural variations from the regular epidermis or markedly differ from it (Eeckhaut and Jangoux 1993). Small variations occur in the cirri, buccal papillae that surround the mouth of some species, body margin, and parapodia, where ciliated sensory cells insinuate between epidermal cells. These are supposed to be mechanoreceptor sites that give information on the structural variations of the host integument; they could also participate in self-recognition of individuals (Eeckhaut and Jangoux 1993). Ciliated sensory cells are dendritic processes of nervous cells, the cell bodies of which lie mostly in the ventral nerve cord. They usually run either singly or in pairs from bundles of basiepidermal nerve processes and reach the apex of the epidermis. Each sensory process bears up to five small cilia that cross the cuticle and have the usual microtubular arrangement (9 × 2 + 2). Their basal body is prolonged by a ciliary rootlet. The sensory epidermis in the four pairs of lateral organs differs markedly from the regular epidermis. In *Myzostoma cirriferum* (see Eeckhaut and Jangoux, 1993) and other myzostomids, there are almost always four pairs of ventral lateral organs alternating with the parapodia. A lateral organ consists of a villous and ciliated, dome-like central part that is surrounded or covered by a peripheral fold (Fig. 7.10.7). The dome-like central part is the sensitive region of the organ and consists of ciliated sensory cells, secretory cells, and complex vacuolar cells that have numerous long microvilli and multivesicular bodies (Figs. 7.10.7, 8). Lateral organs are presumed to allow the myzostomids to recognize the host integument and prevent them from becoming displaced onto the surrounding inhospitable substratum (Eeckhaut and Jangoux 1993).

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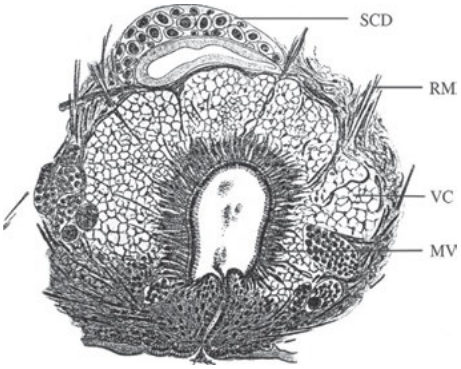


Fig. 7.10.7: Structure of the lateral organ of *Asteriomyzostomum asteriae* (Marenzeller, 1895). Redrawn from Stummer-Traunfels (1926). MV, microvillus; RM, reticular muscle; SCD, secretory cell of the dome; VC, vacuolar cell.

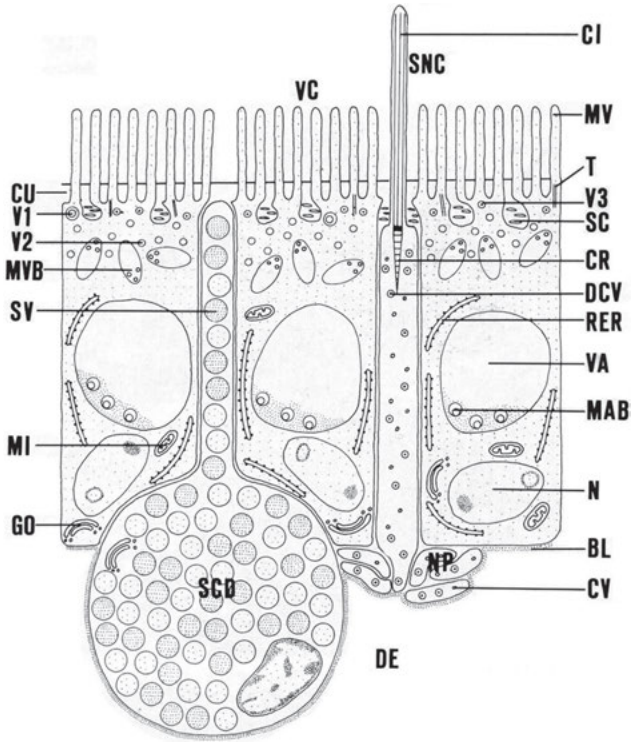


Fig. 7.10.8: Schematic drawing of a section through the epidermis of the lateral organ of *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Eeckhaut and Jangoux (1993), Eeckhaut and Lanterbecq (2005). BL, basal lamina; CI, cilium; CR, ciliary rootlet; CU, cuticle; CV, clear vesicle; DCV, dense cored vesicle; DE, dermis; GO, Golgi apparatus; MAB, multiannular body; MI, mitochondrion; MV, microvillus; MVB, multivesicular body; N, nucleus; NP, nerve process; RER, rough endoplasmic reticulum; SC, subcuticular chamber; SCD, secretory cell of the dome; SNC, sensory cell; SV, secretory vesicle; T, tonofilaments; V1, V2, and V3, vesicles of the first, second, and third types; VA, vacuole; VC, vacuolar cell.

Feeding and digestive system

Ectocommensals of crinoids and many parasitic myzostomids that induce cysts or galls on crinoids feed on particles that they divert thanks to their introvert (i.e., most species of the genus *Myzostoma*; all species of *Contramyzostoma* and *Endomyzostoma*). *Mesomyzostoma*, *Mycomyzostoma*, and *Protomyzostomum* species feed on host tissues, which is probably also the case for *Asteromyzostomum* species. *Pulvinomyzostomum pulvinar*, *Asteriomyzostomum asteriae*, and *Notopharyngoides* species live in the digestive lumen of their hosts where they ingest particles. No indication about the feeding behavior of *Stelechopus hyocrini* exists.

The anatomy of the digestive system of Myzostomida is very similar in almost all species. It consists of a pharynx, which is included in the introvert, a stomach with usually two or three pairs of blind, branching caeca, and an intestine (Fig. 7.10.9A) (Platel 1962, Eeckhaut et al. 1995). The only exceptions to this general scheme are that (i) there are no digestive diverticula in the female of *Mycomyzostoma calcidicola* and in *Stelechopus hyocrini* (Fig. 7.10.9B), (ii) there are one right and one left U-shaped digestive diverticula in *Contramyzostoma bialatum*, (iii) the male of *M. calcidicola* has no digestive system, and (iv) the introvert is absent in the representatives of the Pharyngidea. The ultrastructure of the myzostomid digestive system is only known for *Myzostoma cirriferum* (see Eeckhaut et al. 1995), but the cell types described in the digestive system of this species have also been observed in *Contramyzostoma sphaera*, *Myzostoma capitocutis*, *Myzostoma cuniculus*, and *Myzostoma horologium*.

A cuticle similar to the one that is found in the epidermis covers the myzostomid pharyngeal epithelium. The structure of the epithelium differs on the lip (i.e., the part that surrounds the mouth) and in the pharynx *sensu stricto* (Fig. 7.10.10A, B). The lip is made of ciliated sensory cells, supporting cells, and salivary gland cells (Fig. 7.10.10A). Supporting cells are goblet-shaped cells made of an upper part, contacting the cuticle, and an inner part where the nucleus lies, both being connected by a thin cell process. The upper part of the cell is filled with Alcian blue-positive, ovoid vesicles. Salivary gland cells are common in myzostomids; they have been described in representatives of all genera, except in *Mycomyzostoma* (see Eeckhaut 1998) and *Pulvinomyzostomum* (see Jägersten 1940a). They lie in the parenchyma at the junction between the pharynx and the stomach. In *Myzostoma cirriferum*, they are about 20 in number, each being made of a large cell body from which starts a long, narrow cell process that

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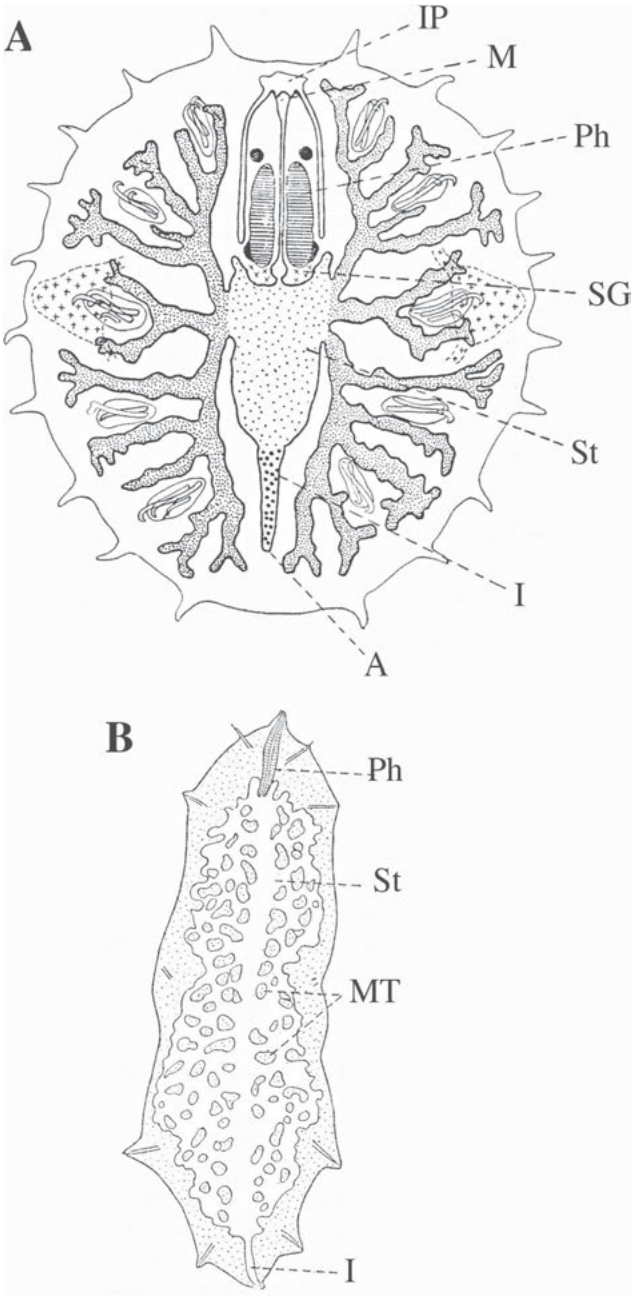


Fig. 7.10.9: Digestive system of *Myzostoma cirriferum* Leuckart, 1836 (A) and *Stelechopus hyocrini* Graff, 1884 (B). A, Redrawn from Platel (1962); B, Redrawn from Jägersten (1940a). A, anus; I, intestine; IP, introvert pouch; M, mouth; MT, muscular trabecula; Ph, pharynx; SG, salivary gland; St, stomach.

ends on the lip. The cytoplasm is full of vesicles filled with electron-dense material that is assumed to be released in the pharyngeal lumen to digest food particles (Eeckhaut et al. 1995). Behind the lip, the pharyngeal lumen is only bordered by secretory cells that look very similar to epidermal covering cells but have many more apical, Alcian blue-positive, electron-dense vesicles (Fig. 7.10.10B). Muscle cells, similar to those of the epidermis, have been observed in the pharynx of *M. cirriferum* (see Eeckhaut and Jangoux 1993).

Eeckhaut et al. (1995) proposed a model explaining how food particles are swallowed and carried into the stomach in ectocommensal species. When in search of food, the introvert continuously retracts and protrudes until it is applied at an appropriate place. Retraction results from the contraction of the longitudinal muscle cells that extend through the parenchyma of the introvert. The mechanism for protrusion appears to be more indirect because the introvert does not contain any antagonistic muscular or fibrillar (e.g., collagen fiber) system. The introvert of myzostomids has no internal cavity, and changes in volume are due to the fact that muscles and parenchymal cells move from the introvert to the trunk and vice versa. The initiator of protrusion is probably located outside the introvert and could be the dorsoventral muscle cells of the trunk; protrusion would depend on the forcing action of these muscle cells, which would push the pharynx and parenchyma into the relaxed introvert. Once the introvert is extended into an ambulacral groove of the host, food particles are swallowed due to the action of the muscle cells of the lip first and then those of the pharynx. The contraction of radial muscle cells of the lip increases the mouth diameter, thus sucking up food particles from the host's groove. The muscle sheet of the pharynx made mainly of alternating radial and circular muscle cells then starts to work. The contraction of radial cells enlarges the diameter of the pharyngeal lumen (sucking up the food particles), whereas the contraction of circular muscle cells reduces the diameter of the pharyngeal lumen (pushing down the food particles). The resulting peristaltic wave carries food particles into the inner organs of the digestive system, namely, the stomach, the digestive caeca, and the intestine, each possessing a non-cuticularized epithelium surrounded by circular muscle cells.

The epithelium of the myzostomid stomach is made of a single cell type that is ciliated and cylindrical (Fig. 7.10.10C). In *Myzostoma cirriferum*, these cells bear many microvilli and several cilia that have the usual 9 × 2 + 2 microtubular arrangement and no rootlet below their basal body. Their cytoplasm includes numerous lipidic droplets that disappear when individuals are starving. Food particles carried by the pharyngeal peristalsis are conveyed toward the digestive caeca due to the action of the stomachal ciliature. Once in the caeca, particles are endocytosed by caecal cells, the single cell type occurring

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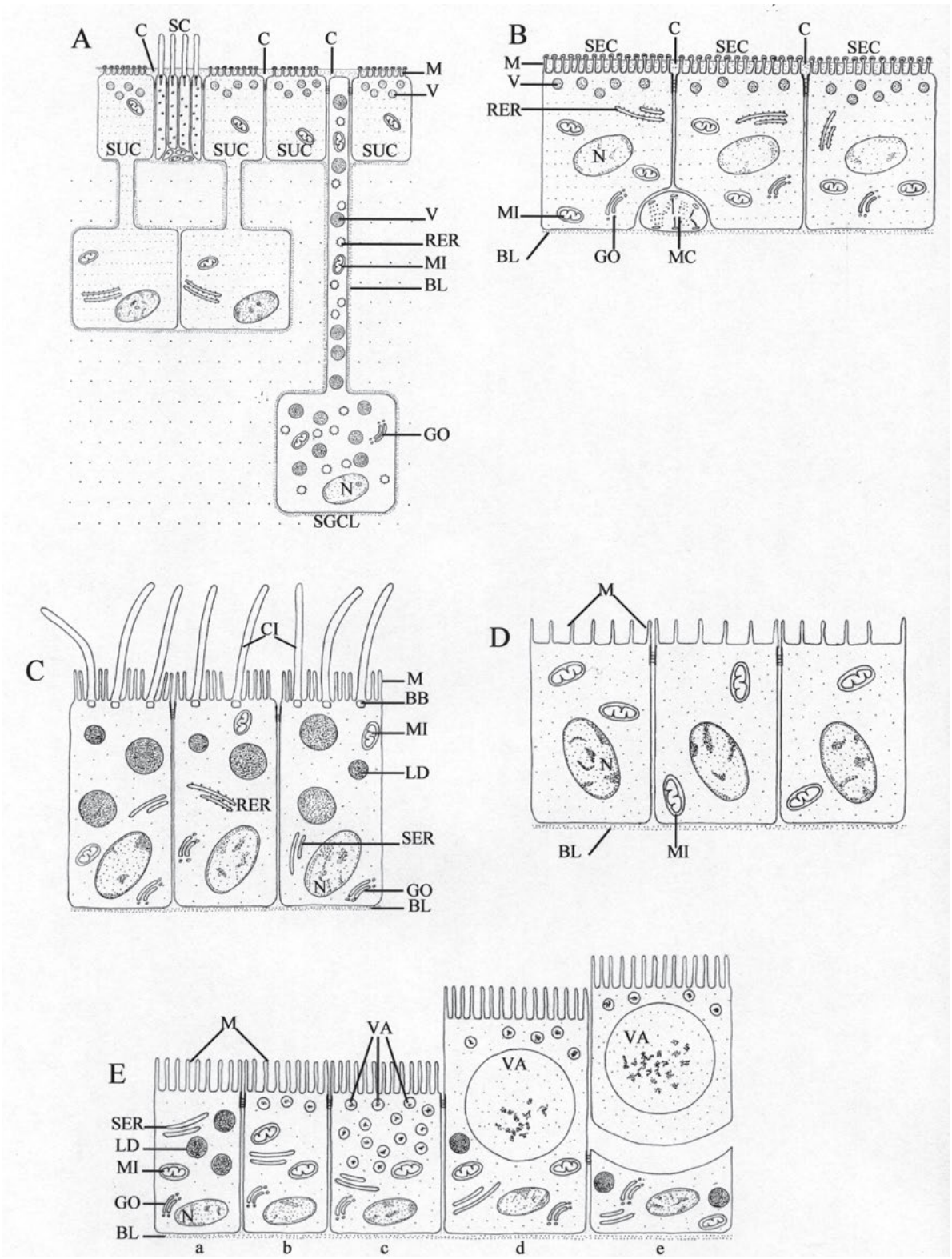


Fig. 7.10.10: Schematic drawings of the epithelia of different parts of the digestive system of *Myzostoma cirriferum* Leuckart, 1836: the lip (A), the pharynx (B), the stomach (C), the intestine (D), and the digestive caeca (E). a–e, successive metabolic stages of a caecal cell observed during the intradigestive process (from Eeckhaut and Lanterbecq 2005). BB, basal body; BL, basal lamina; C, cuticle; Cl, cilium; GO, Golgi apparatus; LD, lipidic droplet; M, microvillus; MC, myoepithelial cell; MI, mitochondria; N, nucleus; RER, rough endoplasmic reticulum; SC, sensory cell; SEC, secretory cell; SER, smooth endoplasmic reticulum; SGCL, salivary gland cells of the lip; SUC, supporting cell; V, vesicle; VA, vacuole.

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in the caecal epithelium, and transferred into a single large vacuole — viz. a phagolysosome — in which they are digested. That vacuole regularly increases in size due to its fusion with additional phagosomes (Fig. 7.10.10E). When it has reached a size roughly corresponding to half the caecal cell volume, the vacuole, together with a fringe of cytoplasm that surrounds it, is expelled into the caecal lumen by an apocrine process. Detached cell fragments are forced out of the caecal lumen to the stomachal lumen due to a contraction of the caecal musculature. The cell fragments progressively gather together in the stomachal lumen, being embedded in an Alcian blue-positive agglutinating matrix that is supposedly produced as a secretion of the pharyngeal secretory cells. A spindle-shaped fecal mass is finally formed, transferred to the intestine, and expelled to the outside by the contraction of the stomachal and intestinal musculatures. The intestinal epithelium is made of a single flattened cell type that harbors many microvilli but lacks cilia (Fig. 7.10.10D).

Excretion and excretory organs

The excretory system of myzostomids consists of protonephridia. Their ultrastructure has been described in *Myzostoma cirriferum* for both adults (Pietsch and Westheide 1987) and larvae (Eeckhaut et al. 2003). The presence of protonephridia has not yet been investigated in any other species. In adults of *M. cirriferum*, five pairs of protonephridia were first described in the trunk (Pietsch and Westheide 1987), but a closer examination using confocal laser scanning microscopy revealed six pairs of 90-µm-long, S-shaped protonephridia in this species (Müller and Westheide 2000). Nephridiopores are located ventrally in two rows of six that are parallel to the sagittal plane. Each protonephridium comprises three terminal cells and one duct cell (Fig. 7.10.11). Each terminal cell has six to nine flagella (without rootlets and with a 9 × 2 + 2 microtubular arrangement), which are each surrounded by rod-like cell processes. The duct cell bears microvilli and cilia. Weir-like fenestrations in the peripheral wall of the terminal cells make up the connection between the central lumina and the parenchymal extracellular space.

Usually, a pair of ducts connecting the uterus to the intestine occurs in myzostomids, and these have long and erroneously been named metanephridia. Spermatozoa have been observed in the lumen of these ducts, and the only obvious function that can actually be assigned to them is to expel the excess of free spermatozoa, thus possibly preventing polyspermy during fertilization.

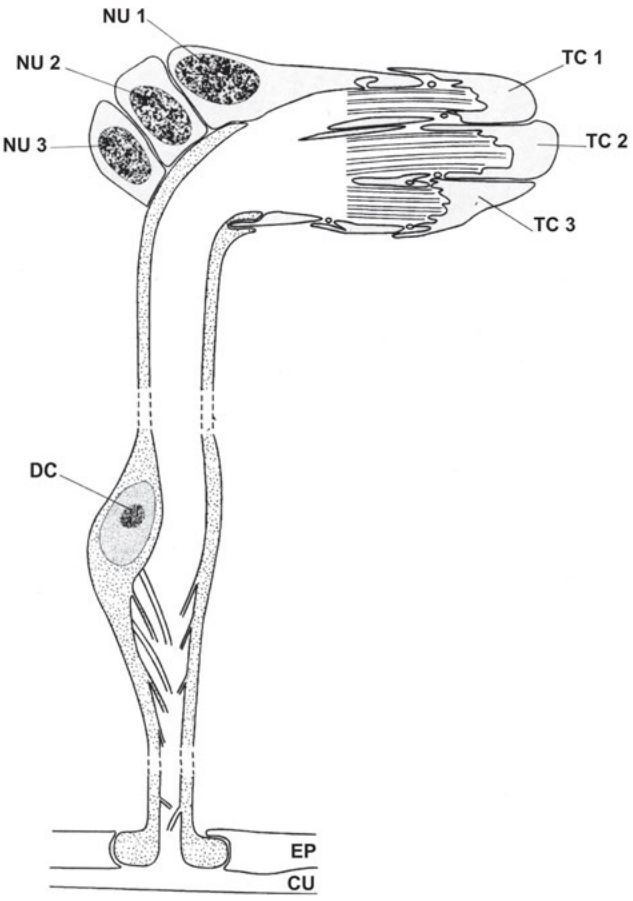


Fig. 7.10.11: Protonephridium of *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Pietsch and Westheide (1987). CU, cuticle; DC, duct cell; EP, epidermal cell; NU 1-3, nuclei of terminal cells; TC 1-3, terminal cells.

Genital systems and gametogenesis

Female genital system and oogenesis

Most myzostomids are functional simultaneous hermaphrodites, although the male genital system develops a bit earlier than the female genital system during organogenesis. In some other species, a male and a female are found and are often interpreted as the two stages of a protandrous hermaphroditic species, the dwarf male being supposed to transform into a female once it lives alone (see discussions between Beard 1884, 1898 and Wheeler 1896, 1899 about the sexual phases of *Myzostoma*). Only *Mycomyzostoma calcidicola* is considered to be dioecious (Eeckhaut 1998). The breeding period is only known for the European species *Myzostoma cirriferum* in which it extends throughout the year (Eeckhaut and Jangoux 1997).

The female genital system of adult myzostomids consists of a branched duct and a diffuse ovary (i.e., female

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germinal cells growing in between parenchymal cells), both located on the dorsal part of the trunk in most species. The female genital system is found ventrally or has an ovary developed both ventrally and dorsally in some other species (e.g., *Myzostoma belli*, *Myzostoma cryptopodium*, and *Notopharyngoides platypus*); however, usually, the branched genital duct follows the course of the digestive organs of the trunk (i.e., intestine, stomach, and digestive caeca). The female genital system lies above it in such a way that a section through the dorsal part of most individuals will show the epidermis, then the parenchyma with developing female germinal cells, below that the genital duct, and finally the digestive system (Fig. 7.10.12A, B). In fully mature specimens, germinal cells often invade the whole dorsal part of the trunk, with parenchymal cells scattered between them.

The way the female genital system is developing has been described in few myzostomids although only by means of photonic microscopy (Wheeler 1896, Jägersten 1939a). Two ovaries would lie dorsal to the stomach in very young *Myzostoma cirriferum* and *Myzostoma glabrum* (Fig. 7.10.12C) (Wheeler 1896). They consist of oogonia that are surrounded by small spaces supposed to be epithelial cavities. The spaces around the growing oogonia develop to form the dorsal central cavity from which start the uterine diverticula. Each oogonium is associated with accessory cells (also called nurse cells) to form triads that fall into the uterus and reach the uterine diverticula. There they implant into the epithelium and grow to form oocytes (Fig. 7.10.12D) (Jägersten 1939a). Eeckhaut and Lanterbecq (2005) analyzed the ultrastructure of the developing germinal cells and that of the genital duct in *M. cirriferum*. In this species, the genital duct consists of a central cavity that they called uterus (some authors differentiate the anterior part as the uterus and the posterior part as the oviduct) and uterine diverticula. The uterus is a sagittal cavity that lies above the stomach and intestine and opens to the outside through a posteroventral gonopore. The uterine diverticula branch off from the anterior part of the uterus, dichotomize, and end at the body margin. According to the state of maturity of individuals, the uterus and uterine diverticula may be flat and empty or thick and full of fertilized eggs. The lumen of both organs is bordered by an epithelium. The epithelium consists of ciliated cells and microvillous cells (Fig. 7.10.12B). Ciliated cells form the dorsal wall of the uterine diverticula, and the latter is observed in the ventral wall of the uterine diverticula and borders the uterus lumen both ventrally and dorsally. The ciliated cells are flattened cells joined together by septate junctions and zonula adhaerentes that bear numerous 9 × 2 + 2 cilia. Each cilium has a basal body and one ciliary rootlet with two branches. As a result of the current they created, the ciliated cells drive fertilized eggs toward the uterus. In the uterine diverticula, microvillous cells are separated from caecal cells of the digestive system by the basal lamina; in the uterus, they are underlain by circular muscle cells whose contractions expel the fertilized eggs through the gonopore. They have numerous microvilli and may act as storage cells.

Eeckhaut and Lanterbecq (2005) did not observe triads described by previous authors in *Myzostoma cirriferum*. The developing germinal cells are not separated by a basal lamina from the surrounding parenchymal cells, nor are they enclosed by an epithelium (Fig. 7.10.12B). Oogonia, previtellogenic oocytes, and vitellogenic oocytes occur in the parenchyma, and the zone where they grow is the ovary of myzostomids (Fig. 7.10.12B) according to Eeckhaut and Lanterbecq (2005). The older they are, the closer to the uterine diverticula they come, and vitellogenic oocytes pierce the epithelium of the diverticula and fall into the lumen where they are fertilized (Fig. 7.10.12B). Oogonia have a voluminous, nucleolated nucleus where heterochromatin is condensed into chromosomes. Previtellogenic oocytes are bigger cells with an irregular-shaped nucleus. The cell membranes of both the oogonia and previtellogenic oocytes are smooth and deprived of microvilli. The vitellogenic oocytes are cells of 20 to 30 μm in diameter, with a nucleus similar in shape to that of the previtellogenic oocytes (Fig. 7.10.12B). Yolk granules occur within the cytoplasm and cortical granules are found at the periphery of the cell just under the cell membrane, which is outlined by a thin vitelline envelope. The vitelline envelope is crossed by microvilli, some of which forming cytoplasmic bridges between the germinal cells and follicle cells. Nurse cells have been observed in some Myzostomatidae (Eckelbarger 1992). They are abortive germ cells that maintain cytoplasmic continuity with the developing oocytes through intercellular bridges. According to Wheeler (1896), nurse cells are absorbed by the developing oocytes, but Jägersten (1939a) suggested that nurse cells transform into follicle cells and eventually are disposed in several layers around the oocytes.

Fertilized eggs only occur in the lumen of the uterine diverticula and uterus. The cytoplasm includes an electron-dense body that is supposed to come from the fertilizing spermatozoon (Eeckhaut and Lanterbecq 2005) Cortical granules are empty, their membrane having fused with the oolema (Fig. 7.10.12B). The fertilizing envelope is

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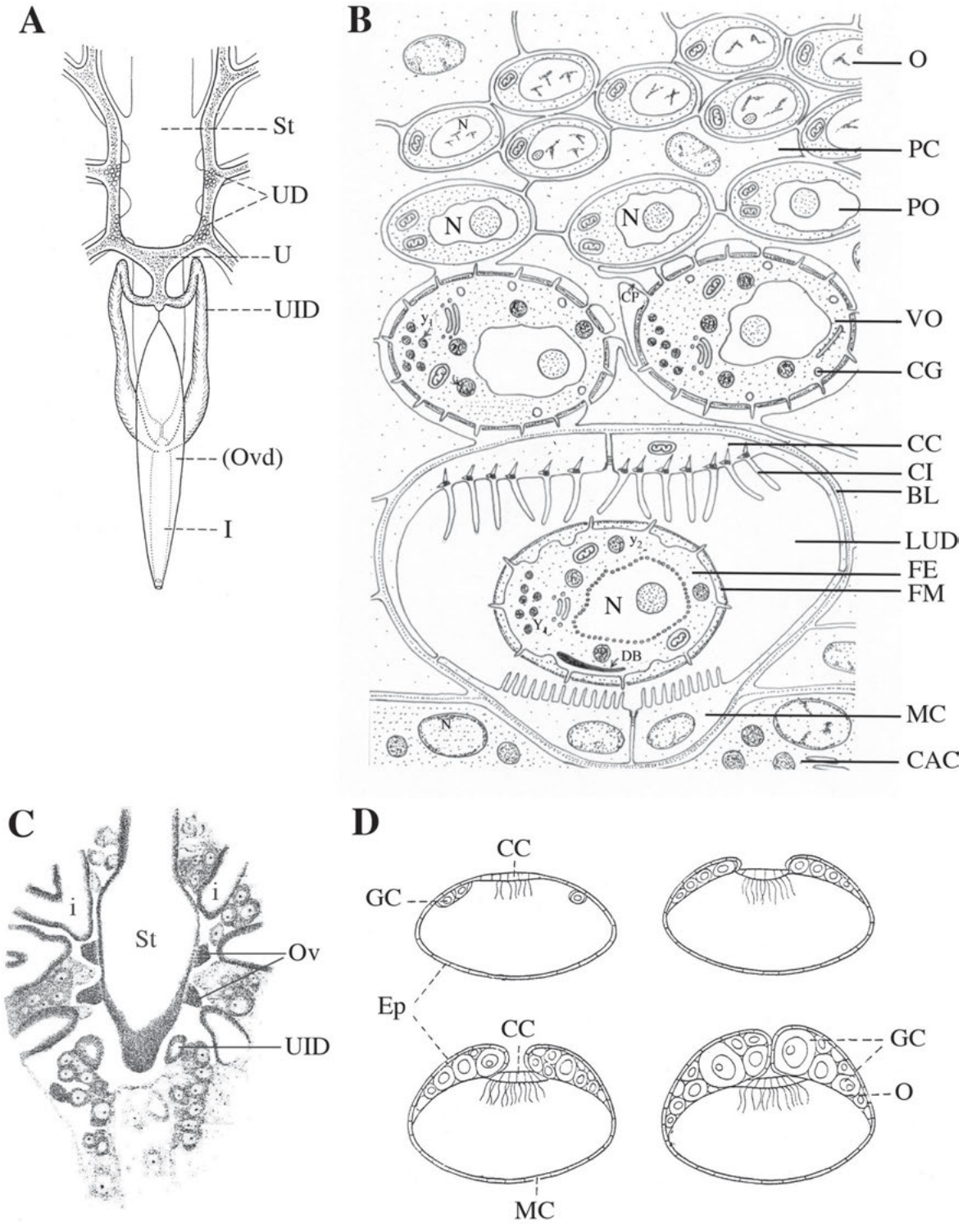


Fig. 7.10.12: Oogenesis and female genital system of *Myzostoma cirriferum* Leuckart, 1836. The female genital tract (A) and portion of the ovary *sensu* Eeckhaut and Lanterbecq (2005) (B); position of the ovary *sensu* Wheeler (1896) (C) and growing of the germinal cells above the epithelium of the uterine diverticula (D). A, D, Redrawn from Jägersten (1939a); B, Redrawn from Eeckhaut and Lanterbecq (2005); C, Redrawn from Wheeler (1896). BL, basal lamina; CAC, caecal cell; CC, ciliated cell; CG, cortical granule; CI, cilium; CP, cytoplasmic process; DB, dense body; Ep, epithelium of the uterine diverticula; FE, fertilized egg; FM, fertilizing membrane; GC, germinal cell; I, intestine; i, intestinal diverticula; LUD, lumen of an uterine diverticulum; MC, microvillous cell; N, nucleus; O, oogonium; Ov, ovary; (Ovd), oviduct (according to Jägersten 1939); PC, parenchymal cell; PO, previtellogenic oocyte; St, stomach; U, uterus; UD, uterine diverticula; UID, uterointestinal duct; VO, vitellogenic oocyte;$Y_{1,2}$, yolk granules of types 1 and 2.

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formed of the upper, old vitelline envelope and of a new, inner layer made of the material secreted by cortical granules. Microvilli cross the fertilizing envelope. The nuclear membrane is fragmented into numerous small vesicles of 10 nm in diameter (Fig. 7.10.12B). In some eggs where the fragmentation is advanced, the vesicles are scattered into the nucleocytoplasm (Fig. 7.10.12B).

Male genital system and spermatogenesis

The male genital system of myzostomids is basically paired: there are usually two male genital apparati that are ventral and each separated from the other by the nerve cord. Each male genital apparatus consists of one or two diffuse testes (according to the species) and one genital duct, the latter consisting of a penis, a seminal vesicle, one or two vasa deferentia, and numerous vasa efferentia (Fig. 7.10.13A–C). Except for the vasa efferentia that are lined by a matrix, the lumen of all male organs is bordered by an epithelium, itself surrounded by muscles. Epithelial cells are joined together by zonula adhaerentes and septate junctions. Muscles form a continuous (at the level of the seminal vesicles) or discontinuous (at the level of the penises and vasa deferentia) sheath of circular muscle cells. The wall of the vasa efferentia is a thick basal lamina (also named the tunica propria) that is continuous with the one of the vasa deferentia.

Structural variability in the male genital system of myzostomids includes the presence of an epithelium lining at least part of the vasa efferentia in some species and the absence of seminal vesicles or their division into a narrow proximal duct and a sac-like distal portion in some others (Jägersten 1939a). Compact, rather than diffuse, testes occur in many Endomyzostomatidae and in *Stelechopus hyocrini* (Jägersten 1939a, see also Grygier 2000).

The ultrastructure of myzostomidan spermatozoa and spermatogenesis has been extensively studied (Bargalló 1977, Afzelius 1983, 1984, Mattei and Marchand 1987, 1988), but the fine structure of male genital ducts is only known for *Myzostoma cirriferum* (see Eeckhaut and Lanterbecq 2005). In this species, the lumen of the penis is bordered by nonciliated and ciliated cells similar to those found in the epidermis (Fig. 7.10.14). Their shape varies according to whether the penis is retracted or extended and will be cylindrical or flat, respectively. These cells are covered by a cuticle, whereas all the other epithelial cells of the male genital system are not. Vacuolar and spumous gland cells form the epithelium of the seminal vesicles (Fig. 7.10.14). The first are located at the base of each seminal vesicle, close to the penis, and are full of large vacuoles that are expelled with the spermatophores formed in the seminal vesicles. They will form the base of it and will participate in the lysis of the integument of the receiver individual during the intradermic penetration (described below). The rest of the seminal vesicle is lined by flat spumous gland cells. They contain vacuoles whose content is assumed to be secreted to form the matrix that coats the spermatophore contents. The vasa deferentia are lined by vesicular gland cells that possess rod-shaped, electron-dense vesicles apically. These rod-shaped vesicles are found in the lumen of the seminal vesicles and at the base of the spermatophores between the vacuolar gland cells and the male germinal cells that came from testes (see Fig. 7.10.18A, C). The vasa efferentia are dichotomously branched ducts connected to the testes; they convey the germinal cells to the vasa deferentia. The testes comprise many follicles scattered in the parenchyma. The follicles include many cysts, also called spermatocysts (see Fig. 7.10.18), each consisting of one cyst cell that encloses developing germinal cells. The number of germinal cells surrounded by a cyst cell varies according to the stage of development of the former (from 1 to 64 in *M. cirriferum*). Germinal cells that are surrounded by the same cyst cell are all at the same stage. Nothing is known about the cyst structure in young myzostomids, but it is probable that, initially, a single germinal cell becomes surrounded by a cyst cell and divides later. The youngest cyst cells observed in mature myzostomids are those containing spermatogonia, which are ovoid cells of 5 µm in diameter (Fig. 7.10.15A). Spermatogonia have a large, nucleolated nucleus where the chromatin condenses into chromosomes. Young spermatids are still ovoid cells with intranuclear, electron-dense spheres that have been considered as either heterochromatin (Fig. 7.10.15B) (Afzelius 1984, Eeckhaut and Jangoux 1991) or protein granules (Mattei and Marchand 1988). Spermatids gradually lengthen and acquire a flagellum with a $9 \times 2 + 0$ axoneme (Fig. 7.10.15C). At the end of spermiogenesis, the spermatids separate from the cytoplasmic remnants and transform into spermatozoa (Fig. 7.10.15D, E). Myzostomid spermatozoa are elongated cells of about 30 µm long and 1 µm in diameter (Fig. 7.10.16). They have a long flagellum whose length is almost twice that of the spermatozoon body. The flagellum arises from one extremity of the cell; it bends as soon as it leaves the cell body and borders the latter along its whole length, being attached to the cell membrane through extracellular processes. It ends in a 40-µm-long free portion that extends out opposite to the flagellar pole of the spermatozoon and that is supposed to beat forward according to Mattei and Marchand (1988). The spermatozoon nucleus is highly elongated

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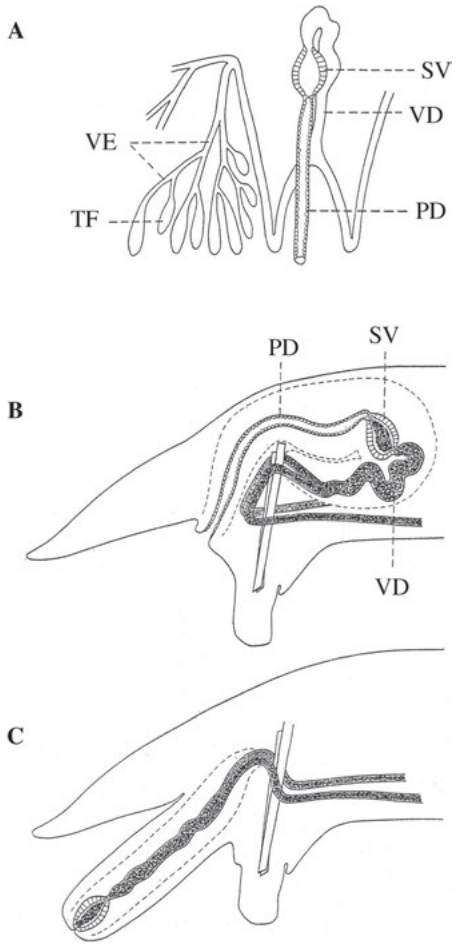


Fig. 7.10.13: Schematic drawings of half of the male genital system of *Myzostoma ambiguum* Graff, 1887: viewed from above (A) and from the front side (B, C) when it stands still (B) and during mating (C). Redrawn from Jägersten (1939a). PD, penial duct; TF, testicular follicle; SV, seminal vesicle; VD, vasa deferentia; VE, vasa efferentia.

and typically includes one row of 40 to 50 dense spheres (Fig. 7.10.16E). The nucleus has been considered as being opened with the cytoplasm by Mattei and Marchand (1987). One or two enlarged mitochondria and a manchette of 16 to 22 microtubules extend from one pole of the spermatozoon to the other (Fig. 7.10.16). The microtubules are located between the nucleus and the cell membrane in the cytoplasm facing the attached part of the flagellum. On the opposite side, a myelin-like sheath presumably derived from the Golgi apparatus caps the nucleus over its whole length. An acrosome is not obvious in *Myzostoma* spermatozoon.

Cysts that contain spermatogonia are located in the outermost ends of the follicles, close to the myzostomid body margin. With the division of spermatogonia, cysts occupy more space and push the rear cysts into the vasa efferentia first and then into the vasa deferentia. Only cysts that include spermatozoa enter vasa deferentia. There, contractions of circular muscle cells force the cysts into the seminal vesicles, where spermatophores form (Fig. 7.10.17).

Reproduction and development

Development

Reproduction in myzostomids is realized by the emission of spermatophores followed by the intradermic penetration of sperm cells. Emissions of spermatophores have been observed in *Myzostoma ambiguum* (see Kato 1952), *Myzostoma cirriferum* (see Jägersten 1939a, Eeckhaut and Jangoux 1991), *Myzostoma alatum* (see Eeckhaut and Jangoux 1992), and *Myzostoma capitocutis*, *Myzostoma nigromaculatum*, *Myzostoma polycyclus*, and *Contramyzostoma sphaera*. All are ectocommensal species, except the last one, whose individuals live singly in cysts. In ectocommensals, matings involve two mature individuals that contact each other, one of them ejecting one spermatophore that attaches to the integument of the other individual. The spermatophore in the other seminal vesicle does not participate in this process. Contacts between the two myzostomids are very brief, and

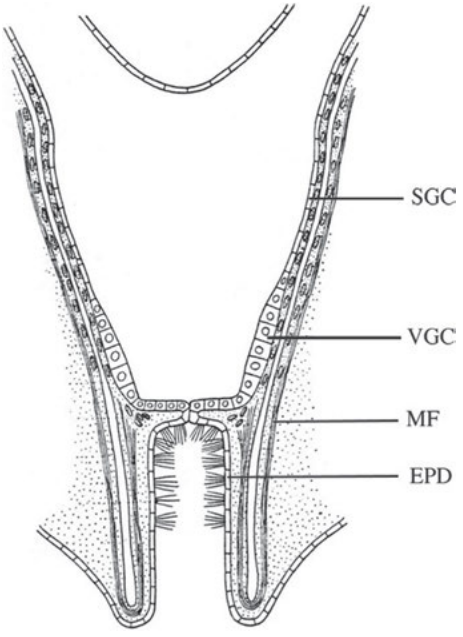


Fig. 7.10.14: Seminal vesicle and penis in *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Jägersten (1939a). EPD, epithelium of the penial duct; MF, muscle fiber; SGC, spumous gland cell; VGC, vacuolar gland cell.

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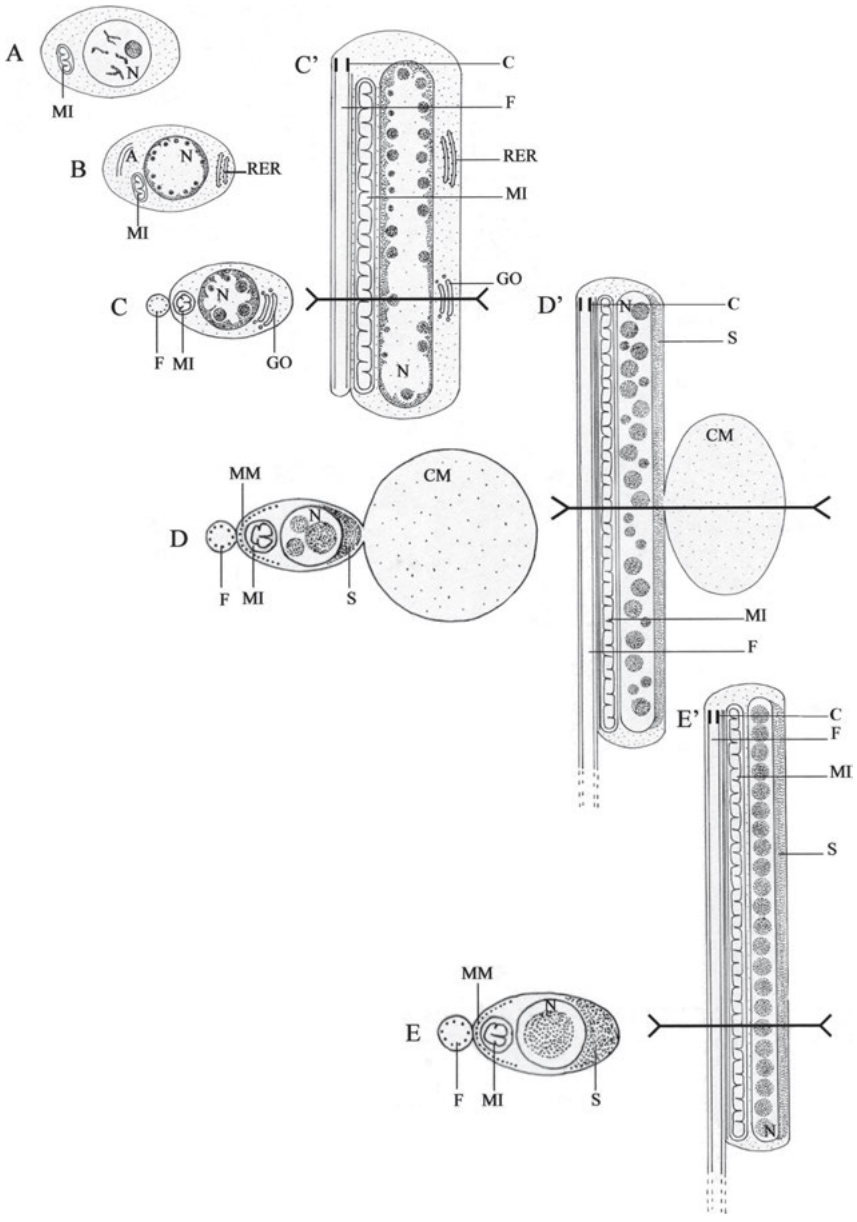


Fig. 7.10.15: Schematic drawings of male germinal cells undergoing spermatogenesis in *Myzostoma cirriferum* Leuckart, 1836 (from Eeckhaut and Lanterbecq 2005). A, Spermatogony; B, Young spermatid; C, C', a more advanced spermatid sectioned transversely (C) and (C') sagitally; D, D', old spermatid; E and E', spermatozoon. A, axoneme; C, centriole; CM, cytoplasmic mass; F, flagellum; GO, Golgi apparatus; MI, mitochondria; MM, manchette of microtubules; N, nucleus; RER, rough endoplasmic reticulum; S, myelin-like sheet.

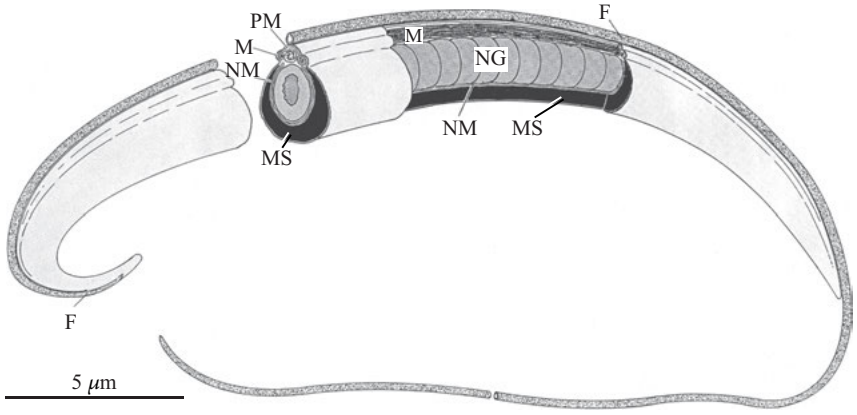


Fig. 7.10.16: Three-dimensional schematic drawing of a spermatozoon (courtesy of W. Westheide). F, flagellum; M, mitochondrion; MS, myelin sheath; NG, nuclear grain, NM, nuclear membrane, PM, palisade of microtubules.

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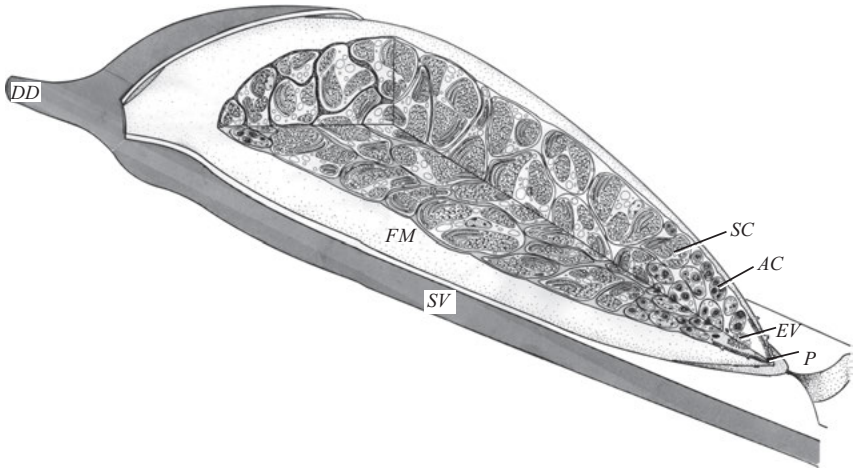


Fig. 7.10.17: Schematic drawing of the spermatophore in place in the seminal vesicle (courtesy of W. Westheide). AC, abortive cyst; DD, deferent duct; EV, enzymatic vacuole; FM, fibrillar matrix; P, penis; SC, spermiocyst; SV, seminal vesicle.

the two separate after mating. Spermatophores are generally attached to the back of the receiver, but they can be emitted successfully to any part of the receiver's body. In most cases, receiver individuals have one attached spermatophore, sometimes two. In *Contramyzostoma sphaera*, gamete exchange occurs when an individual extends a very long penis to contact another individual lying in an adjacent cyst.

Emitted spermatophores are white V-, club-, or ball-shaped baskets according to the species considered. They are 50 to 500 µm long and are formed by a translucent extracellular matrix containing cysts. The cysts are packed close together and tend to form numerous sinuous chains, which interlace each other. In *Myzostoma cirriferum*, spermatophores consist of three regions: the body with the curved horns, the foot, and the basal disc (Fig. 7.10.18). The body-horns region forms the upper two thirds of the spermatophore and includes spermiocysts each of which contains about 64 spermatozoa (Fig. 7.10.18). The foot extends below the body-horns region and includes cysts with abortive germinal cells (Fig. 7.10.18). These cysts are assumed to prevent the spermiocysts from being attacked by the lytic enzymes that create a hole in the receiver's integument. The basal disc of the spermatophore attaches to the receiver's cuticle. It is composed of upper, electron-dense, rod-shaped vesicles of unknown function and lower vacuoles filled with a fibrillar material that is responsible of the degradation of the integument (Fig. 7.10.18). The two kinds of vesicles are respectively synthesized by the vesicular gland cells of the vasa deferentia and the vacuolar gland cells of the seminal vesicles.

After attachment, the spermatophores pierce the integument and release all the cysts through it (Fig. 7.10.19). Intradermic penetration has been observed in *Myzostoma ambiguum* (see Kato 1952), *Myzostoma cirriferum* (see Eeckhaut and Jangoux 1991), and *Myzostoma alatum* (see Eeckhaut and Jangoux 1992). Penetration can be observed *in vivo* thanks to the presence of white trails representing the spermatophore contents that are introduced into the translucent body of the receiver. These trails appear 10 to 30 minutes after attachment, and after 1 to 5 hours, the spermatophores are reduced to matrix only. In *M. cirriferum*, four phases have been distinguished during the intradermic penetration process: fixation, degradation, penetration, and expansion (Eeckhaut and Jangoux 1991). Fixation occurs between the basal disc of a spermatophore and the cuticle of the receiver individual. The membranes of the basalmost spermatophoral vacuoles (those with fibrillar content) disappear; consequently, the lower part of the basal disc appears as a single large fibrillar mass that sends digitations through the cuticle. During the degradation phase, the digitations flow through both the cuticle and the epidermis. The cuticle is strongly altered and epidermal cell membranes become degraded, allowing the lytic material to penetrate the cells. Invasion of the parenchymal layer by the digitations has not been observed. Penetration starts when the cysts pass into the integument. At the very beginning of this phase, the cytoplasmic membranes of all cyst-cells fuse together, leading to the formation of an extremely large syncytium (Fig. 7.10.19). The whole syncytium encloses both the spermatozoa and the abortive germinal cells. At the point of penetration, both the cuticle and the epidermis disappear. Epidermal and parenchymal cells in contact with the penetrating syncytium degenerate: their nuclei become nearly entirely heterochromatic and their cytoplasm becomes highly reduced and deprived of organelles. The expansion phase corresponds to the extension of the whole syncytium into the parenchyma of the receiver. Once at the level of the uterine diverticula, the

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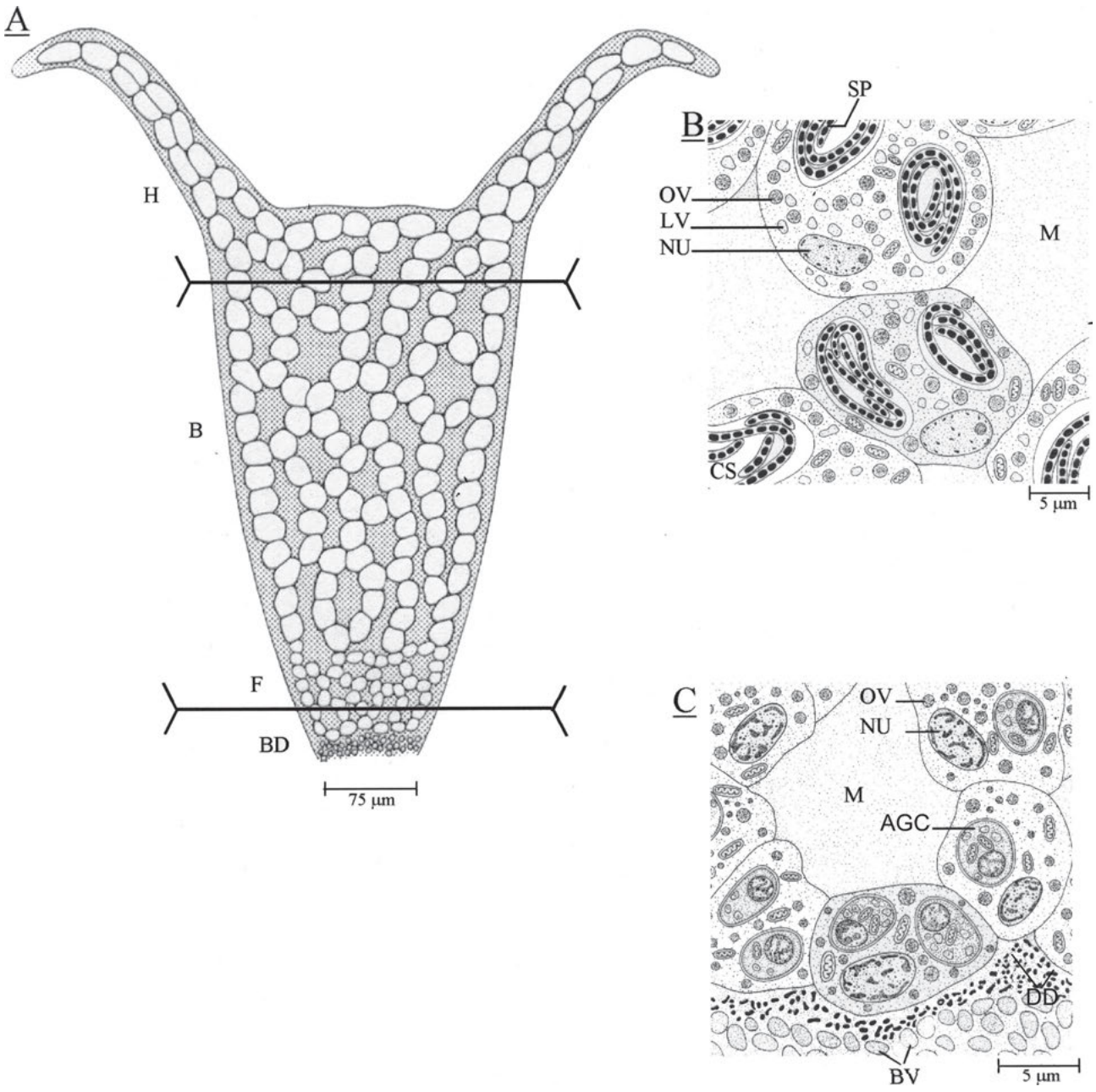


Fig. 7.10.18: Spermatophore of *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Eeckhaut and Jangoux (1991). A, Schematic drawing of a spermatophore just after emission (*in vivo* observation); B, Structure of cysts containing spermatozoa (at the level of the body and horns of the spermatophore); C, Structure of the basal part of the spermatophore with abortive cysts (at the level of the foot) and the dense vesicles and lucent vacuoles found in the basal disc. AGC, abortive germinal cell; B, body; BD, basal disc; BV, basal vesicle; DD, dense droplet; F, foot; H, horn; LV, lucent vesicle; M, matrix; NU, nucleus; OV, osmiophilic vesicle; SP, spermatozoon.

syncytium breaks up and the spermatozoa are released free into the uterine lumen where they fertilize the vitellogenic oocytes.

Fertilization is internal in myzostomids, and the maturation is blocked up to the laying. The first and second maturation divisions occur about 2 hours after the layings and give rise to two polar bodies, the first appearing at the animal pole (Fig. 7.10.20A, B) (Kato 1952). The cleavages are spiral, and at least the first three are preceded by the development of polar bodies. Embryonic development has been observed in numerous *Myzostoma*, including *M. cirriferum*, *M. ambiguum, M. alatum, M. capitocutis*, as well as *Notopharyngoides aruense*, *Hypomyzostoma crosslandi*, *Mesomyzostoma* sp., *Contramyzostoma sphaera*, and

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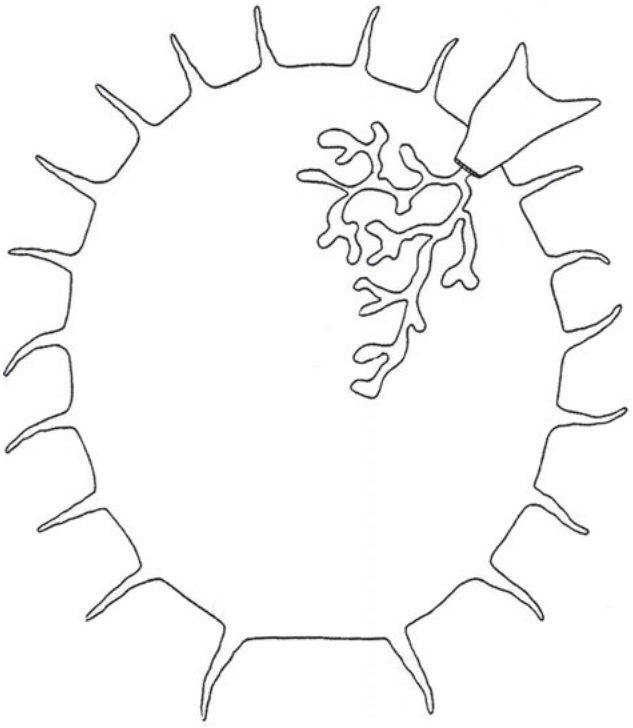


Fig. 7.10.19: Schematic drawings illustrating the intradermic penetration of sperm cells in *Myzostoma cirriferum* Leuckart, 1836. Redrawn from Jägersten (1939a). The drawing shows the development of the spermatic syncytium extending through the dermis of the individual.

Endomyzostoma sp. (see Wautier 2009). The first cleavage is preceded by the formation of a first polar lobe at the vegetal pole about 2 hours after laying, the eggs constrict perpendicularly to the VG axis (Fig. 7.10.20C, D). Shortly afterward, the polar lobe merges with the CD blastomere (Fig. 7.10.20E, F). The second cleavage (1 hour later) is also preceded by the formation of a polar lobe arising from the CD blastomere. The polar lobe fuses with the D blastomere forming the four-blastomere stage. The first cilia appear about 18 h after the laying. Three larvae develop successively: the protrochophore, the trochophore, and the metatrochophore (Fig. 7.10.20). The protrochophore (Fig. 7.10.21A) is a ball-shaped larva present in culture from 18 to 48 hours after egg laying. It has no internal organs, and its body is made of three cell types: covering cells and ciliated cells that are external and surrounded by a cuticle and resting cells that fill the blastocoel (Eeckhaut et al. 2003). The trochophore (Fig. 7.10.21B) is a pear-shaped larva that develops 20 to 72 hours after egg laying; the body includes the same three cell types as the previous stage. The metatrochophore (Fig. 7.10.21C–E) is a pear-shaped larva that develops between 40 hours and 14 days and is characterized by the presence of two bundles of chaetae. The number of chaetae varies from species to species. It is generally of four as in *Myzostoma cirriferum* (see Jägersten 1939b, Eeckhaut et al. 2003) and *Endomyzostoma* sp. (see Wautier 2009). It is of six in *Myzostoma ambiguum* (see Kato 1952) and six to eight in *Myzostoma seymourcollegiorum*, the last species having two supplementary bundles of two chaetae each at the end of the development (Rouse and Grygier 2005). When fully developed, the metatrochophore has a digestive system (made of a pharynx, an esophagus, and a digestive pouch), two pairs of protonephridia, and a nervous system composed of a supraesophageal ganglion, circumesophageal connectives, and dorsal and ventral nerves. The digestive system would open through an anus at the end of the development (Kato 1952). Metamorphosis generally occurs 7 days after egg laying. At that time, the metatrochophore loses its chaetae and becomes pleated ventrally.

Biology and ecology

Infestation and life cycle

Eighty-nine percent of the myzostomids live on the surface of crinoids, both comatulids and stalked crinoids, where they divert food from the ambulacral grooves. They are *Myzostoma* and *Hypomyzostoma* species to which should probably be added *Stelechopus hyocrini* whose relationship with its host has not been described (Graff 1884) with *Eenymeenymyzostoma cirripedium* and *Pulvinomyzostomum messingi*, both observed on the surface of stalked crinoids. The number of ectocommensal myzostomids per infested crinoids is very variable and depends on the myzostomid species, on the crinoid species and on the season (Fishelson 1974, Fabricius and Dales 1993, Deheyn et al. 2006). At the extreme, Woodham (1992) observed more than 2000 individuals of *Myzostoma cirriferum* on a single crinoid in a Scottish population of *Antedon bifida*. Crossing the Channel, Eeckhaut and Jangoux (1997) studied a Brittany population of *A. bifida*, where 90% of the largest crinoids were infested with an average of 21 myzostomids per host. The population of *A. bifida* was monitored through a 5-year period. They found that the infestation varies according to the season: it is at maximum in winter, decreases in spring, and becomes stabilized at a low level from summer to the next winter. The huge infestation in winter is due to the recruitment of young individuals into the population of *M. cirriferum*. Eeckhaut and Jangoux (1997) estimated that the longevity of this species is about 6 months.

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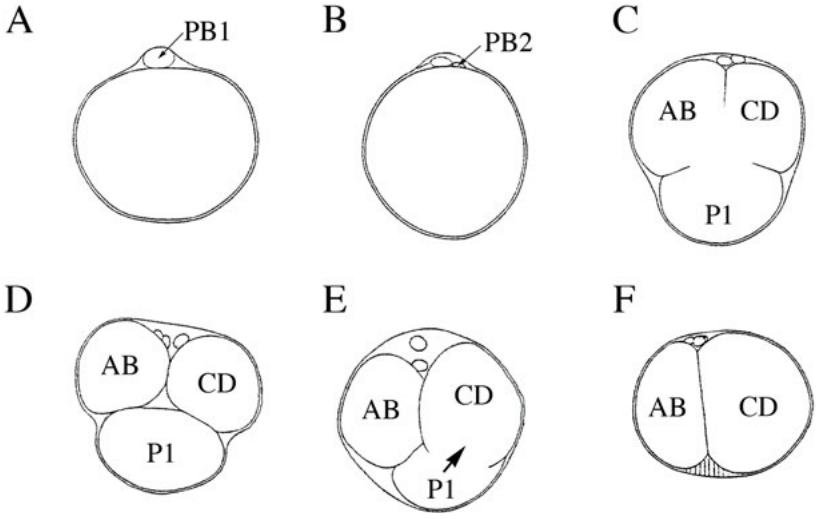


Fig. 7.10.20: Schematic drawings of the early development and cleavage in *Myzostoma ambiguum* Graff, 1887. Redrawn from Kato (1952). AB, CD, blastomeres; P1, first polar lobe; PB1-2, polar bodies.

The life cycle and mode of infestation of ectocommensal myzostomids has been deduced from analyses made quite exclusively on the European *Myzostoma cirriferum* (Eeckhaut and Jangoux 1993b, 1997). However, partial published information about other ectocommensal myzostomids, such as *Myzostoma ambiguum* (see Kato 1952), *Myzostoma alatum* (see Eeckhaut and Jangoux 1992), *Myzostoma glabrum* (see Jägersten 1939a), and *Myzostoma seymourcollegiorum* (see Rouse and Grygier 2005), and various unpublished observations support the view that the life cycle of *M. cirriferum* can be extended to the majority of the ectocommensal myzostomids. Fertilization is internal through transmission of spermatophores (Eeckhaut and Jangoux 1991). Fertilized eggs are emitted through the posterior female gonopore. It is very usual to obtain fertilized eggs of ectocommensal myzostomids in just separating them from their hosts and that at any time of the year. Fertilized eggs have been obtained in ectocommensal species from tropical and temperate waters. This suggests that most ectocommensal myzostomids reproduce throughout the year or a great part of the year. Eggs develop into trochophores and metatrochophores, the last having bundles of chaetae. Metatrochophores are considered as food particles by the crinoids and they are thus taken by the pinnular podia. Larvae attach to the ambulacral grooves thanks to their chaetae first. The metamorphosis happens quickly, giving rise to small "worms" with a first pair of permanent chaetae, larval chaetae being lost during the process. Juveniles stay in the ambulacral grooves and acquire progressively their adult shape (generally they become ovoid or discoid), adult appendages (parapodia, cirri, and lateral organs), and adult color pattern. This is also during this stage that the anterior body part transforms into an introvert that becomes retractable into an anterior pouch. In acquiring the sexual maturity, myzostomids leave the ambulacral grooves and become free moving on the surface of the crinoids. They divert food particles carried by host ambulacral grooves thanks to their introvert. In *Myzostoma cirriferum*, free-swimming larval stage lasts about 10 days and the postmetamorphic stage last about 6 months with a juvenile phase of ~55 days (Eeckhaut and Jangoux 1997). During the time that myzostomids stay still in the ambulacral grooves, hosts often react in creating small cysts around them. Cysts in that case are roof-like deformities that cover part or the entire myzostomid body. They result in fusion of several podia and ambulacral lappets. Such cysts have been observed surrounding juveniles of *Myzostoma* and *Hypomyzostoma* species.

About 20 myzostomid species are considered as parasites at the adult stage as they induce deformities of host's organs. Most of these myzostomids parasite the integument of crinoids and induce abnormalities that have been designed as cysts and galls (Stummer-Traunfels 1926, Jangoux 1990), the parasitic myzostomids being named cysticolous and gallicolous species. Cysts were considered subepidermal deformities either made of host soft tissues or made of host soft tissues reinforced by neoformed small ossicles (Fig. 7.10.22A) (Stummer-Traunfels 1926, Jangoux 1990). Galls (Fig. 7.10.22B) were thought to be "under skeletal ossicles" (Stummer-Traunfels 1926, Jangoux 1990), meaning intradermal. They are always made of host soft tissues but also of original ossicles highly deformed by the presence of parasites. Since these definitions, new deformities induced by myzostomids have been analyzed: none of the deformities, galls and cysts, are in reality intradermal, and the difference between galls and cysts

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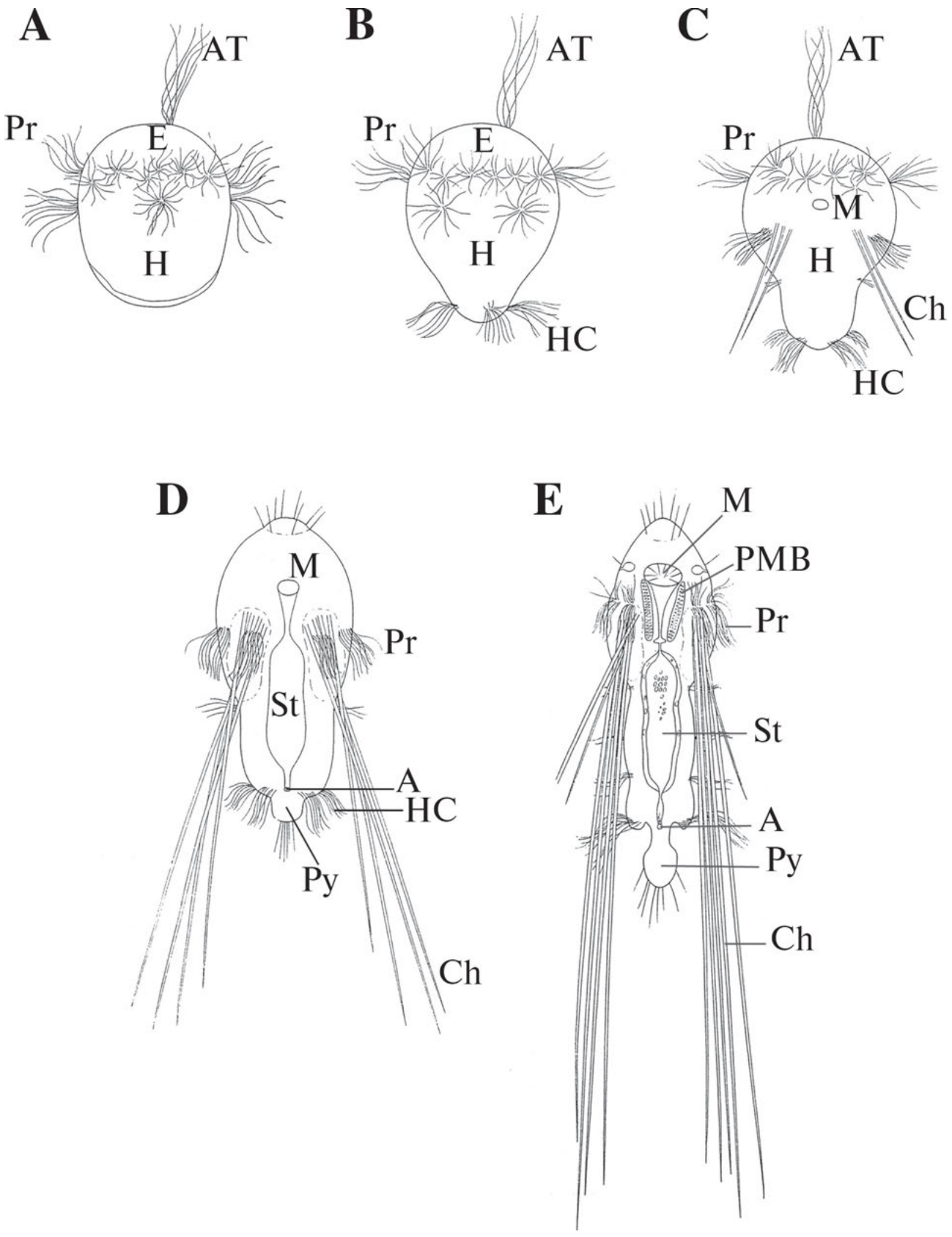


Fig. 7.10.21: Larval development in *Myzostoma glabrum* Leuckart, 1842. Redrawn from Jägersten (1939b). A, Protrochophore; B, Trochophore; C–E, Young, intermediate, and late metatrochophore, respectively. A, anus; AT, apical tuft; Ch, chaeta; E, episphere; H, hyposphere; HC, hypospheral ciliated crown; M, mouth; PMB, pharyngeal muscle bulb; Pr, prototroch; Py, pygidium; St, stomach.

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can only rely on the presence of evident deformed original ossicles in the first and the huge number of neoformed ossicles in the second. Whatever they are in galls or cysts, myzostomids occur single, in heterosexual couple, or by pair in more or less spacious cavities. The cavities are always lined by a thin modified host epidermis. The wall of the myzostomid shelter is thus made by a thin modified host epidermal layer that lined the cavities, the host dermis, and, externally, the nonaltered host epidermis. The dermis included soft tissues but also the new formed

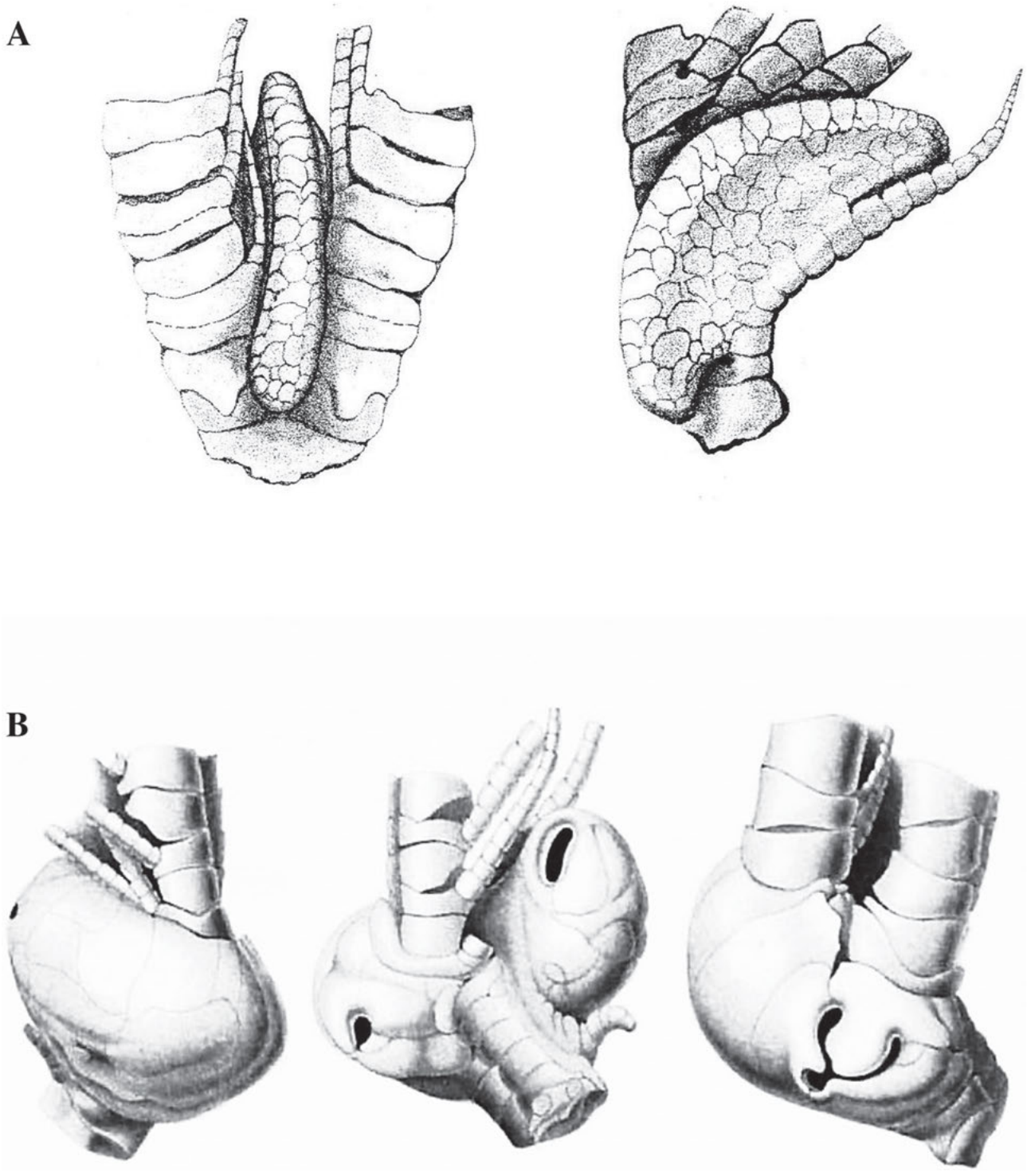


Fig. 7.10.22: Cysts and galls induced by myzostomids. A, Cyst induced by *Endomyzostoma cysticolum* Graff, 1884 (redrawn from Remscheid 1918); B, Gall induced by *Endomyzostoma tenuispinum* Graff, 1884 (redrawn from Graff 1884).

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minute ossicles or the deformed original ossicles. The number and shape of neoformed ossicles varied greatly. In the shelter induced on *Saracrinus nobilis* by *Mycomyzostoma calcidicola*, there are 70 to 90 new polygonal ossicles, 1 nodal ossicle, 2 to 3 internodal ossicles, and 1 to 3 cirral ossicles.

Gallicolous myzostomids belong to the *Endomyzostoma* genus. Cysticolous myzostomids are *Endomyzostoma*, *Myzostoma*, *Mycomyzostoma*, *Notopharyngoides*, *Contramyzostoma*, and *Protomyzostomum* species. Galls and cysts that they induced measured from a few millimeters to a few centimeters long. They appear as soft swellings or hard calcified shelters that are mainly observed at the level of the pinnules, arms, and calyx of crinoids. Most often, they have two openings, sometimes only one or none. One opening is located close to the host ambulacral groove that enables the myzostomids to catch food from the groove, the other opening lying at the opposite side where feces are expulsed. Unpublished observations and the work of Wautier (2009) suggest that gallicolous and cysticolous myzostomids have a similar life cycle than ectocommensal species. Indeed, spermatophores have also been observed on the dorsal part of female stages of *Endomyzostoma* spp., and the histology of male stage reports a quite similar male genital system with cyst cells and spermatophores. Furthermore, trochophore larvae have been observed in a new *Endomyzostoma* species from the southwest of Madagascar (Wautier 2009). Yet, the location of galls and cysts is close of the ambulacral grooves, which suggests that larvae are caught as food particles in the same way as those of ectocommensal myzostomids. One cysticolous species, *Mycomyzostoma calcidicola*, probably infests crinoids in a different way, as the cysts that look like rugby balls of a few centimeter in diameter are located in the middle part of the host stalks. The cysts have a large internal cavity with generally no opening. Each cyst is inhabited by a dwarf male and a large female, the latter probably eating the host tissues or liquids. Cysts induced by *Myzostoma*, e.g., *Myzostoma toliarense* and *Notopharyngoides* species, and *Contramyzostoma sphaera* are soft swellings covering partly or quite totally the body of the parasites. The last species, in particular, has very long penises, enabling these hermaphrodites to fertilized individuals that occur in adjacent cysts. Cysts induced by *Contramyzostoma bialatum* are pits dug into the crinoid arms at the level of the ambulacral grooves. Those of *Protomyzostomum* species are hard calcified swellings induced on the arms or discs of basket stars. To these gallicolous and cysticolous species should be added the three *Asteromyzostomum* that insert their mouth into the body wall of asteroids, most often at the level of the ambulacral grooves.

Parasites of the digestive system are represented by 11 species belonging to the genera *Pulvinomyzostomum*, *Notopharyngoides*, *Asteriomyzostomum*, and *Eenymeenymyzostoma*. *Pulvinomyzostomum pulvinar* and *Pulvinomyzostomum inaki* infest crinoids where a large female is found with one dwarf male that flanks its side into the anterior part of the digestive system. About one third of the *Leptometra phalangium* collected off Banyuls-sur-mer (Mediterranean) was infested (Eeckhaut and Jangoux 1992). Small males can be observed single in the host mouth or in the calyx ambulacral grooves. There is no size difference between infested and noninfested crinoids. The parasitosis is certainly light, with *P. pulvinar* only diverting some food particles from the host gut. This is also the case for *Notopharyngoides* infestations. There are three Indo-West Pacific *Notopharyngoides* species: *N. platypus*, *N. aruensis*, and *N. ijimai*. They are single or by pair into the anterior part of the host gut. They do not have dwarf males but are functional hermaphrodites. They lay eggs when disturbed and have trochophores that evolve into metatrochophores. Younger individuals are sometimes found in cysts on host arm or disc.

Asteriomyzostomum asteriae infests the pyloric caeca from two species of the asteriid starfish, *Sclerasterias neglecta* and *Sclerasterias richardi*, in the Mediterranean, and *Asteriomyzostomum fisheri* stands in the body cavity of the goniasterid cushion star *Ceramaster leptoceraumus* in the Pacific. *Asteriomyzostomum hercules* infests the cardiac stomach of the asteroid *Coronaster volsellatus*. The prevalence is moderately high (although without quantitative data); when infected, one to two endoparasites were found per one host. *Asteriomyzostomum jinshou* infests the rectal sac of the asteroid *Mediaster brachiatus*, with a prevalence of 12 on 280 individuals (4.3%). *Asteriomyzostomum monroeae* infests the pyloric caecum of *Henricia* sp., with a prevalence of 7 on 27 individuals (25.9%). *Eenymeenymyzostoma nigrocorallium* was observed on three species of antipatharians in Madagascar on 73% of the colonies sampled, with one to five individuals on 20-cm-long infested coral fragment with a maximum of 39 specimens on a 139-cm-long entire coral colony. Individuals inhabit the gastrovascular ducts of their hosts, and the infestation is most of the time invisible by eye.

Parasites of coelom and gonads are from *Mesomyzostoma*, *Protomyzostomum*, and *Asteriomyzostomum* genera. *Asteriomyzostomum fisheri* has been observed in the body cavity of the sea star *Tosia leptoceramus* off southern California (Wheeler 1905). The way they infest the sea stars

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and their life cycle is unknown. *Mesomyzostoma reichenspergi* has been described from the coelom crinoid arm and pinnules, whereas *Mesomyzostoma katoi* was from the gonads of crinoids. Yet, there are three undescribed *Mesomyzostoma* species, one infesting the coelom of arms and pinnules of Japanese crinoids and two observed in crinoid discs, probably in the coelomic channels (Rouse and Eeckhaut personal observation). There are generally one to five mesomyzostomids per host. Mesomyzostomids are hermaphrodites and probably reproduce into the coelomic channels. When separated from their hosts, they lay eggs that evolve into metatrochophores. It is probable that mesomyzostomids infest their hosts thanks to the feeding apparatus of crinoids. Once caught in the pinnules, larvae could metamorphose, dig into the integument and reach the coelomic channels where they stay when adults. The Arctic *Protomyzostomum* infest basket stars, were the Antarctic species occur in brittle stars. Ecology of *Protomyzostomum polynephris* is the best known (Fedotov 1912, 1914). Fedotov (1916) supposed that *P. polynephris* penetrates into the host as a free-swimming larva through the large bursal slits. The infection of *Gorgonocephalus* is favored by the circumstance that they live in large groups on deep-water rocks. The larva having entered the bursal cavity should metamorphose and perforate its wall to penetrate into the body cavity in which it crawls to the gonads rupturing the connective tissue septa on its way. The parasites are found in different parts of the ophiuroid disc. Usually, they penetrate into the mass of the gonads and, by devouring the genital products, they stimulate the formation of cavities. Before reaching the gonads, the parasites seem to feed on other tissues. Up to 119 individuals have been observed in a single host, although lower infestations with few individuals also occur. The degree of infestation reaches about 50%, and the largest observed parasite was of 5 to 9 cm long. *P. polynephris* eat the gonads of their host, *Gorgonocephalus eucnemis*, leading to partial to total castration of the hosts. *P. polynephris* are found in soft or calcified gonadal cysts where multiple individuals are found.

Host specificity

The host specificity of the taxon "Myzostomida" is high, as almost all of them infest echinoderms, mainly crinoids but sometimes ophiuroids and asteroids. Five unnamed species are notable exceptions and infest a Japanese hexactinellid sponge (Okada 1920), a Puerto Rican black coral (Goenaga 1977), black corals from Costa Rica and gorgonians off Indonesia (Rouse personal communication), and black corals from Madagascar (Terrana and Eeckhaut 2017). Myzostomids belonging to the same genus infest one echinoderm class, except the genus *Myzostoma*, where some species infest crinoids and other ophiuroids. According to Grygier (1990), who studied a wide range of museum samples, host specificity of Indo-West Pacific myzostomid species may be species-specific, family-specific, or nonspecific. Two ecological studies taking into consideration myzostomids have been performed on tropical crinoids, those of Fabricius and Dales (1993) and Deheyn et al. (2006). In Fabricius and Dales (1993), all the myzostomid species were confounded. About 20% of the symbionts were myzostomids found on about one third of the crinoid species examined. In Deheyn et al. (2006), a total of 1064 specimens of symbionts belonging to 47 species were found on crinoids. Myzostomids (18 species) represented 59% of all symbiont specimens, shrimps (16 species) represent 20%, and polychaetes (3 species) represent 13%. Crabs, galatheids, gastropods, polychaetes, nematodes, ophiuroids, and fishes were also found on crinoids but in lower number. Polychaetes, myzostomids, and shrimps infested more than 50% of the crinoid individuals. The number of individuals per infested crinoid was the highest for myzostomids, with 8.3 on average, whereas it was lower for the other symbiotic taxa, with an average of 1 or 2 individuals per infested host. Myzostomids were abundant on Comasteridae, less on Himerometridae, Colobometridae, and Mariametridae.

Coevolution

During their common history, cospeciations occurred in myzostomids and their crinoid hosts (in both stalked crinoids and comatulid crinoids (Lanterbecq et al. 2010). The number of host-switches was much higher in comatulids than in stalked crinoids with internal host-switches that occurred in Comasteridae and in the non-comasterid comatulid clade, although not evident in stalked crinoids (Lanterbecq et al. 2010). External host-switches evidently existed from Comasteridae to non-comasterid and vice versa and may exist from stalked crinoids to non-comasterids (Lanterbecq et al. 2010). Genetic isolations existed inside myzostomid populations during cospeciations, host-switches, and/or duplications (Fig. 7.10.23). These events occurred in parasites and commensals and were at the origin of the myzostomid diversification. Host-switches, however, were more common in commensals than in parasites, which are explained by their ability to contact other hosts. Whether parasites or commensals, myzostomid populations living on crinoids were in a similar situation to terrestrial populations living on islands: if batches of

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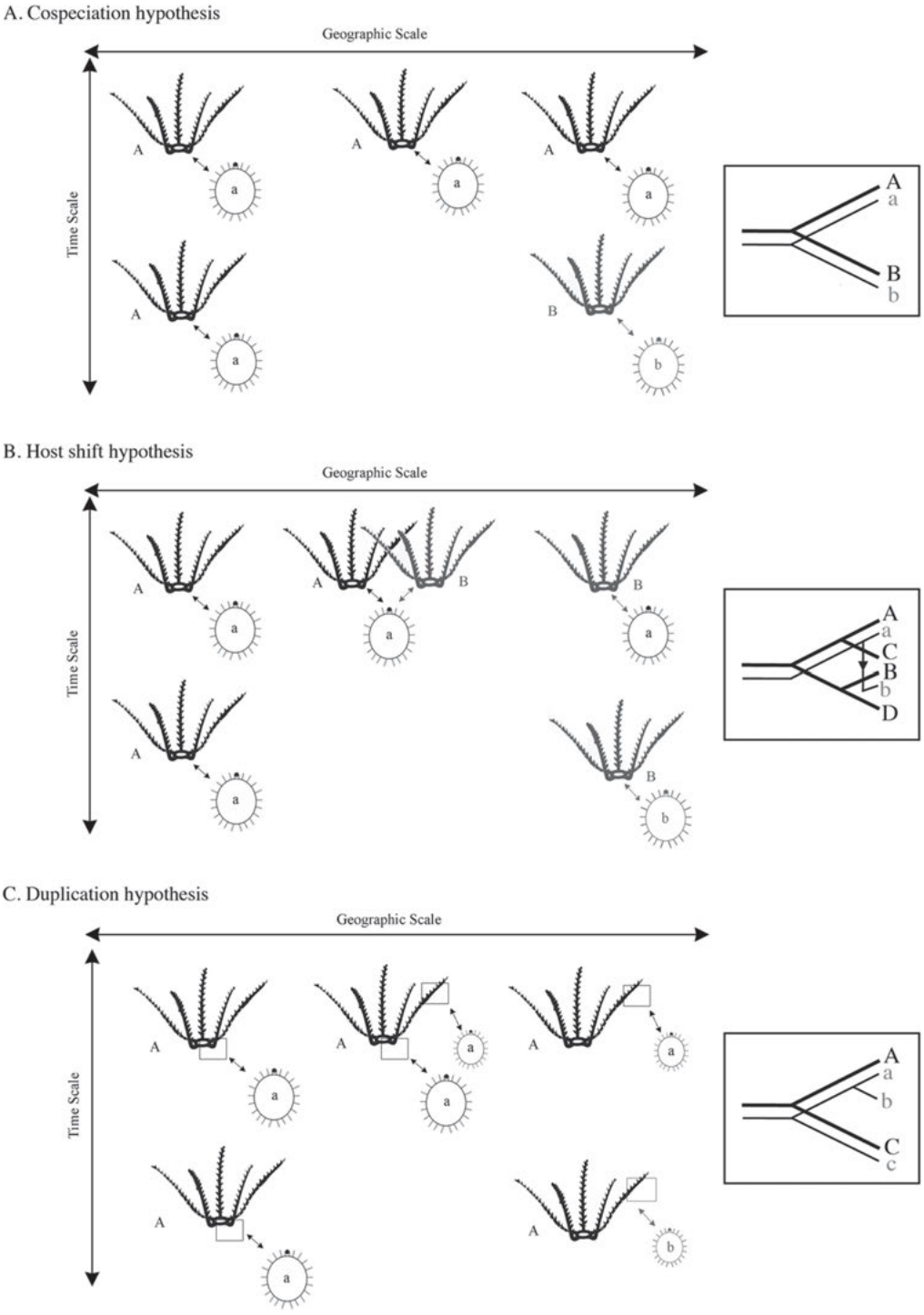


Fig. 7.10.23: Evolutionary events that possibly occurred in the crinoid-myzostomid system (from Lanterbecq et al. 2010). Considering geographical and time scales, the evolutionary events are cospeciation (A), host-shift (B), or duplication (C). Different colors (black and gray) and letters refer to different species. The different biological events are represented on the right, with thick and thin lines representing the host and associate trees, respectively. (A) Cospeciation hypothesis: when a crinoid species *A* has speciated in a new species *B*, the myzostomid-associate *a* cospeciated and became a new species *b* through time. (B) Host-shift hypothesis (followed by speciation): if two crinoid species (*A* and *B*) live together in the same geographic area, it is thinkable that the myzostomid *a*, associated with the crinoid species *A*, has colonized the crinoid species *B* and then became a new species *b* by geographic isolation on the crinoid *B* (through time). (C) Duplication hypothesis: the isolation of myzostomid individuals on one crinoid species is possible, as some ectocommensal myzostomids often show a preferred location on crinoids (e.g., the pinnules or the calyx); thus, regarding at large geographical scale, individual batches of a given myzostomid species *a* might show such preferences that could eventually lead to its speciation in *b* if the preferred location is maintained through time.

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individuals were genetically isolated for long enough, they were liable to speciate by allopatry.

In nature, the occurrence of crinoid-switches by myzostomids could be explained by the opportunism that characterized some species. Indeed, on a small geographical scale, some myzostomids often appear to be species specific, but these myzostomids often infest more than one crinoid species when viewed on a wider geographical scale (Eeckhaut et al. 1998). For instance, *Myzostoma fissum*, which is found in the whole Indo-West Pacific Ocean, has only been recorded on *Dichrometra flagellata* in Hansa Bay (Papua New Guinea), where 25 crinoid species co-occur, although it is sometimes observed on other species (mainly on Mariametridae) in other regions (Eeckhaut et al. 1998). Such opportunistic myzostomids would be prone to speciation if the host species become separated.

Phylogeny and taxonomy

Phylogenetic position within Metazoa

Although solutions of the phylogenetic analyses appear varied and sometimes in contradiction to each other, the first analyses that were made (Eeckhaut et al. 2000, Zrzavy et al. 2001) lead to wrong answers due to the poor knowledge about the used genes and about the phylogenetic resolution that they can give. The most convincing results are those of Bleidorn et al. (2007), who worked with mitochondrial and nuclear DNA. It is indeed very improbable that the unique order of 10 protein-coding genes and 2 ribosomal genes shared by myzostomids and annelids appeared twice independently during the evolution of these organisms. However, in the protostome tree of life published in *Nature*, Dunn et al. (2008) reported a total of 39.9 Mb of expressed sequence tags from 29 animals belonging to 21 phyla, including one myzostomid, *Myzostoma seymourcollegiorum*. They found it outside annelids but they also emphasized that its position was very unstable and not very reliable. Myzostomida are now undoubtedly linked to Annelida (Bleidorn et al. 2007, Struck et al. 2011, Hartmann et al. 2012, Weigert et al. 2014). Below are the various positions accorded to myzostomids through time and a summary of the phylogenetic analyses concerning them.

Myzostomids have been first considered as Trematoda (Leuckart 1827) based on the presence of a branching gut with all of its diverticula and of several pairs of presumed suckers on the ventral side, which were later defined as sense organs and considered as the homolog of the lateral organs of polychaetes (Wheeler 1896). Based on the morphology of their larvae, they were also considered as Crustacea (Semper 1858) or Stelechopoda (i.e., a taxon grouping myzostomids with Tardigrada and Pentastomida) (Graff 1877). Mecznikow (1866) and Beard (1884) conducted some investigations on their development and pointed out the possible affinity of myzostomids with polychaetes based on the general similarity of the larval shape (trochophora-type larvae bearing a metatroch and a telotroch, with two pairs of long chaetae). Benham (1896) was the first to suggest them as a separate class of annelids (rather than derived polychaete annelids), a position supported later by other investigators (e.g., Fedotov 1929, Kato 1952). Jägersten (1940a) grouped Myzostomida and Annelida (as two separate classes) into a coelomate protostome clade called Chaetophora. Mattei and Marchand (1987), based on ultrastructural similarities between the spermatozoa of Myzostomida and Acanthocephala (they both present filiform spermatozoa bearing an anterior flagellum and lacking of accessory centriol), considered these two taxa as sister groups defining a phylum they called Procoelomata. Because myzostomids exhibit characters such as parapodia with chaetae and acicula, a trochophora-type larva, and are segmented (though the segmentation is incomplete), they are classified in all textbooks (e.g., in Ruppert et al. 2004) and encyclopedias as a family of Polychaeta, an order of Polychaeta or a class of Annelida (e.g., in Grzimek's *Animal Life Encyclopedia*) (see Eeckhaut 2003). This suggestion is also based on the very intuitive idea that the body plan of ectocommensal myzostomids evolved from that of an errant polychaete ancestor that lost the notopodial chaetal system, with a migration of the neuropodia onto the ventral side of the body. The overdevelopment of the ventral side of myzostomids and the regression of locomotory and sense organs would have happened several times independently and led to the body plans of parasitic myzostomids.

The two first phylogenetic analyses were based on morphological data. The cladistic analysis of Haszprunar (1996) suggested that Myzostomida are the sister group of a clade including Sipuncula, Echiura, and Annelida. Rouse and Fauchald (1997) investigated polychaete systematics and found that Myzostomatidae were either associated to the Spintheridae (a family including ectoparasitic species of sponges) or they clustered with polychaetes with a hypertrophied axial pharynx. In the study of Rouse and Pleijel (2001), which is a modification of that of Rouse and Fauchald (1997), Myzostomida are included in Phyllodocida.

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Chenuil et al. (1997) compared the secondary structure of a small part of the large ribosomal subunit RNA gene (LSU hereafter) to that of other metazoans, including polychaetes and oligochaetes, and pointed out the difference existing between myzostomids and annelids. Zrzavy et al. (1998) used phenotypical data (morphological, ultrastructural, developmental, and ecological characters) and molecular data (no SSU sequences were available for myzostomids), and the analyses suggested that Myzostomida are the sister group of a clade including Echiura, Pogonophora, and annelids.

Eeckhaut et al. (2000) inferred the phylogenetic position of Myzostomida within Metazoa by analyzing the DNA sequences of two slowly evolving nuclear genes: the SSU and the elongation factor-1α (EF-1α hereafter). All analyses yielded best trees with Myzostomida not nested within Annelida and suggested that myzostomids are closer to flatworms than they are to annelids. The analyses of Zrzavy et al. (2001) comprised SSU and LSU sequences of *Myzostoma glabrum* together with phenotypical characters. The analyses showed myzostomids as the sister group of Cycliophora, closely related to the rotifer-acanthocephalan clade (=Syndermata). The myzostomid-cycliophoran-syndermate clade, accommodated within Platyzoa, was strongly supported by most analyses. Zrzavy et al. (2001) proposed the new name Prosomastigozoa for this group, due to the presence of highly derived spermatozoa with an anteriorly directed flagellum, at least present in myzostomids and syndermates (cycliophoran sperm ultrastructure was insufficiently known). Two other works (Littlewood et al. 2001, Rota et al. 2001) also inferred the phylogenetic position of non-myzostomidan clades but used myzostomidan sequences in the ingroup.

Bleidorn et al. (2007) presented evidence from mitochondrial and myosin II data that Myzostomida have an annelid origin. The unique order of 10 protein-coding and 2 ribosomal genes shared by myzostomids and annelids, but not by any other metazoan taxon, is compelling evidence supporting annelid affinities for Myzostomida. Although the analyses of mitochondrial data recover myzostomids as sister to all annelids, they appear as derived within annelids in the case of the myosin II data with strong support in all analyses. These results were supported by another study including data from two additional myzostomids (Bleidorn et al. 2009a, b). In 2009, Bleidorn et al. were also able to identify seven Hox genes for the myzostomid *Myzostoma cirriferum*. The presence of *Lox5*, *Lox4*, and *Post2* supports the inclusion of Myzostomida within Lophotrochozoa. Signature residues within flanking regions of Lox5 are also found in annelids but not in Platyhelminthes. As such, the available Hox genes data of myzostomids also support an annelid relationship.

To date, the annelid origin of Myzostomida is evident, as shown by recent phylogenomic results based on EST libraries. Even if EST-based phylogenomic studies including myzostomids disagree in their placement (Dunn et al. 2008, Bleidorn et al. 2009a, b, Struck et al. 2011), the authors consider myzostomids as annelid relatives (Hejnol et al. 2009, Hartmann et al. 2012). This hypothesis is also supported by the presence in *Myzostoma cirriferum* of several microRNA families that are exclusively shared by annelids and myzostomids (Helm et al. 2012). In conclusion, most of the analyses, especially the most recent, support a close affinity of myzostomids with annelids. Interestingly, however, dozens of symplesiomorphies were discovered by means of ancestral state reconstruction in the complete 18S and 28S rDNAs shared by the stem groups of Metazoa and Myzostomida (Wang and Xie 2014). By contrastive analyses on the datasets with or without such symplesiomorphic sites, Wang and Xie (2014) suggested that Myzostomida and other basal groups could be basal lineages of Bilateria.

Phylogeny and body plan evolution

Lanterbecq et al. (2006) reported the first molecular phylogeny of Myzostomida and investigated the evolution of their various symbiotic associations in using nuclear (18S rDNA) and mitochondrial (16S rDNA and COI) sequence data from 37 myzostomid species representing nine genera. Since this work, other phylogenetic analyses with important new species have been realized: Summers and Rouse (2014) with 75 myzostomid species, Jimi et al. (2017) with rare *Asteromyzostomum* and *Asteriomyzostomum*, and Terrana and Eeckhaut (2017) with the first species infesting black corals. Fig. 7.10.24 illustrates one analysis in the study of Terrana and Eeckhaut (2017). Three of the families are monophyletic: Asteromyzostomatidae, Protomyzostomatidae, and Mesomyzostomatidae (Summers and Rouse 2014). Three genera including more than one terminal are monophyletic (*Endomyzostoma*, *Mesomyzostoma*, and *Protomyzostomum*) and *Pulvinomyzostomum* is paraphyletic or monophyletic (results varying with analyses). *Myzostoma* is paraphyletic (polyphyletic before erection of *Eenymeenymyzostoma* for *Myzostoma cirripedium*), and two genera are polyphyletic (*Contramyzostoma* and *Notopharyngoides*).

Based on the integration of phylogenetic, ontogenetic, and morphological data, the following hypothesized evolutionary scheme can be proposed for explaining the diversity of the extant myzostomid body plans can be proposed. According to ontogeny and morphology, the

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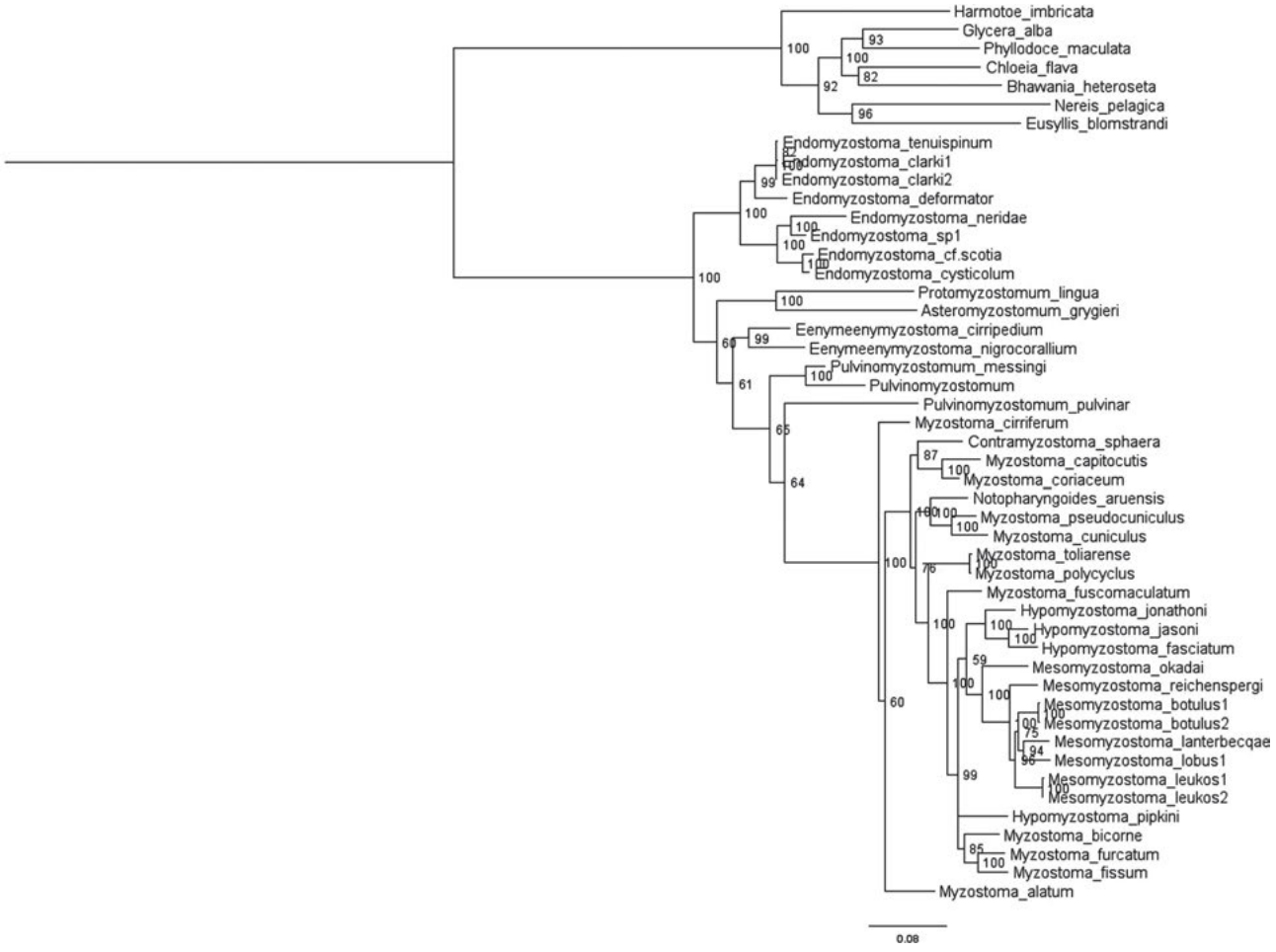


Fig. 7.10.24: The phylogeny of myzostomids. Results were obtained with a Bayesian analysis using 16S-18S-CO1 alignment (ML results in the same tree) (Terrana and Eeckhaut 2017). Numbers above branches indicate posterior probability obtained in the Bayesian analysis and in the maximum likelihood analysis.

first organisms that enter in association with crinoids would have been worms with six segments and five pairs of parapodia structured in cirrate neuropodia and notopodia.

The most recent analyses indicate that the last common ancestor of the all living myzostomids would be endoparasitic (Summers and Rouse 2014, Jimi et al. 2017, Terrana and Eeckhaut 2017). Reconstruction analysis also indicated that the host animals for the last common ancestor of the entire myzostomids would be stalked crinoids (Summers and Rouse 2014, Jimi et al. 2017, Terrana and Eeckhaut 2017). As galls and cysts-forming *Endomyzostoma* is the monophyletic sister group of all the other myzostomids, and as fossilized galls similar to those created by current *Endomyzostoma* species exist, a lifestyle similar to *Endomyzostoma* for myzostomid ancestors is suggested. Ancestral-state reconstruction showed that the host group of the last common ancestor of the ophiuroid symbionts (Protomyzostomidae) and the asteroid symbionts (Asteriomyzostomidae and Asteromyzostomidae) was likely to be sea stars. The black coral associate, *E. nigrocorallium*, evolved most probably from stalked crinoid-infesting species (Terrana and Eeckhaut 2017). Endoparasites of the digestive system of crinoids appeared multiple times, independently, through the lineages of *Pulvinomyzostomum* and *Notopharyngoides*.

The biggest family, Myzostomatidae, appeared after Endomyzostomatidae, Protomyzostomatidae, Asteromyzostomatidae, Asteriomyzostomatidae, and Pulvinomyzostomatidae. In Myzostomatidae, most are *Myzostoma* species that are hermaphroditic and move freely on crinoid body surface (Lanterbecq et al. 2009). The body of these myzostomids have an introvert and a discoid trunk. They developed pairs of needle-shaped cirri and had well-formed parapodia. In Myzostomatidae appeared three main morphotypes that can still be observed in the extant myzostomid fauna: *Myzostoma*, *Hypomyzostoma*, and *Mesomyzostoma* types. *Myzostoma*-type species developed their walking

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ability. These myzostomids keep a discoid trunk, but it often becomes very flat and flexible. Their parapodia are perfectly well adapted to a walking mode of locomotion on crinoids (Eeckhaut and Lanterbecq 2005) and they are able to move quickly at the crinoid surface. Furthermore, they often mime the colors and the color pattern of their hosts. It is also remarkable to observe that, in becoming discoid, trunks of such segmented, bilateral worms tend to become pentameric as the hosts are, 10 planes of symmetry dividing these organisms in two almost equal body parts. This surely helped *Myzostoma*-type myzostomids to merge with the crinoid surface. From time to time, parasites appeared, probably from a *Myzostoma*-type ancestor (Lanterbecq et al. 2009), presenting a particular body shape perfectly adapted to the host body part that they infested. *Contramyzostoma* and *Notopharyngoides* species are examples of these parasites. All show a reduction of their locomotory appendages and sensory organs.

Hypomyzostoma-type myzostomids developed their mimicry abilities. Their body is thick and they do not move quickly on crinoid surface but stay attached on pinnules or on the aboral sides of the arms. To merge to pinnules, some of them have developed caudal appendages and dorsal ridges. They also took their color pattern. To live on arms, they become very elongated and developed transversal ridges similar to arm ossicles. From these elongated *Hypomyzostoma*-type myzostomids appeared *Mesomyzostoma*-type species that parasite the coelom and gonads of crinoids. They become thread shaped to insert into the coelomic sinuses and in the gonads. They do not have sensory organs anymore, and their parapodia are reduced to the chaeta.

Taxonomy

Jägersten (1940a) divided Myzostomida into the orders Pharyngidea and Proboscidea based on differences in the ontogenesis of the anterior body of a few *Myzostoma* species (Proboscidea) and *Pulvinomyzostomum pulvinar* (Pharyngidea). He observed that a proboscis differentiates in Proboscidea, whereas an extrusible pharynx develops in Pharyngidea. Ontogenetically, it means that the blastopore (that becomes the mouth) is located at the apex of the proboscis in *Myzostoma* species while it forms the ventral opening through which the pharynx is everted in *P. pulvinar*. Jägersten (1940a) then built a classification in which all *Myzostoma* species are separated from all the other genera (for most of which, the ontogeny of the anterior body part was, however, unknown). Since then, the authors have described new myzostomid species, without a detailed knowledge of their ontogeny, and created new genera more or less haphazardly placed in one of the two orders. Most of the time, parasites were considered as Pharyngidea and ectocommensals as Proboscidea. Myzostomid taxonomy and anatomy were reviewed by Nansen (1885), Stummer-Traunfels (1926), Jägersten (1940a), Prenant (1959), and Grygier (2000). An extensive description of the taxa and a recent key to the orders and families of Myzostomida can be found in the work of Grygier (2000).

Proboscidea species have a protrusible proboscis, better named introvert (Fig. 7.10.1), as this body part, while extruded or invaginated, is never located "before the mouth" of these organisms. A prebulbar nerve ring is present and a peribulbar nerve ring, when present, is incomplete. Salivary glands end at the end of the introvert. The parapodia are well developed. The marginal cirri are well developed in most species but can be totally absent. The parapodial cirri are present in about 20 species. Sensory lateral organs lie in four pairs ventrally. The digestive system is complete with two to three pairs of dichotomized digestive caeca. Most proboscidea are hermaphrodites, mainly simultaneous, sometimes protandrous. The fertilization is internal; eggs are emitted in the water column and give rise to larvae of the trochophore type. Proboscidea includes only one family, Myzostomatidae, which is the biggest in terms of species.

Pharyngidea species do not have any introvert but sometimes a protrusible pharynx. In adults of Pharyngidea, the opening located on the trunk of individuals is thus the mouth. A peribulbar nerve ring is present. Salivary glands end at the level of the mouth. In general, the parapodia, cirri, and lateral organs are reduced or absent. They are often protandrous hermaphrodites with big females and dwarf males or dioecious. The fertilization is internal, and eggs are emitted in the water column and give rise to larvae of the trochophore type.

In the light of phylogenetic analyses based on molecular data, these two taxa, Proboscidea and Pharyngidea, are obsolete and only the names of families are still relevant in modern taxonomy. The World Register of Marine Species considers Myzostomida as an order in the super class "Annelida *incertae cedis*" (WoRMS 2019). They are often considered as an order in Class Polychaeta. Myzostomida includes nine recognized families.

Myzostomatidae Beard, 1884. Myzostomatidae comprises three genera: *Myzostoma*, *Hypomyzostoma*, and *Notopharyngoides*.

Myzostoma Leuckart, 1836

Type species *Myzostma cirriferum* Leuckart, 1836

Diagnosis: *Myzostoma* comprises about 140 species, including *M. cirriferum* on which most of the ecological and ultrastructural works have been done. *Myzostoma*

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shows an enormous range of morphological variations. The body of *Myzostoma* species is made of a posterior flat ovoid or discoid trunk and an anterior protrusible introvert. The margin of the trunk bears from 0 to more than 100 cirri that are small buds, needle-like or long and flexible body extensions. About 20 species have hump-like parapodial cirri. Five pairs of well-developed parapodia and four pairs of lateral organs are located lateroventrally. A pair of penises lies close to the parapodia of the third pair. A female genital pore is present close to the anus that opens posteroventrally. Some species bear caudal appendages, dorsal tubercles, or dorsal ridges.

Distribution: Grygier (1990) distinguished three groups within *Myzostoma*. The *costatum* group (Fig. 7.10.25A) includes flat-bodied, round, or oval species with a radiating pattern of dorsal ridges that extend outward as marginal teeth. This assemblage occurs throughout the Indian Ocean and east to the Mollucas and Torres Straits. It includes species such as *Myzostoma costatum*, *Myzostoma plicatum*, *Myzostoma cristatum*, and *Myzostoma rubrofasciatum sensu* Boulenger, 1913. One species, *Myzostoma carinatum*, is from the Caribbean. Some dorsally costate species have long caudal processes, such as *M. fissum, Myzostoma adhaerens*, and *Myzostoma furcatum*. They occur in the Indian Ocean but also extend well into the Pacific. The *ambiguum* group (Fig. 7.10.25B) has species with flat, round to shield-shaped bodies, and the anterior and posterior one to two pairs of marginal cirri are much longer than the others. This assemblage includes species such as *M. ambiguum, Myzostoma antennatum, Myzostoma longimanum*, *Myzostoma longicirrum*, and *Myzostoma vastum*. All are Pacific, except *M. vastum*, which is from the Caribbean. The *wyvillethompsoni* group (Fig. 7.10.25C) includes species with long, oval bodies and prominent parapodial cirri, the first three pairs directed anteromedially and the last two pairs posteromedially. The group includes *Myzostoma wyvillethompsoni*, *Myzostoma wheeleri*, and *M. cirripedium* found on stalked crinoids in the Philippine-Molluccan region and *Myzostoma ingolfi* observed on a South Californian ophiuroid. *M. carpenteri* is from Northwest Atlantic (Remscheid 1918) and *Myzostoma cirriferum* and *Myzostoma vincentinum* are from Northeast Atlantic; a few species are also recorded from Antarctic (Stummer-Traunfels 1908).

Ecology: Most are found on comatulid crinoids. A few *Myzostoma* infest stalked crinoids and others live on the surface of ophiuroids. Adults are ectocommensals; juveniles of a few species induce cysts at the level of the ambulacral grooves of the arms.

Main literature on species description: Atkins (1927), Boulenger (1913, 1916), Carpenter (1885), Fauvel (1916), Eeckhaut and Jangoux (1992), Eeckhaut et al. (1994, 1998), Graff (1883, 1884a, 1884b, 1884c, 1885b, 1887), George (1950), Grygier (1989, 1990, 1992), Jägersten (1937, 1940b), Lanterbecq and Eeckhaut (2003), McClendon (1906), Remscheid (1918), Rouse (2003), Rouse and Grygier (2005), Stummer-Traunfels (1908, 1910), Subramaniam (1938).

Hypomyzostoma Perrier, 1897

Type species *Hypomyzostoma folium* (Graff, 1884)

Diagnosis: *Hypomyzostoma* (Fig. 7.10.25D) consist of 12 species, including *H. crosslandi*, *Hypomyzostoma nanseni*, *Hypomyzostoma sulcatum*, *Hypomyzostoma elongatum*, *Hypomyzostoma folium*, *Hypomyzostoma taeniatum*, *Hypomyzostoma membranaceum*, *Hypomyzostoma fasciatum*, *Hypomyzostoma maculatum*, *Hypomyzostoma dodecaphalcis*, *Hypomyzostoma jasoni*, and *Hypomyzostoma jonathoni*. The trunk is thick, convex dorsally, concave ventrally, and very elongated in the sagittal plane. The parapodia that bear ventral cirri are well developed and lie in two parallel rows, the first pair being much closer to the anterior trunk margin than the posterior one. The lateral organs are very near the trunk margin that has no well-developed cirri but is scalloped. Transverse color stripes are very characteristic of the genus. The introvert is long and thin without buccal papillae.

Distribution: Strictly Indo-West Pacific.

Ecology: Only present on comatulid crinoids where they mainly stay on the arms. Juvenile-stage parasites of the integument at least in some species, adults free-moving on hosts.

Main literature on species description: Boulenger (1913), Eeckhaut et al. (1998), Graff (1877, 1884, 1887), Grygier (1992), Jägersten (1937), Remscheid (1918), Summers et al. (2014).

Notopharyngoides Benham, 1896

Type species *Notopharyngoides platypus* (Graff, 1887)

Diagnosis: *Notopharyngoides* (Fig. 7.10.25E) comprises three species, *N. platypus*, *N. aruensis*, and *N. ijimai*. This is an Indo-Pacific group found in the Red Sea and in the Pacific as far north as Japan. Their trunk is very thick, round or discoid, concave dorsally, and convex ventrally. The individuals are big, often more than 1 cm long. The parapodia and lateral organs lie at the center of kidney-shaped, flattened folds. Such integument folds are also present ventrally on the trunk margin and in the sagittal plane. The cirri are only present in *N. platypus*. The introvert pouch opens ventrally or dorsally.

Distribution: Indo-Pacific group found in the Red Sea and in the Pacific as far north as Japan.

Ecology: Only present on comatulid crinoids where they infest the anterior part of the digestive system or induce cysts on the calyx or the base of the arms.

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Main literature on species description: Eeckhaut et al. (1998), Graff (1887), Grygier and Nomura (1998), Hara and Okada (1921), Remscheid (1918).

Pulvinomyzostomatidae Jägersten, 1940. Pulvinomyzostomatidae (Fig. 7.10.25F) includes three species, *Pulvinomyzostomum pulvinar*, *P. inaki*, and *P. messingi*.

***Pulvinomyzostomum* Jägersten, 1940**

Type species *Pulvinomyzostomum pulvinar* (Graff, 1884)

Diagnosis: The first two species present a large female and a dwarf male that often occur together, the last is a free-living species on the surface of stalked crinoids. It is thought, although not experimentally demonstrated, that when females are absent males evolve into females. Female trunk is very thick, wider than long, concave dorsally, and convex ventrally. There are no cirrus and parapodia are not well developed. The mouth, anus, and female genital pore lie dorsally. The male trunk is flat and ovoid. Five pairs of small parapodia are present ventrally with two male genital pores at the level of the third pair. Six to 10 pairs of slit-like lateral organs are present. The mouth and anus are terminal in the sagittal plane.

Distribution: *Pulvinomyzostomum pulvinar* is from the Mediterranean Sea and the Atlantic coast of Brittany, *P. inaki* from Costa Rica (1866 m), and *P. messingi* off southwestern Oregon (1650 m).

Ecology: Parasite of the digestive system observed on *Leptometra* and *Antedon* comatulid crinoids.

Main literature on species description: Eeckhaut and Jangoux (1992), Jägersten (1940a), Summers et al. (2014).

Endomyzostomatidae Perrier, 1897. Endomyzostomatidae (Fig. 7.10.25G), formerly Cystimyzostomatidae, include about 10 species in three genera: *Endomyzostoma* (formerly *Cystimyzostomum* Jagersten, 1940), *Contramyzostoma*, and *Mycomyzostoma*.

Sexuality is variable in *Endomyzostoma* species. *Endomyzostoma pentacrini* and *Endomyzostoma deformator* are functional hermaphrodites, and the others are supposed to be protandrous hermaphrodites with females and dwarf males. It is to remark that, at the time of the description of the species, the way myzostomids reproduce, i.e., through intradermic sperm penetration, was unknown. Consequently, spermatic syncytia, which are very usual on the dorsal dermis in myzostomids, could have mistakenly be considered as testicles. Yet, it is not possible to distinguish protandrous hermaphrodites from dioecious states in myzostomids without knowing the entire life cycle of the species.

***Endomyzostoma* Perrier, 1897**

Diagnosis: In *Endomyzostoma* (Fig. 7.10.25G), the trunk of females and hermaphrodites is big similar in shape as the one of *Pulvinomyzostomum pulvinar* but often longer than wide. Parapodia, cirri, and lateral organs are reduced or absent. The mouth and anus are generally terminal. Male stage is round or oval and always very flat. They lack lateral organs; cirri and parapodia are extremely reduced.

Distribution: Mainly Indo-West Pacific with species described in Antarctic (Remscheid 1918, Summers et al. 2014) and Southwest Atlantic (McClendon 1906).

Ecology: Parasites of the integument of comatulid crinoids and stalked crinoids, inducing galls or cysts.

Main literature on species description: Boulenger (1916), Eeckhaut and Améziane-Cominardi (1994), Graff (1884a, b), Grygier (1988), McClendon (1906), Remscheid (1918), Stummer-Traunfels (1908), Wheeler (1896), Summers et al. (2014).

***Contramyzostoma* Eeckhaut, Grygier & Deheyn, 1998**

Type species *Contramyzostoma sphaera* Eeckhaut, Grygier & Deheyn, 1998

Diagnosis: *Contramyzostoma* (Fig. 7.10.25H) includes two species. The assignment of *Contramyzostoma* to Endomyzostomatidae by Eeckhaut and Jangoux (1995) is based on the behavior of the first described species and is probably erroneous. Both species are small and characterized by a development of the ventral side laterally, which is particularly evident in *Contramyzostoma bialatum*. In the last species, the ventral side forms two cylindrical wings developed on the right and left parts of the animal. The dorsum is reduced to a plate in the two species that bear the external appendages (cirri, parapodia, and lateral organs). The mouth and anus open dorsally. In *C. bialatum*, only the female stage is known, whereas the other *Contramyzostoma* species, *Contramyzostoma sphaera*, is simultaneous hermaphrodite. It is probable that this genus is polyphyletic.

Distribution: *C. bialatum* was described from Singapore and *C. sphaera* from Hansa Bay, North of Papua New Guinea.

Ecology: Parasites of the integument of comatulid crinoids inducing soft cysts.

Main literature on species description: Eeckhaut and Jangoux (1995), Eeckhaut et al. (1998).

***Mycomyzostoma* Eeckhaut, 1998**

Type species *Mycomyzostoma calcidicola* Eeckhaut, 1998

Diagnosis: *Mycomyzostoma* (Fig. 7.10.25I) is a monospecific genus with the single species, *M. calcidicola*. The species is considered as dioecious. The female body is made of a ball-shaped trunk with a peduncle that is an

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everted pharynx. There is no cirrus, parapodium, and lateral organs. An anogenital pore opens opposite to the mouth. The male is much smaller, flat, and rectangular in outline. Digestive system, lateral organs, and cirri are absent. The parapodia are represented by hooks and support rods. A pair of genital pores is present at the level of the parapodia of the third pair.

Distribution: Reported around New Caledonia, West Pacific.

Ecology: Parasite of the stalked crinoid *S. nobilis*, inducing cysts.

Main literature on species description: Eeckhaut (1998).

Mesomyzostomatidae Stummer-Traunfels, 1923. Mesomyzostomatidae (Fig. 7.10.25J) is a monogeneric family with three species, *M. reichenspergi*, *M. katoi*, and *Mesomyzostoma lanterbecqae*.

***Mesomyzostoma* Remscheid, 1918**

Type species *Mesomyzostoma reichenspergeri* Remscheid, 1918

Diagnosis: Heinzeller et al. (1995) described a new species of myzostomid that invades the coelom of a comatulid crinoid that is temptatively placed here in the family. There are three undescribed species in Rouse's collection, one from Japan and two from Lizard Island (personal observation). The two described species are flatworm-like, but they bear five pairs of hooks, remnants of parapodia. Three to four pairs of hooks have been described in *M. katoi*. Marginal cirri and lateral organs are absent. The mouth and anus open on the trunk margin. The species are simultaneous hermaphrodites with a female genital pore that opens close to the anus and male genital pores close to the third pair of hooks.

Distribution: *M. reichenspergi* was collected in Aru Island, Indonesia (Remscheid 1918) and *M. katoi* in Japan (Okada 1933). Undescribed species were observed around Japan and in Lizard Island.

Ecology: Undescribed and described species parasite the gonads and/or the coelomic channels of the arms, pinnules, and calyx of comatulid crinoids.

Main literature on species description: Remscheid (1918), Okada (1933), Summers et al. (2014).

Protomyzostomatidae Stummer-Traunfels, 1923. Protomyzostomatidae (Fig. 7.10.25K) is a monogeneric family including seven described species: *Protomyzostomum polynephris, Protomyzostomum cystobium, Protomyzostomum sagamiense*, *Protomyzostomum astrocladi* (Fedotov 1912, 1914, 1916, 1925), *Protomyzostomum glanduliferum* (see Bartsch and Faubel 1995), and *Protomyzostomum lingua* with *Protomyzostomum roseus* (see Summers et al. 2014).

***Protomyzostomum* Fedotov, 1912**

Type species *Protomyzostomum polynephris* Fedotov, 1912

Diagnosis: Adults of the species *P. polynephris* are the largest myzostomids described so far. The body is made of a very long and flat trunk that, in life, is rolled up or irregularly folded. There are no cirrus and the lateral organs are faint. The small parapodia, five pairs, are close to the margin. The mouth and the anus are terminal, in the sagittal plane.

Distribution: Four *Protomyzostomum* spp. are from the Arctic Ocean or North Pacific and one is from Japan. *P. glanduliferum* Bartsch and Faubel, 1995 with an undescribed species (Grygier 2000) that has been recorded from Antarctica. *P. lingua* is from Antarctica (Discovery Bank; 379 m) and *P. roseus* is from California (Monterey Canyon; 1160 m).

Ecology: The Arctic and Pacific species infest gonads of basket stars or induce cyst on their arms or discs, and the two others infest that of brittle stars and occur in the ventral coelom, above the jaws and the basal arm vertebrae.

Main literature on species description: Fedotov (1912, 1914, 1916, 1925), Bartsch and Faubel (1995), Okada (1922), Jägersten (1940a), Nigmatullin (1970), Summers et al. (2014).

Asteriomyzostomatidae Jägersten, 1940. Asteriomyzostomatidae (Fig. 7.10.25L) include five species in the genus *Asteriomyzostomum*: *A. asteriae* Marenzeller, 1895, *A. fisheri* Wheeler, 1905, *A. hercules* Jimi, Moritaki & Kajihara, 2017, *A. jinshou* Jimi, Moritaki & Kajihara, 2017, and *A. monroeae* Jimi, Moritaki & Kajihara, 2017.

***Asteriomyzostomum* Jägersten, 1940**

Type species *Asteriomyzostomum asteriae* (Marenzeller, 1895)

Diagnosis: An undescribed species was observed in *Hippasteria imperialis* around Goto Island (East China Sea) (Grygier personal communication). The body of described species is flat, oval, and wider than long. Five pairs of reduced parapodia are located ventrally close to the margin. Four pairs of lateral organs alternate with parapodia. There is no cirrus. The anus and the female genital opening are located dorsally, at two thirds the body length. Asteriomyzostomatidae are functional hermaphrodites. The penes are poorly developed and open close to the parapodia of the third pair.

Distribution: *A. asteriae* is reported from starfishes in the Mediterranean and *A. fisheri* is reported from a cushion star in the Pacific (South California). The three other species — *A. hercules, A. jinshou*, and *A. monroeae* — are described from deep-sea asteroids that were collected at two sites in

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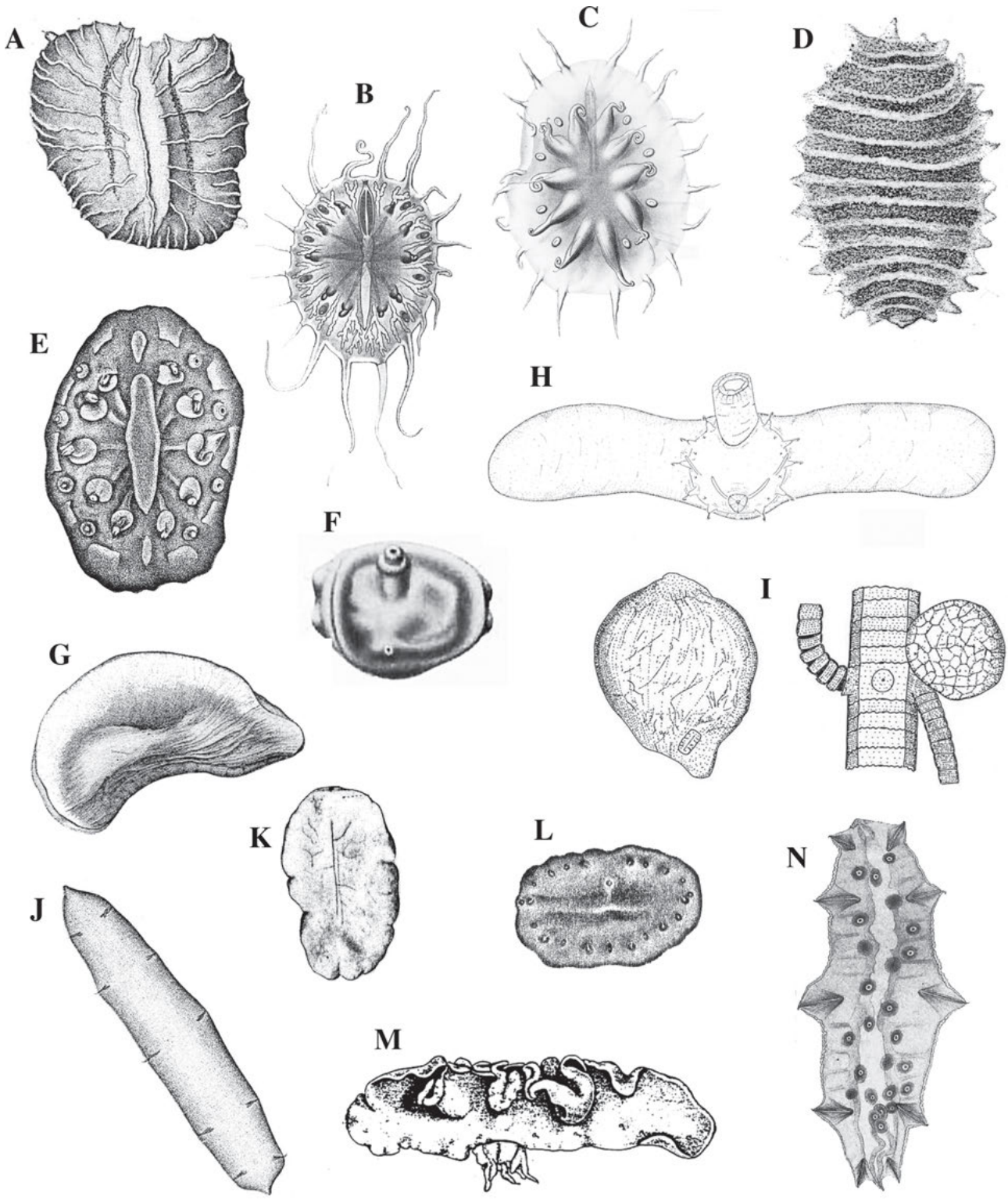


Fig. 7.10.25: Various myzostomidan genera and morphologies. A, *Myzostoma cristatum* Remscheid, 1918; B, *Myzostoma ambiguum* Graff, 1887; C, *Myzostoma wyvillethompsoni* Graff, 1884; D, *Hypomyzostoma taeniatum* (Remscheid, 1918); E, *Notopharyngoides aruensis* (Remscheid, 1918); F, female stage of *Pulvinomyzostomum pulvinar* Graff, 1884; G, *Endomyzostoma cysticolum* (Graff, 1883); H, *Contramyzostoma bialatum* Eeckhaut & Jangoux, 1995; I, *Mycomyzostoma calcidicola* Eeckhaut, 1998, with its cyst; J, *Mesomyzostoma reichenspergi* Remscheid, 1918; K, *Protomyzostomum polynephris* Fedotov, 1912; L, *Asteriomyzostomum asteriae* (Marenzeller, 1895); M, *Asteromyzostomum witjasi* Wagin, 1954; N, *Stelechopus hyocrini* Graff, 1884. A, D, F, K, Dorsal view; B, C, E, H, J, L, N, Ventral view; G, I, M, Side view. A, D, E, G, J, Redrawn from Remscheid (1918); B, Redrawn from Graff (1887); C, F, N, Redrawn from Graff (1884); H, Redrawn from Eeckhaut and Jangoux (1995); I, Redrawn from Eeckhaut (1998); K, Redrawn from Fedotov (1912); L, Redrawn from Stummer-Traunfels (1903); M Redrawn from Wagin (1954).

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the Kumano Sea, off central Japan, eastern North Pacific by dredging (Cape Miki at depths of 196 to 291 and 270 to 341 m and off Minami-Ise at a depth of 140 to 360 m).
Ecology: *A. asteriae* infests the pyloric caeca from two species of the asteriid starfish, *S. neglecta* and *S. richardi*, in the Mediterranean, and *A. fisheri* stands in the body cavity of the goniasterid cushion star *C. leptoceraumus* in the Pacific. *A. hercules* infests the cardiac stomach of the asteroid *C. volsellatus*. *A. jinshou* infests the rectal sac of the asteroid *M. brachiatus*. *A. monroeae* infests the pyloric caecum of *Henricia* sp.
Main literature on species description: Marenzeller (1895), Stummer-Traunfels (1903), Wheeler (1905), Jimi et al. (2017).

Asteromyzostomatidae Wagin, 1954. Asteromyzostomatidae (Fig. 7.10.25M) are represented by six species, all belonging to *Asteromyzostomum*.

***Asteromyzostomum* Wagin, 1954**
Type species *Asteromyzostomum witjasi* Wagin, 1954
Diagnosis: The trunk of *Asteromyzostomum* species is wider than long and folded up dorsally making them mushroom-shaped. The parapodia are reduced to ventral button-like structures with small chaetae. Cirri are absent. The posterior trunk folds bear about 40 oval lateral organs. The mouth is ventral and surrounded by well-developed circumoral tentacles. The anus opens just ventral to the posterior end of the trunk. Species are hermaphrodites with the female gonopore opening posterior to the anus. Two penes are described and located between the third and fourth pairs of parapodia.
Distribution: Three are described from the Russian Arctic (Wagin 1954), two unnamed species come from Antarctica (Elephant Island) and Atlantic (Grygier 2000), and an unnamed species off Mie Prefecture, Japan (Jimi et al. 2017).
Ecology: All are external parasites attached by circumoral tentacles into the integument of sea stars.
Main literature on species description: Wagin (1954), Grygier (2000), Summers and Rouse (2014), Jimi et al. (2017).

Stelechopidae Graff, 1884. The family Stelechopidae (Fig. 7.10.25N) is represented by the single species *Stelechopus hyocrini*.

***Stelechopus* Graff, 1884**
Type species *Stelechopus hydrocrini* Graff, 1884
Diagnosis: Individuals have small, flat, elongated trunk with five small parapodia located ventrolaterally, marginally, or dorsolaterally. Cirri are absent and only two pairs of lateral organs have been observed. The mouth and the anus are terminal. Organisms are hermaphrodites with the female genital tract opening posterior to the anus. Male system opens through two gonopores located at the level of the parapodia of the third pair.
Distribution: South of the Indian Ocean, off Crozet Island.
Ecology: Ectocommensal of the stalked crinoids *Hyocrinus* and *Bathycrinus*.
Main literature on species description: Graff (1884), Jägersten (1940a).

Eenymeenymyzostomatidae Summers & Rouse, 2015. Eenymeenymyzostomatidae includes two species in one genus, *E. cirripedium* (see Graff 1885) and *E. nigrocorallium* (see Terrana and Eeckhaut 2017).

***Eenymeenymyzostoma* Summers & Rouse, 2015**
Type species *Eenymeenymyzostoma cirripedium* (Graff, 1885)
Diagnosis: During their phylogenetic analyses, Summers and Rouse (2014) found *M. cirripedium* well outside all other members of *Myzostoma*, and *Eenymeenymyzostoma* n. gen. and Eenymeenymyzostomatidae n. fam. were erected (Summers and Rouse 2014, 2015). *Myzostoma metacrini* McClendon, 1906 is a junior synonym of *E. cirripedium*. Other potential members of *Eenymeenymyzostoma* n. gen. include 10 other species described from stalked crinoids. *E. nigrocorallium* is the first species of myzostomids associated with black corals described. The morphology of *E. nigrocorallium* is very particular compared to its related sister species, *E. cirripedium*. It is characterized by the presence of five pairs of extremely reduced parapodia located on the body margin and the lack of introvert, cirrus, and lateral organ. Individuals are hermaphroditic with the male and female gonads located both on the dorsal side of the trunk. They have a highly developed parenchymomuscular layer on the ventral side and the digestive system lies in the midpart of the trunk.
Distribution: *E. cirripedium* was described from Sagami Bay (Japan, 218 m) (Graff 1885) and *E. nigrocorallium* from the Great Reef of Toliara (Madagascar).
Ecology: *E. cirripedium* is a free-living myzostomid species described from stalked crinoids. *E. nigrocorallium* was observed on three species of antipatharians from the Great Reef of Toliara in Madagascar: *Stichopathes* sp., *Cirrhipathes* sp. aff. *anguina*, and a second species of *Cirrhipathes*. Myzostomids are found on 73% of the colonies sampled, with one to five individuals on 20-cm-long infested coral fragment with a maximum of 39 specimens on a 139-cm-long entire coral colony. Individuals inhabit the gastrovascular ducts of their hosts, and the infestation is most of the time invisible by eye.

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Main literature on species description: Graff (1885), Summers and Rouse (2014), Terrana and Eeckhaut (2017).

References

Abel, O. (1920): *Lehrbuch der Paläozoologie*. 1st ed. Gustav Fischer, Jena: 1–500.

Afzelius, B.A. (1983): The spermatozoon of *Myzostomum cirriferum* (Annelida, Myzostomida). *Journal of Ultrastructure Research* 83: 58–68.

Afzelius, B.A. (1984): Spermiogenesis in *Myzostomum cirriferum* (Annelida; Myzostomida). *Videnskabelige Meddelelser Fra Dansk Naturhistorick Forening i Kjobenhavn* 145: 11–21.

Arendt, Y.A. (1961): On damages of sea lilies, called *Schizoproboscina*. *Paleontologitshesky Zhurnal* 2: 101–106. [in Russian]

Atkins, D. (1927): Report on the Myzostomida collected by Mr F.A. Potts in Torres Strait, together with a description of a species obtained by Professor J. Stanley Gardiner from the Maldives. *Proceedings of the Royal Society of London* 23: 339–357.

Bachmayer, F. (1964): Ein Korallenriff in Niederösterreich. *Veröffentlichungen aus dem Naturhistorischen Museum, Wien, Neue Folge* 5: 102–111.

Bargalló, R. (1977): Polimorfisme dels gàmetes masculins. III. Consideracions espermatològiques a propòsit dels Myzostòmids. *Butlletí de la Societat Catalana de Biologia* 2: 33–39.

Bartsch, I. & Faubel, A. (1995): *Protomyzostomum glanduliferum* n. sp., a new myzostomid from the Antarctic ophiuroid *Ophiacantha disjuncta*. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92: 35–43.

Beard, J. (1884): On the life-history and development of the genus *Myzostoma* (F.S. Leuckart). *Mitteilungen aus der zoologischen Station zu Neapel* 5: 544–580.

Beard, J. (1898): The sexual condition of *Myzostoma glabrum* (F.S. Leuckart). *Mitteilungen aus der zoologischen Station zu Neapel* 13: 293–324.

Benham, W.B. (1896): Archiannelida, Polychaeta, Myzostomidaria. In: Farmer, S.F. & Shipley, A.E. (eds.), *The Cambridge Natural History*. Macmillan, London: 241–334.

Bleidorn, C., Eeckhaut, I., Podsiadlowski, L., Schult, N., McHugh, D., Halanych, K.M., Milinkovitch, M.C. & Tiedemann, R. (2007): Mitochondrial genome and nuclear sequence data support Myzostomida as part of the annelid radiation. *Molecular Biology and Evolution* 24: 1690–1701.

Bleidorn, C., Lanterbecq, D., Eeckhaut, I. & Tiedemann, R. (2009a): A PCR survey of hox genes in the myzostomid *Myzostoma cirriferum*. *Development, Genes and Evolution* 219: 211–216.

Bleidorn, C., Podsiadlowski, L., Zhong, M., et al. (2009b): On the phylogenetic position of Myzostomida: Can 77 genes get it wrong? *BMC Evolutionary Biology* 9: 150.

Bo, M., Rouse, G.W., Martin, D. & Bavestrello, G. (2013): A myzostomid endoparasitic in black corals. *Coral Reefs* 33: 273.

Boulenger, C.L. (1913): Report on the Myzostomida collected by Mr. Cyril Crossland in the Red Sea in 1905. *Proceedings of the Royal Society of London*: 85–108.

Boulenger, C.L. (1916): Myzostomida. British Antarctic (Terra Nova) Expedition 1910. *Natural History Reports in Zoology* 2: 135–140.

Brett, C.E. (1978): Host-specific pit-forming epizoans on Silurian crinoids. *Lethaia* 11: 217–232.

Carpenter, P.H. (1885): On three new species of *Metacrinus*. With a note on a new *Myzostoma* by L. Von Graff. *Transactions of the Linnean Society of London* 2: 435–446.

Chenuil, A., Solignac, M. & Bernard, M. (1997): Evolution of the large-subunit ribosomal RNA binding site for protein L23/25. *Molecular Biology and Evolution* 14: 578–588.

Clarke, J.M. (1921): Organic dependence and disease: their origin and significance. *Bulletin of the New York State Museum* 221–222: 1–113.

Deheyn, D.D., Lyskin, S. & Eeckhaut, I. (2006): Assemblages of symbionts in tropical shallow-water crinoids and assessment of symbionts' host-specificity. *Symbiosis* 42: 161–168.

Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., Sörensen, M.V., Haddock, S.H.D., Schmidt-Rhaesa, A., Okusu, A., Kristensen, R.M., Wheeler, W.C., Martindale, M.Q. & Giribet, G. (2008): Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452: 745–749.

Eckelbarger, K.J. (1992): Polychaeta: Oogenesis. In: Harrison, F.W. & Gardiner, S.L. (eds.), *Microscopic Anatomy of Invertebrates, Vol. 7 Annelida*. Wiley-Liss, New York: 109–127.

Eeckhaut, I. (1998): *Mycomyzostoma calcidicola* gen. nov., sp. nov., the first extant parasitic myzostome infesting crinoid stalks, with a nomenclatural appendix by M.J. Grygier. *Species Diversity* 3: 89–103.

Eeckhaut, I. (2003): Myzostomida. In: Craig, S.F., Thoney, D.A., Schlager, N., Trumpey, J.E. & Hutchins, M. (eds.), *Grzimek's Animal Life Encyclopedia. Vol. 2: Protostomes*. Gale Group: 59–63.

Eeckhaut, I. & Améziane-Cominardi, N. (1994): Structural description of three myzostomes parasites of crinoids and of the skeletal deformities deformities they induce on their hosts. In: David, B., Guille, A., Feral, J.-P. & Roux, M. (eds.), *Echinoderms through time, Proceedings of the Eight International Echinoderm Conference*. Balkema, Rotterdam: 203–209.

Eeckhaut, I. & Jangoux, M. (1991): Fine structure of the spermatophore and intradermic penetration of sperm cells in *Myzostoma cirriferum* (Annelida, Myzostomida). *Zoomorphology* 111: 49–58.

Eeckhaut, I. & Jangoux, M. (1992): Development and behaviour of *Myzostoma alatum* and *Pulvinomyzostomum pulvinar*, two myzostomid symbiotes of the comatulid *Leptometra phalangium* (Echinodermata). In: Scalera-Liaci, L. & Canicatti, C. (eds.), *Echinoderms through Time*. Balkema, Rotterdam: 229–236.

Eeckhaut, I. & Jangoux, M. (1993a): Integument and epidermal sensory structures of *Myzostoma cirriferum* (Myzostomida). *Zoomorphology* 113: 33–46.

Eeckhaut, I. & Jangoux, M. (1993b): Life cycle and mode of infestation of *Myzostoma cirriferum* (Annelida), a symbiotic myzostomid of the comatulid crinoid *Antedon bifida* (Echinodermata). *Diseases of Aquatic Organisms* 15: 207–217.

Eeckhaut, I. & Jangoux, M. (1995): *Contramyzostoma bialatum* (Annelida: Myzostomida), a new genus and species of parasitic myzostome infesting comatulid crinoids. *Raffles Bulletin of Zoology* 43: 343–353.

Eeckhaut, I. & Jangoux, M. (1997): Infestation, population dynamics, growth and reproductive cycle of *Myzostoma cirriferum* (Myzostomida), an obligate symbiont of the comatulid crinoid *Antedon bifida* (Crinoidea, Echinodermata). *Cahiers de Biologie Marine* 38: 7–18.

Eeckhaut, I. & Lanterbecq, D. (2005): Myzostomida: A review of their ultrastructure and phylogeny. In: Bartholomaeus, T. &

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Purschke, G. (eds.), *Morphology, Molecules and Evolution of the Polychaeta and Related Taxa. Developments in Hydrobiology* 179: 253–275.

Eeckhaut, I., VandenSpiegel, D. & Grygier, M.J. (1994): Myzostomida (Annelida) from Singapore with related Indo-Pacific distribution records and description of three new species. *Raffles Bulletin of Zoology* 42: 669–688.

Eeckhaut, I., Dochy, B. & Jangoux, M. (1995): Feeding behaviour and functional morphology of the introvert and digestive system of *Myzostoma cirriferum* (Myzostomida). *Acta Zoolologica (Stockholm)* 76: 307–315.

Eeckhaut, I., Grygier, M.J. & Deheyn, D. (1998): Myzostomes from Papua New Guinea, with related Indo-West Pacific distribution records and description of five new species. *Bulletin of Marine Science* 62: 841–886.

Eeckhaut, I., McHugh, D., Mardulyn, P., Tiedemann, R., Monteyne, D., Jangoux, M. & Milinkovitch, M.C. (2000): Myzostomida: A link between trochozoans and flatworms? *Proceedings of the Royal Society of London B* 267: 1383–1392.

Eeckhaut, I., Fievez, L. & Müller, M.C. (2003): Larval development of *Myzostoma cirriferum* (Myzostomida). *Journal of Morphology* 258: 269–283.

Fabricius, K.E. & Dale, M.B. (1993): Multispecies associations of symbionts on shallow water crinoids of the central Great Barrier Reef. *Coenoses* 8: 41–52.

Fauvel, P. (1916): *Polychètes. Résultats du voyage de la Belgica en 1897–1899 sous le commandement de A. de Gerlache de Gomery.* J.E. Buschmann, Anvers: 44 pp.

Fedotov, D.M. (1912): *Protomyzostomum polynephris*, eine neue Myzostomidenart. *Zoologischer Anzeiger* 39: 649–653.

Fedotov, D.M. (1914): Die Anatomie von *Protomyzostomum polynephris* Fedotov. *Zeitschrift für wissenschaftliche Zoologie* 109: 631–696.

Fedotov, D.M. (1916): On the parasitism of *Protomyzostomum* in *Gorgonocephalus eucnemis*. *M. Tr. Zool. Zh. SSSR* 1: 161–218. [in Russian with English summary]

Fedotov, D.M. (1925): Über eine neue Art von *Protomyzostomum* (*Pr. astrocladi*, sp. n.) aus *Astrodadus*. *Zoologischer Anzeiger* 63: 183–194.

Fedotov, D. (1929): Beiträge zur Kenntnis der Morphologie der Myzostomiden. *Zeitschrift für Morphologie der Tiere* 15: 156–191.

Fishelson, L. (1974): Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. *Marine Biology* 26: 183–192.

Franzen, C. (1974): Epizoans on Silurian-Devonian crinoids. *Lethaia* 7: 287–301.

George, A.I. (1950): On *Myzostoma striata,* n. sp. from the Madras harbour. *Proceedings of the Indian Academy of Sciences Section B* 32: 215–221.

Goenaga, C. (1977): *Two new species of Stichopathes (Zoantharia; Antipatharia) with observations on aspects or their biology.* M.S. thesis, University of Puerto Rico.

Graff, L. (1877): *Das Genus Myzostoma (F. S. Leuckart).* Wilhelm Engelmann, Leipzig: viii, 82 pp., plates I–XI.

Graff, L. von (1883): Verzeichnis der von der United States Coast Survey steamers "Hassler" und "Blake" von 1867 zu 1879 gesammelten Myzostomiden. *Bulletin of the Museum of Comparative Zoology, Harvard College* 11: 125–133.

Graff, L. von (1884a): On the Myzostomida of the "Porcupine" and "Triton" dredgings. *Proceedings of the Royal Society of Edinburgh* 12: 378–380.

Graff, L. von (1884b): Report on the Myzostomida collected during the voyage of H.M.S. Challenger during the years 1873–76. *Reports on the Scientific Results of the Voyage of H.M.S Challenger during the years 1873–76. Zoology* 10: 1–82, plates I–XVI.

Graff, L. von (1884c): Nye Arter af Myzostomider i Universitetets Zoologiske Museum i Kjobenhavn. *Videnskabelige Meddelelser Fra Dansk Naturhistorick Forening i Kjobenhavn* 6: 81–85.

Graff, L. von (1885a): Ueber einige Deformitaten an fossilen Crinoiden. *Palaeontographica* 31: 185–191, plate XVI (I).

Graff, L. von (1885b): Description of a new species of *Myzostoma*. *Transactions of the Linnean Society of London, 2nd Series. Zoology* 2: 444–446, plate LII (fig. 19).

Graff, L. von (1887): Report on the Myzostomida collected during the voyage of H.M.S. Challenger during the years 1873–76. Supplement. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76. Zoology* 20: 1–16, plates I–IV.

Grygier, M.J. (1988): Unusual and mostly cysticolous crustacean, molluscan and myzostomidan associates of echinoderms. In: Burke, R.D., Mladenov, P., Lambert, P. & Parsley, R.L. (eds.), *Echinoderm Biology.* Balkema, Rotterdam: 775–784.

Grygier, M.J. (1989): Three new species of *Myzostoma* (Myzostomida). *Proceedings of the Biological Society of Washington* 102: 793–804.

Grygier, M.J. (1990): Distribution of Indo-Pacific *Myzostoma* and host specificity of comatulid-associated Myzostomida. *Bulletin of Marine Science* 47: 182–191.

Grygier, M.J. (1992): Hong Kong Myzostomida and their Indo-Pacific distributions. In: Morton, B. (ed.), *The Marine Flora and Fauna of Hong Kong and Southern China, III. Proceedings of the 4th International Marine Biology Workshop.* Hong Kong University Press, Hong Kong: 131–147.

Grygier, M.J. (2000): Class Myzostomida. In: Beesley, P.L, Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia, Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula.* CSIRO Publishing, Melbourne: 297–330.

Grygier, M.J. & Nomura, K. (1998): Cysticolous Myzostomida. *Notopharyngoides platypus* from *Comanthina nobilis* (Echinodermata: Crinoidea), at Kushimoto, Honshu, Japan. *Species Diversity* 3: 17–24.

Hara, J. & Okada, Y. (1921): Two new species of *Myzostoma*. *Annotes zoologicae Japonica* 10: 33–39.

Hartmann, S., Helm, C., Nickel, B., Meyer, M., Struck, T.H., Tiedemann, R., Selbig J. & Bleidorn, C. (2012): Exploiting gene families for phylogenomic analysis of myzostomid transcriptome data. *PLoS ONE* 7: e29843.

Haszprunar, G. (1996): The Mollusca: Coelomate turbellarians or mesenchymate annelids? In: Taylor, J.D. (ed.), *Origin and Evolutionary Radiation of the Mollusca.* Oxford University Press, Oxford: 3–28.

Heinzeller, T., Aschauer, B., Lange, A. & Welsch, U. (1995): A myzostomid invading the connective tissue of its host *Comanthus parvicirrus* (Crinoidea). In: Emson, R.H., Smith, A.B. & Campbell, A.C. (eds.), *Echinoderm Research.* Balkema, Rotterdam: 3–8.

Hejnol, A., Obst, M., Stamatakis, A., Ott, M., Rouse, G.W., Edgecombe, G.D., Martinez, P., Baguñà, J., Bailly, X., Jondelius, U., Wiens, M., Müller, W.E.G., Seaver, E., Wheeler, W.C., Martindale, M.Q., Giribet, G. & Dunn, C.W. (2009): Assessing the root of bilaterian animals with scalable phylogenomic methods. *Proceedings of the Royal Society B Biological Sciences* 276: 4261–4270.

Helm, C. & Bleidorn, C. (2016): Annelida: Myzostomida. In: Schmidt-Rhaesa, A. Harzsch, S. & Purschke, G. (eds.),

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Structure and Evolution of Invetebrate Nervous Systems. Oxford University Press, Oxford: 241–253.

Helm, C., Bernhart, S.H., Höner zu Siederdissen, C., Nickel, B. & Bleidorn, C. (2012): Deep sequencing of small RNAs confirms an annelid affinity of Myzostomida. *Molecular Phylogenetics and Evolution* 64: 198–203.

Helm, C., Weigert, A., Mayer, G. & Bleidorn, C. (2013): Myoanatomy of *Myzostoma cirriferum* (Annelida, Myzostomida): Implications for the evolution of the myzostomid body plan. *Journal of Morphology* 274: 456–466.

Helm, C., Stevenson, P.A., Rouse, G.W. & Bleidorn, C. (2014): Immunohistochemical investigations of *Myzostoma cirriferum* and *Mesomyzostoma* cf. *katoi* (Myzostomida, Annelida) with implications for the evolution of the myzostomid body plan. *Zoomorphology* 133: 257–271.

Jägersten, G. (1937): Myzostomiden von Prof. Sixten Backs Expedition nach Japan und den Bonin-Inseln 1914. *Arkiv för Zoologi* 29A: 1–37.

Jägersten, G. (1939a): Üeber die Morphologie und Physiologie des Geschlechtsapparats und den Kopulationsmechanismus der Myzostomiden. *Zoologiska Bidrag fran Uppsala* 18: 163–242.

Jägersten, G. (1939b): Zur Kenntnis der Larvenentwicklung bei *Myzostomum*. *Arkiv för Zoologi* 31A: 1–21.

Jägersten, G. (1940a): Zur Kenntnis der Morphologie, Entwicklung und Taxonomie der Myzostomida. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 11: 1–84.

Jägersten, G. (1940b): Neue und alte *Myzostomum*-Arten aus dem Zoologischen Museum Kopenhagen. *Videnskabelige Meddelelser Fra Dansk Naturhistorick Forening i Kobenhavn* 104: 103–125.

Jangoux, M. (1990): Diseases of Echinodermata. In: Kinne, O. (ed.), *Disease of Marine Animals*. Vol. III. Biologische Anstalt Helgoland: Hamburg: 439–567.

Jimi, N., Moritaki, T. & Kajihara, H. (2017): Rare endoparasitic *Asteriomyzostomum* (Annelida: Asteriomyzostomidae) from Japan, including three new species descriptions and their phylogenetic position within Myzostomida. *Parasitology International* 66: 841–847.

Kato, K. (1952): On the development of myzostome. *Science Reports of Saitama University* 1: 1–16.

Kronenberg, K. (1997): *Ultrastructureller Vergleich der Epidermisstrukturen von* Pulvinomyzostomum pulvinar *(Graff) und* Myzostoma alatum *Graff (Myzostomida, Annelida)*. Master's thesis. University of Munich: 55 pp.

Lanterbecq, D. & Eeckhaut, I. (2003): Myzostomida from Madagascar, with the description of two new species. *Hydrobiologia* 496: 115–123.

Lanterbecq, D., Rouse, G., Milinkovitch, M.C. & Eeckhaut, I. (2006): Molecular phylogenetic analyses indicate multiple independent emergences of parasitism in Myzostomida (Protostomia). *Systematic Biology* 55: 208–227.

Lanterbecq, D., Bleidorn, C., Michel, S. & Eeckhaut, I. (2008): Locomotion and fine structure of parapodia in *Myzostoma cirriferum* (Myzostomida). *Zoomorphology* 127: 59–68.

Lanterbecq, D., Rouse, G.W. & Eeckhaut, I. (2009): Bodyplan diversification in crinoid-associated myzostomes (Myzostomida, Protostomia). *Invertebrate Biology* 128: 283–301.

Lanterbecq, D., Rouse, G. & Eeckhaut, I. (2010): Evidence for cospeciation events in the host-symbiont system involving crinoids (Echinodermata) and their obligate associates, the myzostomids (Myzostomida, Annelida). *Molecular Phylogenetics and Evolution* 54: 357–371.

Leuckart, F.S. (1827): *Versuch einer naturgemässen Eintheilung der Helminthen*. Neue Akademische Buchhandlung von Karl Gross, Heidelberg, Leipzig: 88 pp.

Leuckart, F.S. (1830): Untitled paragraph n°92. *Isis von Oken* 23: 612–613.

Leuckart, F.S. (1836): In Beziehung auf der Haarstern (Comatula) und *Pentacrinus europaeus*, so wie auf das Schmarotzerthier auf Comatula. *Notizen aus dem Gebiete der Natur- und Heilkunde gesammelt und mitgetheilt von Dr. L.G.V. Froriep* 59: 129–131.

Littlewood, D.T.J., Olson, P.D., Telford, M.J., Herniou, E.A. & Riutort, M. (2001): Elongation factor 1-alpha sequences alone do not assist in resolving the position of the Acoela within the Metazoa. *Molecular Biology and Evolution* 18: 437–442.

Marenzeller, E. von (1895): *Myzostoma asteriae* n. sp., ein Endoparasit von *Asterias* Arten. *Anzeiger der Akademie der Wissenschaften Wien* 18: 192–193.

Mattei, X. & Marchand, B. (1987): Les spermatozoïdes des Acanthocephales et des Myzostomides. Ressemblances et conséquences phylétiques. *Comptes Rendus de la Academie des Sciences, Série III, Sci. Vie, Paris* 305: 525–529.

Mattei, X. & Marchand, B. (1988): La spermiogénèse de *Myzostomum sp.* (Procoelomata, Myzostomida). *Journal of Ultrastructure and Molecular Structure Research* 100: 75–85.

McClendon, J.F. (1906): The myzostomes of the Albatross expedition to Japan. *Bulletin of the American Museum of Natural History* 22: 119–130.

Mecznikow, E. (1866): Zur Entwicklungsgeschichte von *Myzostomum*. *Zeitschrift für wissenschaftliche Zoologie* 16: 236–243.

Müller, M.C. & Westheide, W. (2000): Structure of the nervous system of *Myzostoma cirriferum* (Annelida) as revealed by immunohistochemistry and cLSM analyses. *Journal of Morphology* 245: 87–98.

Nansen, F. (1885): *Myzostomernes Anatomi og Histologi*. John Griegs Bogtrykkerl: Bergen.

Nansen F. 1887. Anatomie und Histologie des Nervensystemes der Myzostomen. *Jenaer Zeitschrift für Naturwissenschaften* 21:267–321.

Nigmatullin, C.M. (1970): *Protomyzostomum cystobium* n. sp. from cysts on the arms and disc of *Gorgonocephalus caryi* Lyman. In: Wagin, V.L. (ed.), *Voprosy Evolvutsionnoi Morfologii i Biogeografii (Questions of Evolutionary Morphology and Biogeography)*. Kazan University Press, Kazan: 50–66. [in Russian]

Okada, Y. (1920): One species of Myzostomida attached to a hexactinellid sponge. *Dobutsugaku Zasshi [Zoological Magazine Tokyo]* 32: 324–325. [in Japanese]

Okada, Y. (1922): On a new *Protomyzostomum* (*P. sagamjense*, sp. nov) from ovary of *Gorgonocephalus*. *Annotes zoologicae Japonica* 10: 165–169.

Okada, Y. (1933): *Mesomyzostoma katoi* n, sp., an interesting myzostome found in the gonad of *Comanthus japonicus*. *Annotes zoologicae Japonica* 14: 185–189.

Pietsch, A. & Westheide, W. (1987): Protonephridial organs in *Myzostoma cirriferum* (Myzostomida). *Acta Zoologica (Stockholm)* 68: 195–203.

Platel, R. (1962): Histologie du tube digestif de *Myzostomum cirriferum* (Leuckart) (Myzostomides). *Cahiers de Biologie Marine* 3: 261–288.

Prenant, M. (1959): Classe des Myzostomides. In: Grassé, P (ed.), *Traité de Zoologie*. Vol. 5. Masson, Paris: 714–784.

Radwanska, U. & Radwanski, A. (2005): Myzostomid and copepod infestation of Jurassic echinoderms: A general approach, some new occurrences, and/or reinterpretation of previous reports. *Acta Geologica Polonica* 55: 109–130.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Rao, K.H. & Sowbhagyavathi, R. (1972): Observations on the associates of crinoids at Waltair Coast with special reference to myzostomes. *Proceedings of the Indian Academy of Sciences B* 38: 360–366.

Remscheid, E. (1918): Beiträge zur Kenntnis der Myzostomiden. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 35: 179–225.

Roman, J. (1952): Quelques anomalies chez *Clypeaster melitensis* Michelin. *Bulletin de la Société Géologique de France, Série 6* 2: 3–11.

Roman, J. (1953): Galles des Myzostomides chez des Clypeastres de Turquie. *Bulletin du Muséum National d'Histoire Naturelle, Série 2* 25: 650–654.

Rota, E., Martin, P. & Erséus, C. (2001): Soil-dwelling polychaetes: Enigmatic as ever? Some hints on their phylogenetic relationships as suggested by a maximum parsimony analysis of 18S rDNA gene sequences. *Contributions to Zoology* 70: 127–138.

Rouse, G.W. (2003): Encounter 2002 expedition to the Isles of St Francis, South Australia: *Myzostoma australe* (Myzostomida), a new crinoid-associated worm from South Australia. *Transactions of the Royal Society of South Australia* 127: 265–268.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Grygier, M.J. (2005): *Myzostoma seymourcollegiorum* n. sp. (Myzostomida) from southern Australia, with a description of its larval development. *Zootaxa* 1010: 53–64.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford.

Ruppert, E.E., Fox, R.S. & Barnes, R.B. (2004): *Invertebrate Zoology, A Functional Evolutionary Approach*. 7th ed. Brooks Cole Thomson, Belmont CA. 963 pp.

Scholtz, G. (2002): The Articulata hypothesis — Or what is a segment? *Organisms, Diversity and Evolution* 2: 197–215.

Seaver, E.C. (2003): Segmentation: mono- or polyphyletic? *International Journal of Developmental Biology* 47: 583–595.

Seaver, E.C., Thamm, K. & Hill, S.D. (2005): Growth patterns during segmentation in the two polychaete annelids, *Capitella* sp. I and *Hydroides elegans*: comparisons at distinct life history stages. *Evolution and Development* 7: 312–326.

Semper, C. (1858): Zur Anatomie und Entwickelungsgeschichte der Gattung *Myzostoma* Leuckart. *Zeitschrift für wissenschaftliche Zoologie* 9: 48–65.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 47: 95–98.

Stummer-Traunfels, R.R. von (1903): Beiträge zur Anatomie und Histologie der Myzostomem. I. *Myzostoma asteriae* Marenz. *Zeitschrift für wissenschaftliche Zoologie* 85: 495–595.

Stummer-Traunfels, R.R. von (1908): Myzostomidae. National Antarctic Expedition. *Natural History* 4: 1–26.

Stummer-Traunfels, R.R. von (1910): Arktische Myzostomen. Mit einem Anhang: Ueber den Bau der Borstendrüsen bei *Myzostoma gigas* Graff. In: Römer, F. & Shaudinn, F. (eds.), *Fauna Arctica*. Vol. 5. Gustav Fischer: Jena: 75–86.

Stummer-Traunfels, R.R. von (1926): Myzostomida. In: Kükenthal, W. & Krumbach, T. (eds.), *Handbuch der Zoologie, 3*. Walter de Gruyter & Co., Berlin: 132–210.

Subramaniam, M.K. (1938): On *Myzostoma gopalai* species nova from the Madras harbour. *Proceedings of the Indian Academy of Sciences Section B* 7: 270–276.

Summers, M.M. & Rouse, G.W. (2014): Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Ecology Biology* 14: 170.

Summers, M.M. & Rouse, G.W. (2015): Erratum: Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Ecology Biology* 15: 53.

Summers, M., Al-Hakim, I. & Rouse, G.W. (2014): Turbotaxonomy: 21 new species of Myzostomida (Annelida). *Zootaxa* 3873: 301–344.

Tautz, D. (2004): Segmentation. *Development and Cell* 7: 301–312.

Terrana,L. and, Eeckhaut I. (2017). "Taxonomic description and 3D modelling of a new species of myzostomid (Annelida, Myzostomida) associated with black corals from Madagascar" *Zootaxa* 4244(2):277–29.

Wagin, V.L. (1954): *Asteromyzostomum* n. gen. — A new representative of the class Myzostomida (Annelides). *Trudy Leningradskogo Obshchestva Yestestvoispytateley* 72: 16–37. [in Russian]

Wang, Y. & Xie, Q. (2014): The molecular symplesiomorphies shared by the stem groups of metazoan evolution: Can sites as few as 1% have a significant impact on recognizing the phylogenetic position of Myzostomida? *Journal of Molecular Evolution* 79: 63–74.

Warn, J.M. (1974): Presumed myzostomid infestation of an Ordovician crinoid. *Journal of Paleontology* 48: 506–513.

Wautier, M. (2009): *Etude morphologique, embryologique et phylogénétique d'une nouvelle espèce de myzostomide cysticole,* Endomyzostoma tenuitectum *n. sp. (Tuléar, Madagascar)*. Master's thesis, University of Mons-Hainaut, Mons, Belgium.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology Evolution* 31: 1391–1401.

Wheeler, W.M. (1896): The sexual phases of *Myzostoma*. *Mitteilungen aus der Zoologischen Station zu Neapel* 12: 227–302.

Wheeler, W.M. (1899): J. Beard on the sexual phases of *Myzostoma*. *Zoologischer Anzeiger* 22: 281–288.

Wheeler, W.M. (1905): A new *Myzostoma* parasitic in starfish. *Biological Bulletin* 8: 75–78.

Willmer, P. (1990): *Invertebrate Relationships. Patterns in Animal Evolution*. New York: Cambridge University Press.

Woodham, A. (1992): Distribution and population studies on *Myzostoma cirriferum* Leuckart (Myzostomida) in a Scottish sea loch. In: Colombo, G., Ferrari, I., Ceccherelli, V.U. & Rossi, R. (eds.), *Marine Eutrophication and Population Dynamics*. Olsen & Olsen, Fredensborg: 247–255.

WoRMS (2019): Annelida. Accessed at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=882 on 2019-12-21

Yakovlev, N.N. (1939): On the discovery of a peculiar parasite of carboniferous sea lilies. *Doklady Akademii Nauk SSSR* 22: 146–148. [in Russian]

Zrzavy, J., Mihulka, S., Kepka, P., Bezdek, A. & Tietz, D. (1998): Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* 14: 249–285.

Zrzavy, J., Hypsa, V. & Tietz, D. (2001): Myzostomida are not annelids: Molecular and morphological support for a clade of animals with anteriorsperm flagella. *Cladistics* 17: 1–29.

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7.11 Errantia: Protodriliformia

Patricia A. Ramey-Balci, Dieter Fiege, and Günter Purschke

7.11.1 Polygordiidae Czerniavsky, 1881

Introduction

Of the about 85 families of marine polychaete worms, Polygordiidae Czerniavsky, 1881 is a unique and interesting group now composed of a single genus, *Polygordius* Schneider, 1868. To date, as few as 21 nominal species and 2 subspecies have been described from the Mediterranean Sea (6 species), Atlantic Ocean (4 species), Indian Ocean (2 species, 1 subspecies), Pacific Ocean (7 species, 1 subspecies), Black Sea (1 species), and Southern Ocean (1 species), but only 18 species are currently regarded as valid (see below). Polygordiidae have been found in sedimentary environments with high porosity from the intertidal zone down to 5000 m depth. They are small, thin worms lacking external signs of segmentation and defining polychaete characters such as parapodia and chaetae. Living animals are transparent or pinkish; some are opaque with an iridescent cuticle. Due to the lack of polychaete characters and their predominant longitudinal musculature, they superficially resemble nematodes. Initially, they were viewed as segmented Gordian worms and named *Polygordius* accordingly (Schneider 1868). Distinguishing morphological characters for species are limited to the shape and the minute structures on the prostomium and pygidium that require detailed examination using scanning electron microscopy (SEM) for the purpose of species descriptions. Earlier descriptions mainly focused on less reliable characters, including color, prostomial "eyespots", body size, number of segments, and arrangement of blood vessels (Ramey et al. 2006). As a result, the identification of *Polygordius* species is difficult. Recent studies suggested that species richness within this group is underestimated (e.g., Ramey et al. 2006, Avery et al. 2009, Ramey-Balci and Ambler 2014). In fact, four species new to science were recently described from the South Pacific (3 species) and North Atlantic, Caribbean Sea (1 species) (Tustison et al. 2020), and two others are in the process of being described, including one species from the South Pacific (Chilean coastline) (Canete et al. unpublished data), and one species from the Indian Ocean (Ramey et al. unpublished data). All species, with a single exception, have been described from sediments composed of a mixture of coarse sand and shells (or shell-hash), and when present, they are often numerically dominant. This association is so characteristic that certain sedimentary subtidal habitats along the European coast are generically referred to as "*Polygordius*-Schill" (sediments primarily composed of shell-hash) (Fig. 7.11.1.1A) (Hagmeier 1930). Larvae of *Polygordius* may be notably abundant in the plankton (e.g., Fewkes 1883, Ritter 1892, Ramey-Balci and Ambler 2014, Cañete et al. 2019), and two distinct forms are exhibited. Lovén (1843) reported the first *Polygordius* by describing the development of a then unnamed planktonic larval annelid. The description of the first adult *Polygordius* 25 years later marked the beginning of a rich and controversial history regarding the systematic placement of the genus with respect to Annelida (reviewed by Hermans 1969). Because of their rather simple organization, Polygordiidae were considered to represent a "primitive state", ancestral with respect to the "Chaetopodes" in Annelida (Hatschek 1878), and were the first group for which the former taxon Archiannelida was created. Alternate views suggested that they may be highly derived or secondarily simplified, but in either case they are well adapted for interstitial life (Hermans 1969, Westheide 1985, 1987, Worsaae and Kristensen 2005, Ramey 2008a).

Morphology

Adults

Polygordiidae have a thin, slender body, cylindrical in cross-section with slight ventral and ventrolateral grooves along the body in certain species (10–100 mm long, <1 mm wide). Because segmentation is poorly visible externally, especially in fixed specimens, they resemble nematodes in appearance. With nematodes, they also share a smooth body surface (Fig. 7.11.1.1D, E). Unlike meiofaunal polychaetes, external ciliation is usually absent, with the exception of a densely ciliated pygidium in *P. jouinae* (see Ramey et al. 2006). Cilia belonging to the nuchal organs and the scattered receptor cells are generally present (Fig. 7.11.1.2A, B). Most likely, these scattered cilia belong to collar receptors distributed unevenly over body and palps, the only type of receptor cell found in polygordiids so far (Figs. 7.11.1.2B, 7.11.1.3D) (Purschke 2005, Wilkens and Purschke 2009). This pattern is rather unusual for annelids that generally possess a high diversity of different receptor cell types (Purschke 2005). Parapodia and chaetae are absent. The prostomium is rounded or conical with two short palps directed frontally (Fig. 7.11.1.1F, G). The nature of these anterior appendages has been uncertain for a long time, and several terms have been applied (Fauchald and Rouse 1997, Rota and Carchini 1999), but from the innervation pattern it is evident that they in fact represent palps (Wilkens and Purschke 2009). These are solid, lack blood vessels, coelomic cavities, and musculature, and thus

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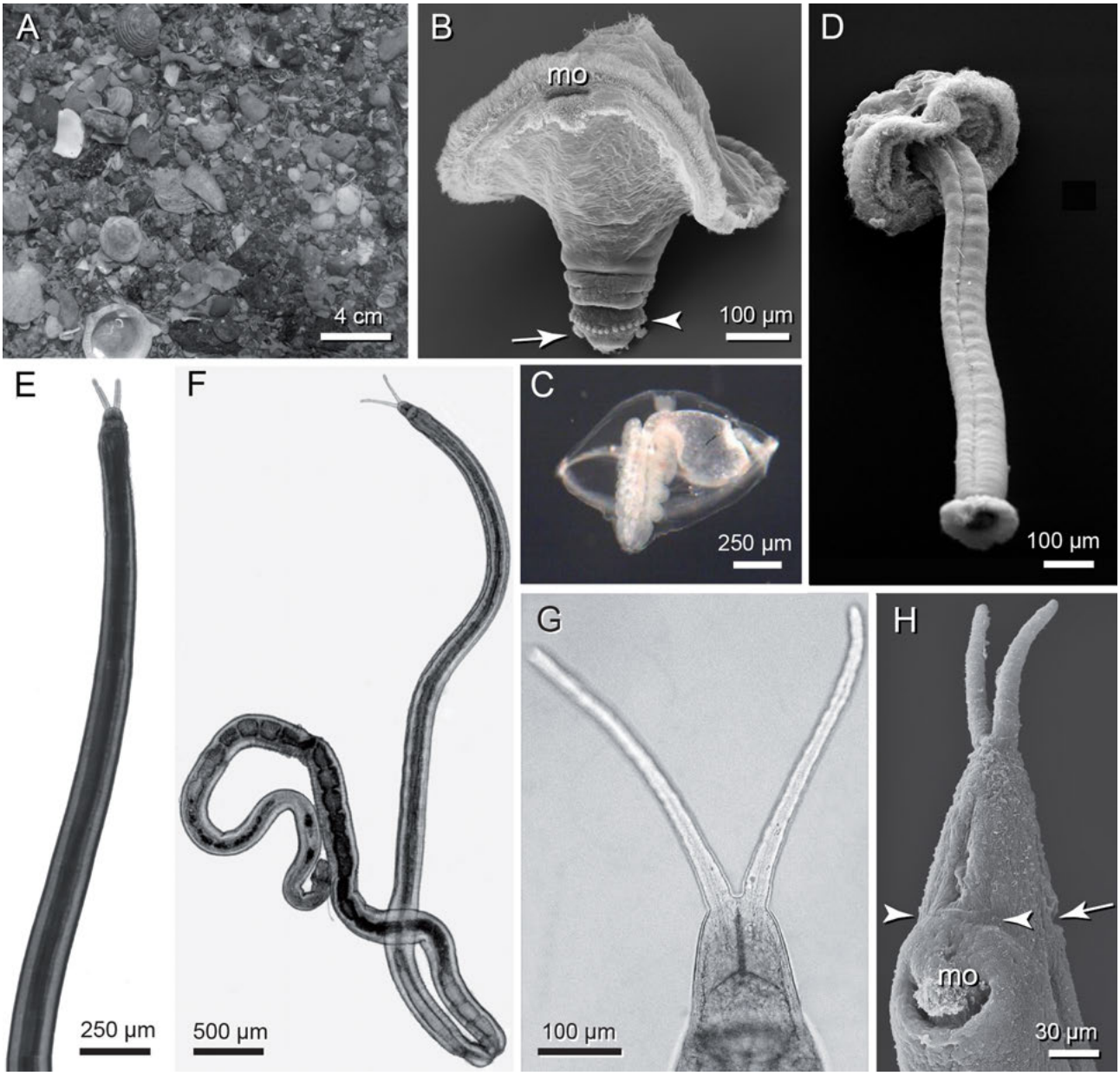


Fig. 7.11.1.1: A, "*Polygordius*-Schill" (shell-hash) (Primel, near Roscoff, Brittany, France: 48°43.306 N, 3°51.015 W, 20 m depth); B, C, *Polygordius* sp. endolarvae (Chincoteague, Virginia, Mid-Atlantic Bight, USA); B, SEM lateroventral view with highly folded worm trunk partially visible (trunk segments usually completely covered by hyposphere), mouth (mo) lined by prototroch and metatroch, posterior ring of pygidial glands (arrowhead) and pygidial cirri (arrow); C, lateral view with folded worm trunk visible through the hyposphere; D, *Polygordius jouinae* exolarvae (Chincoteague, Virginia, Mid-Atlantic Bight, USA), SEM lateral view showing segmented worm trunk emerging medially from bell-shaped episphere and hyposphere; E, *Polygordius lacteus* (syn. *Polygordius erythrophthalmus*) (Beg Meil, Brittany, France), anterior end; F, G, *Polygordius appendiculatus* (Helgoland, North Sea), live specimen; F, Complete specimen (immature); G, Anterior end with paired palps, ventral view; H, *P. jouinae* (Tuckerton, New Jersey, Mid-Atlantic Bight, USA) SEM of anterior end, ventral view showing mouth (mo), headfold (arrowheads), and nuchal organ (arrow).

are purely sensory and therefore cannot be classified as grooved palps (see Fauchald and Rouse 1997, Rouse 2001). Pigmented eyes are absent. Red pigment spots in the prostomium of *P. lacteus* (syn. *P. erythrophthalmus* Giard, 1880) are pigment-containing coelomocytes. Prostomium and peristomium are separated by a more or less pronounced perpendicular head fold in front of the mouth (Fig. 7.11.1.1G, H) (Hempelmann 1906, Rota and Carchini 1999). The heavily ciliated nuchal organs form oval slits positioned slightly oblique to body axis, dorsolaterally at

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the base of the prostomium; their general ultrastructure is similar to that of other polychaetes (Purschke 1997, Wilkens and Purschke 2009). The cuticle is comparatively thick and houses several layers of parallel, prominent collagen fibers in a fine fibrillar matrix different from cuticles found in most other interstitial polychaetes (Fig. 7.11.1.3B, C) (Hempelmann 1906, Rieger and Rieger 1976, Purschke 2002, Hausen 2005). These collagen fibers are responsible for the iridescent appearance of most species due to interference effects. The cuticle in polygordiids is traversed by numerous microvilli that extend far beyond the cuticular surface, and these microvilli form the slightly rough and fibrillar appearance of the body surface in SEM (Figs. 7.11.1.3B, 7.11.1.4I). The epidermis is equipped with mucous glands all over the body. The musculature is mainly composed of longitudinal fibers arranged in four functional groups, including two dorsal and two ventral groups. Circular musculature is either weakly developed or entirely absent (Fig. 7.11.1.3A) (Hempelmann 1906, Hermans 1969, Tzetlin and Filippova 2005). Numerous segmental bundles of oblique muscles run from midventral to midlateral. Groups of longitudinal fibers mainly act as antagonists and are the reason for the nematode-like movements. The longitudinal fibers extend as smaller bundles into the anterior end, pass the nuchal organ and the brain, and almost reach the bases of the

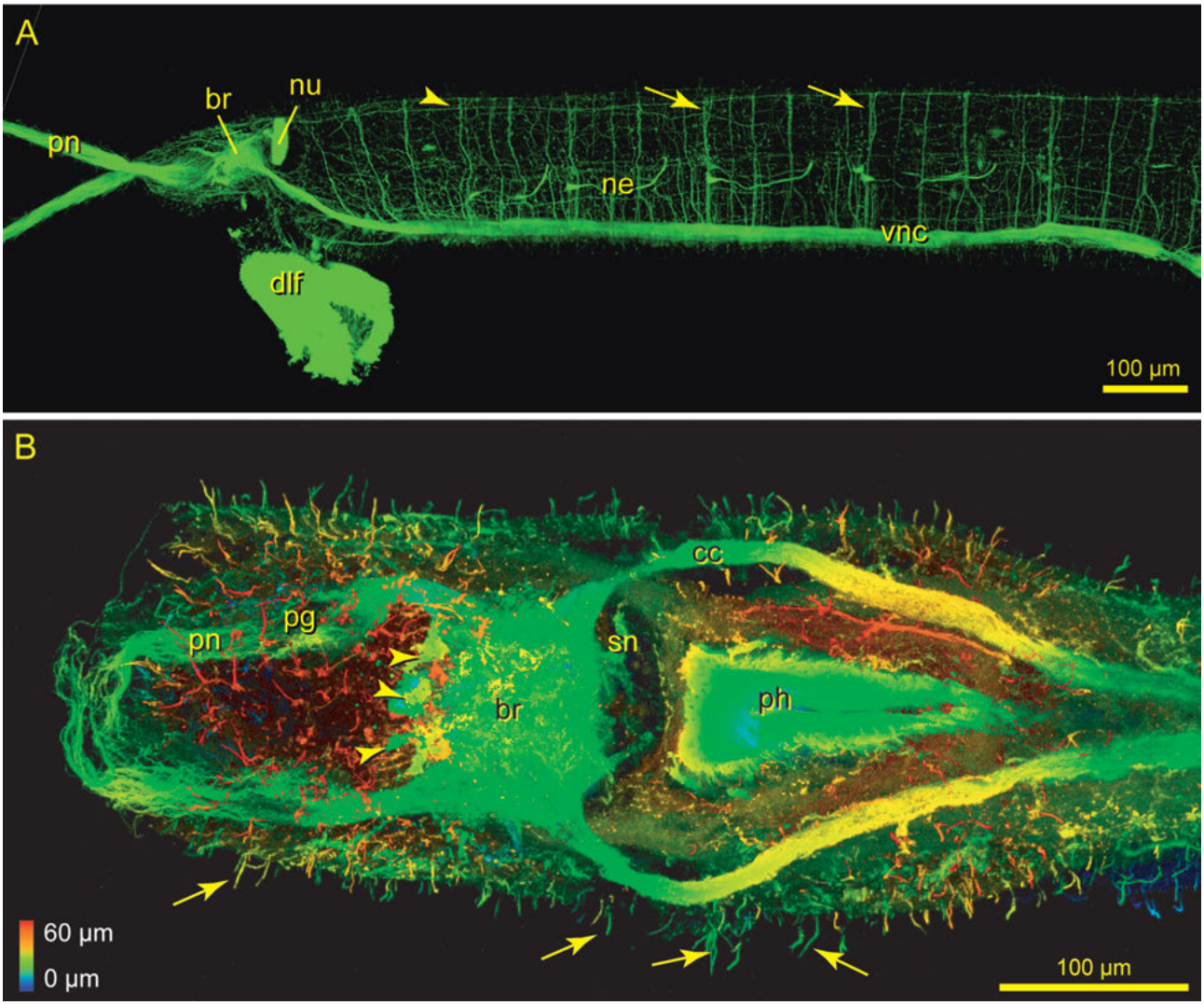


Fig. 7.11.1.2: *P. appendiculatus*. Laser scanning microscopy images after staining with antibodies against acetylated α-tubulin showing the nervous system. A, Lateral view with neuropil of the brain (br), nuchal organ (nu), palp nerves (pn), ventral nerve cord (vnc), nephridia (ne), and protruding dorsolateral folds of the pharynx (dlf). In each segment, a number of segmental nerves arise from the ventral cord in a clearly repetitive pattern (arrows). Arrowhead, dorsal longitudinal nerve; B, Close-up of the brain and circumesophageal connectives (cc) in ventral view. Note numerous unciliated receptor cells distributed over the body surface (arrows). Arrowheads point to a few photoreceptor-like sense organs situated in front of the neuropil of the brain (br). pg, palp ganglion; ph, pharynx; sn, stomatogastric nerve. Originals: A, C. Lehmacher, Osnabrück; B, V. Wilkens, Osnabrück.

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palps, the dorsal pair being longer than the ventral one (Lehmacher et al. 2014). The prostomium contains the brain and two palp ganglia situated anteriorly and two nuchal ganglia posteriorly (Figs. 7.11.1.2A, B). Numerous photoreceptor-like sense organs lie in front of the brain in *P. appendiculatus* and *P. lacteus* and eventually in all species (Fig. 7.11.1.2B) (Wilkens and Purschke 2009, Lehmacher et al. 2016). These are composed of one supportive and usually several sensory cells, the latter comprising rhabdomeric and ciliary photoreceptors variously combined to form several types of sense organs (Lehmacher et al. 2016). Lehmacher et al. (2016) showed that these organs provide useful taxonomic characters in *Polygordius*. The circumesophageal connectives leave the brain as a pair of single cords and separate into dorsal and ventral roots within the neuropil of the brain (Orrhage and Müller 2005, Wilkens and Purschke 2009). These connectives form a wide arc around the mouth and unite ventrally to form a single, compact ventral nerve cord running posteriorly between the ventral longitudinal muscle bundles (Fig. 7.11.1.2A, B). In *P. appendiculatus*, in each segment, the ventral nerve cord gives rise to five larger and several smaller segmental nerves running circularly around the body (Fig. 7.11.1.2A). In addition to the ventral cord, a pair of lateral and a pair of dorsolateral longitudinal nerves pass down the trunk directly from the brain. In species studied anatomically, segmental ganglionic swellings along the ventral nerve cord were not found, although sometimes a distinct subesophageal ganglion is reported for certain species (e.g., Rota and Carchini 1999). However, if labeled with specific antibodies against neurotransmitters, groups of neuronal somata showing a ganglionic arrangement become apparent in the nerve cord of late larvae (Hay-Schmidt 1995). The pygidium has a preanal nerve ring lying underneath the girdle of adhesive glands probably innervating the glands (Hempelmann 1906, Fraipont 1884b).

The intestinal tract forms a strait tube and is divided into pharynx, esophagus, intestine, and rectum. The different sections are not separated by distinct borders; pharynx and esophagus may be distinguished by the presence or absence of a cuticle, but this has not been studied. The intestine bears a characteristic ventral ridge carrying longer cilia. The rectum with its lower epithelium comprises longitudinal folds and no gland cells (Hempelmann 1906). A distinct muscular eversible pharynx (proboscis) is absent, but the mouth cavity is supplied with prominent densely ciliated protrudable dorsolateral folds (Fig. 7.11.1.2A) and a ventral pharyngeal sac directly behind the mouth (Fraipont 1887, Purschke and Tzetlin 1995). The pharynx continues into the esophagus without a distinct border. Although the pharyngeal musculature is poorly developed, a sphincter and retractor muscle fibers are present in the pharyngeal regions. Gland cells are dispersed among the epithelial cells without the formation of distinct and compact salivary glands or other accessory organs (Hempelmann 1906).

Coelomic cavities, mesenteries, and muscular septa are well developed throughout the trunk. The coelom is displaced to the periphery in the buccal region and first segment by a peripharyngeal cavity around the esophagus (Hempelmann 1906). A similar cavity is present around the rectum. The circulatory system is closed and well-developed. A dorsal longitudinal blood vessel bifurcates into a pair of lateral loops at the base of prostomium; these run ventrally backward and unite to form the ventral vessel (Fig. 7.11.1.4A, B). The dorsal blood vessel gives rise to segmental lateral loops; in reproductive segments, these lateral vessels possess blind-ending branches next to the gonads during sexual maturity. A dorsal intestinal blood sinus has been observed in mature animals (Hempelmann 1906, Rota and Carchini 1999). The blood is red, green, or yellow (Remane 1932). Formerly, the structure of the blood vascular system has been used as an important taxonomic character (e.g., Jouin 1970, Rota and Carchini 1999), but its value has been overestimated (see Ramey et al. 2006 for discussion). Excretory organs are metanephridia (Fig. 7.11.1.2A); the first pair is formed by the fusion of the second pair of larval protonephridia with the first pair of metanephridia (Fraipont 1884a, Hempelmann 1906).

A high number of fertile segments is found in both males and females, starting in the first quarter of the body. No genital ducts are present, indicating that the release of gametes is achieved by rupture of the body wall. The spermatozoa comprise a spherical nucleus, a conical acrosome, and a midpiece with four to five spherical mitochondria (Fig. 7.11.1.4C) (Franzén 1974, 1977; i.e., ect-aquasperm of Jamieson and Rouse 1989). In females, relatively large numbers of small eggs (1000s; 22–62 µm; *P. jouinae*) are tightly packed in the coelom and appear clear and irregular in shape when observed in live specimens (Fig. 7.11.1.4D) (Ramey et al. 2006, Ramey 2008b).

In most species, the pygidium is encircled with numerous adhesive glands creating a distinct ring or preterminal inflation where the number, shape, and orientation of glands vary among species and are frequently used diagnostic characters for species distinction. In certain species, the pygidium bears terminally or subterminally (i.e., between pygidial glands and anus) positioned appendages often referred to as pygidial or anal cirri (up to 15). The anus is terminal and often bordered by a number of anal lobes (Fig. 7.11.1.4E–I).

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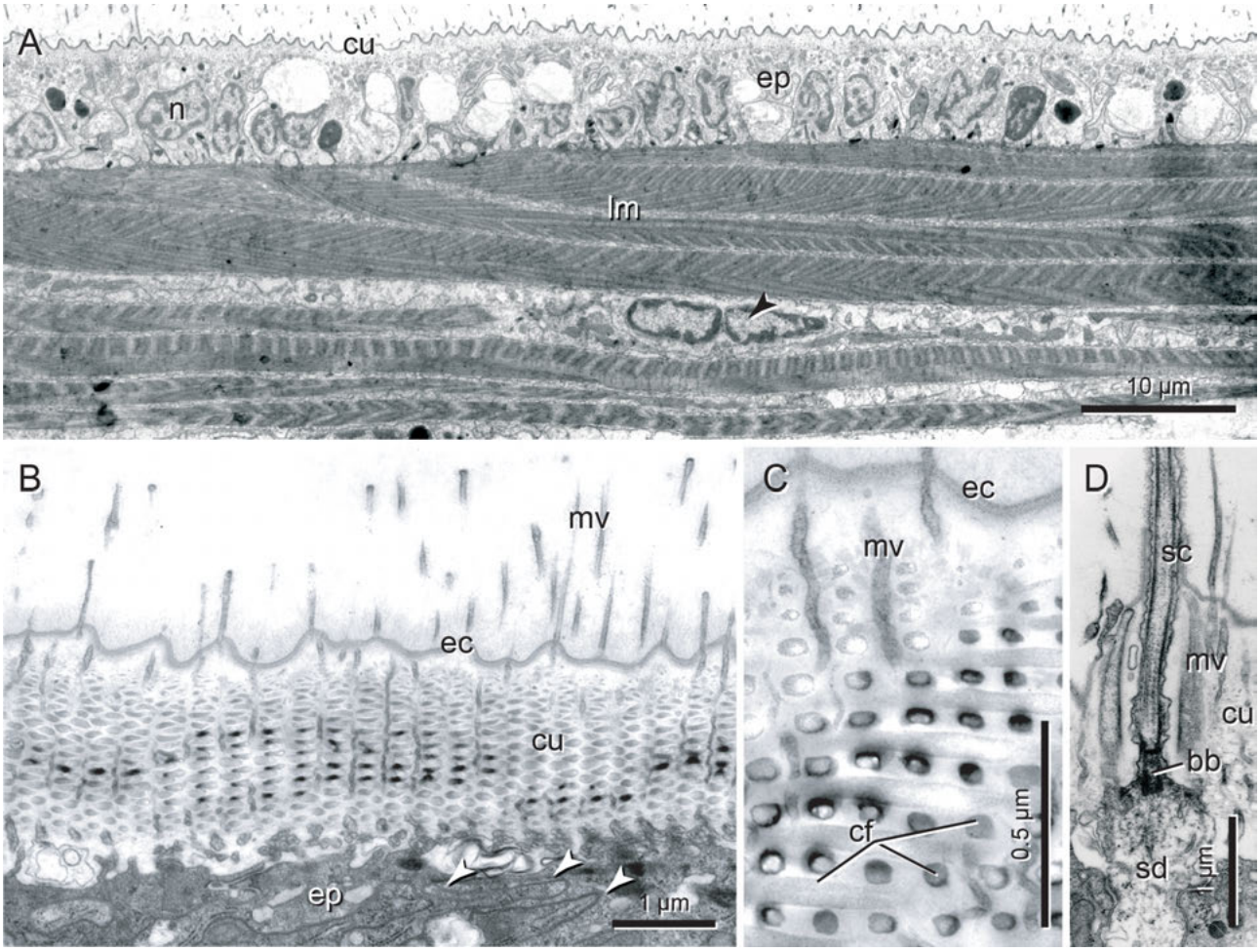
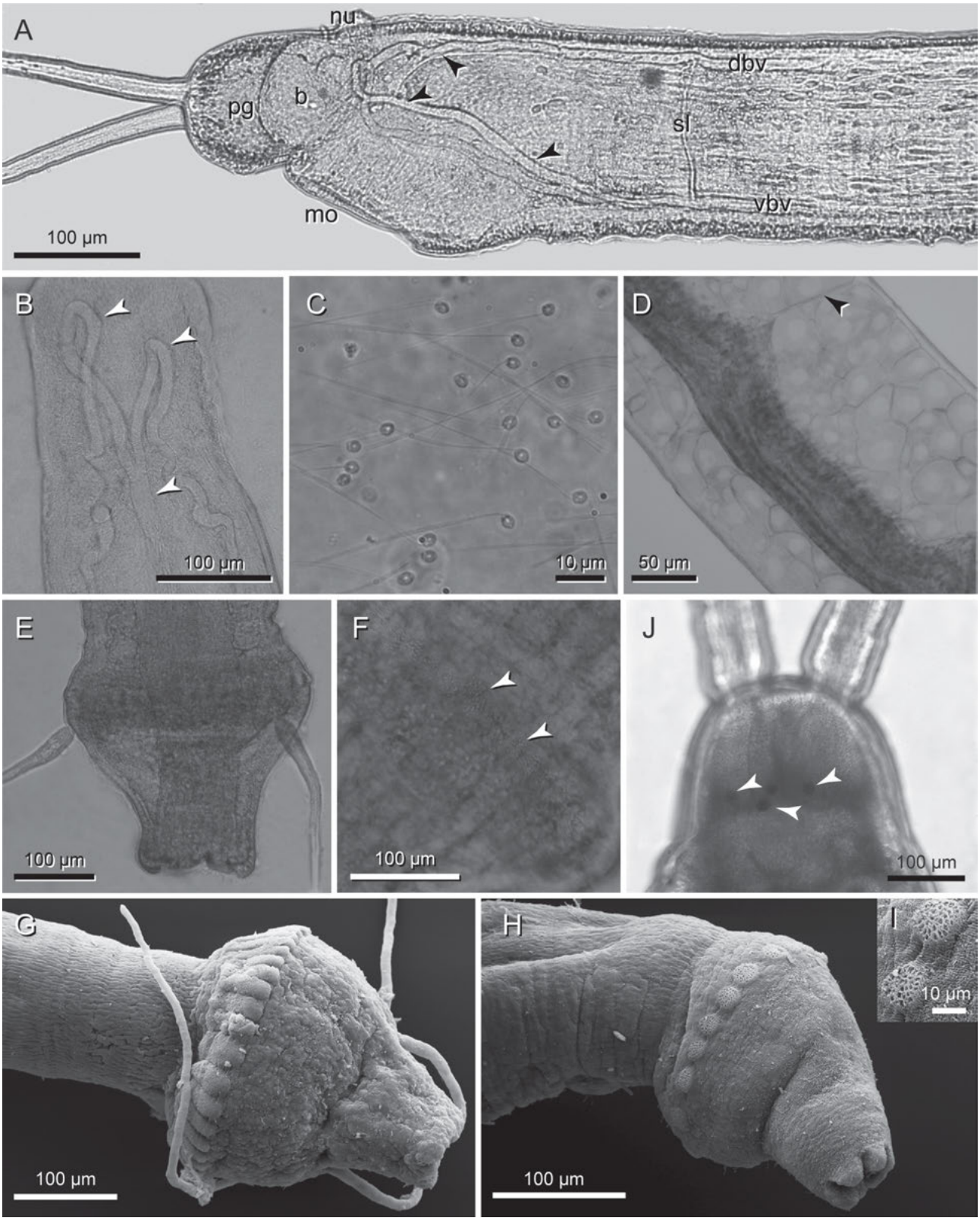


Fig. 7.11.1.3: Transmission electron microscopy (TEM) of cuticle and body wall. A, *P. jouinae*. Longitudinal section through body wall showing cuticle (cu), epidermis (ep), and thick layer of longitudinal muscle fibers (lm). Note the absence of circular muscle fibers; the section shows numerous nuclei (n) of epidermal cells but only two belonging to muscle fibers (arrowhead); B, C, *P. lacteus*, details of cuticle; B, Cuticle (cu) with several layers of collagen fibers (cf), traversed by numerous microvilli (mv) that extend beyond the epicuticle (ec). Arrowheads point to highly convoluted membranes of adjacent epidermal cells; C, Cuticle with epicuticle (ec) and layers of parallel collagen fibers (cf) crossing at about 90°; D, *P. appendiculatus*. Apex of collar receptor; sensory dendrite (sd) with a single cilium (sc) surrounded by a collar of strong microvilli (mv); note the absence of a ciliary rootlet. bb, basal body; sc, sensory cilium; sd, sensory dendrite. Originals: A, B. Leander, Vancouver; B, C, C. Lehmacher, Osnabrück.

Live specimens are transparent to opaque depending on body size. Sexually mature individuals usually show a reddish hue due to enlarged blood sinuses; females appear transparent to white, whereas mature males are milky white due to spermatozoa (Ramey et al. 2006). The cuticle is iridescent in certain species. The presence or absence of pigmented prostomial spots predominantly on the head anterior to the brain feigning eyes is highly variable among individuals and species (e.g., *P. lacteus*) (Fig. 7.11.1.4J). These pigment spots are due to pigment-containing coelomocytes.

▸ **Fig. 7.11.1.4:** A, B, Blood vessels; A, *P. appendiculatus* (Roscoff, Brittany). Lateral view of anterior body showing unpaired dorsal (dbv), ventral blood vessels (vbv), anterior loops (arrowheads), and segmental loop in the first segment (sl); specimens slightly squeezed so that nuchal organs (nu) and mouth (mo) protrude, brain (b), and palp ganglion (pg); B–D, *P. jouinae*; B, Dorsal view of anterior body showing anterolateral loops or circumesophageal blood commissures and dorsal blood vessel (arrowheads); C, Sperm; D, Body cavity full of eggs; arrowhead points to septum; E–I, Pygidia showing preterminal inflation with ring of glands and pair of pygidial cirri; E, F, *P. appendiculatus* (Helgoland, North Sea); E, Overview; F, Details of E showing openings of adhesive glands (arrowheads); G–I, *Polygordius* spp. undescribed; G, H, Pygidia, lateral views; I, Details of H showing openings of pygidial glands in distinct plaques and fibrillar appearance of body surface; J, *P. lacteus* (syn *P. erythrophthalmus*) (Beg Meil, Brittany, France). Anterior end with irregular red pigment spots often mistaken as eyes (arrowheads). Original: A, M. Stüeken, Osnabrück.

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Larvae

Trochophore larvae (650–750 µm long, 550–650 µm wide) possess a hemispherical anterior episphere and a conical posterior hyposphere (Sensenbaugh and Franzén 1987). The prototroch runs around the widest part of the body just anterior to the mouth, whereas the metatroch is situated slightly posterior to it (Fig. 7.11.1.1B). The episphere of young larvae bears a central round apical organ comprising a nerve plexus, pigmented ocelli (eyes), and unpigmented photoreceptor-like structures described as phaosome photoreceptor cells by Sensenbaugh and Franzén (1987). However, from their description, it is evident that it is not a true phaosome, i.e., a single receptor cell with an intracellular vacuole, but rather the photoreceptor-like sense organ as described above for the adults (Wilkens and Purschke 2009). Obviously, the first of these structures are formed early in ontogeny, and new organs of this type are added continuously when development proceeds. Single and/or aggregated cilia are present, but an apical tuft is only observed in early trochophores (Woltereck 1905). Palpal knobs appear later in development but have been observed in early trochophores by Sensenbaugh and Franzén (1987). The apical organ is distinctly set off from the surrounding epidermis. In trochophores of *Polygordius* cf. *appendiculatus*, the ocelli consist of two pigmented supportive cells and a rhabdomeric photoreceptor cell, whereas in the segmented larvae an additional sensory cell is formed (Brandenburger and Eakin 1981). Later in development, these ocelli are lost as neither pigmented ocelli nor traces thereof have been found in adults (Lehmacher et al. 2016). The hyposphere bears a ciliated food groove between prototroch and metatroch, which runs into the ventral mouth opening (Fig. 7.11.1.1B) (see also Ramey-Balci and Ambler 2014). The intestinal tract is bent 90° toward the posterior end and consists of a pharynx, wide stomach, intestine, and anus. The posterior end is equipped with a telotroch around the anus in exolarvae, which is absent in endolarvae (Ramey-Balci and Ambler 2014). The body cavity (blastocoel) is crossed by muscle strands and contains one pair of protonephridia. Development was described in detail by Shearer (1908), and the ultrastructure of exolarvae was studied by Smith and Ruppert (1988). The larval nervous system was described by Fraipont (1884b) for *Polygordius neapolitanus* Woltereck, 1902, Janowsky (1905) for *Polygordius triestinus*, and Hay-Schmidt (1995) for *P. lacteus* as consisting of an apical ganglion, a pair of lateral nerves, a pair of prototroch nerves, a metatroch nerve with an oral nerve plexus, a ventral ganglion, and a paired ventral nerve cord. The larval musculature was described by Hatschek (1886) and Janowsky (1905) for *P. triestinus*.

The larvae are transparent with occasional brown or yellow pigmented prototroch cells.

Biology and ecology

Polygordiidae are found worldwide in intertidal, shallow subtidal/continental shelf and most recently in continental slope sediments at depths from 1000 to 5000 m in Antarctic waters. Although they occupy a broad range of environments, they have a strong habitat affinity for highly energetic areas with coarse grained sediments at both global and local scales (Ramey 2008a, b). These worms are often considered part of the meiofaunal community because they spend their postsettlement life living interstitially among the sediment grains. Therefore, they have often been ignored in macrofaunal community studies (Grassle et al. 2009); however, their size (10–100 mm long, 0.08–1.5 mm wide) makes them part of the macrofaunal community as it is usually defined (organisms retained on a 0.5 mm mesh sieve). This is likewise reflected by their reproductive biology, which does not show any character typical of meiofaunal polychaetes such as direct development, modified sperm, or direct sperm transfer (see Westheide 1984, 1987). Due to their elongated body shape, relatively strong cuticle, and mode of movement, they somewhat resemble and have also been mistaken for large nematodes. *Polygordius* is a subsurface deposit feeder, feeding on sedimentary particulate organic matter (POM) derived from organic-rich flocs containing phytodetritus, decomposing macroalgae, fecal pellets, microorganisms, and, to a lesser extent, seagrass and land-derived detritus (Ramey and Bodnar 2008). The intestine of Polygordiidae has been reported to be infected with parasites (e.g., Fraipont 1887, Rota and Carchini 1999, Leander and Ramey 2006, Ramey et al. 2006).

Limited knowledge of the behavior and general ecology of Polygordiidae mainly comes from studies of *P. jouinae* Ramey, Fiege & Leander, 2006 on the inner continental shelf off New Jersey, USA (Ramey et al. 2006, 2009, Ramey 2008a, b; Ramey-Balci and Ambler 2014). Live observations indicated that this worm displays several behaviors that are particularly well suited to living in highly mobile sediments that are frequently resuspended into the water column. *Polygordius* is able to swim by lateral undulations of the body (Clark and Hermans 1976), but when disturbed it quickly curls into a tight ball, allowing it to fall more rapidly to the sediment surface following resuspension, and on contact with sediment, it moves rapidly into the sediment interstices (Ramey 2008b). Moreover, glands on the pygidium function to anchor the worm to the sediment, as originally observed

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by Schneider (1868) in *P. lacteus* Schneider, 1868 (see Ramey-Balci et al. 2018, supplementary materials 1 and 2 video). *Polygordius* can reach densities as high as 10,942 individuals 0.04 m^{-2} (0.5 mm mesh sieve) (Ramey et al. 2011) and often makes up more than 50% of the macrofaunal community (Ramey et al. 2006). Density has been shown to be significantly, positively correlated with the proportion of medium to very coarse sand and negatively correlated with fine sand (Ramey et al. 2006). The relatively large size of this species (sexually mature adult body, 13–43 mm long and 0.23 to 0.38 wide) likely allows it to move with relative ease through coarse but not finer sediments. Patterns in distribution have been shown to be extremely patchy in time (i.e., seasonally and yearly) and in space, especially at small spatial scales of less than 1 m (Ramey 2008a, b, Ramey et al. 2009). Higher abundances of *P. jouinae* are associated with microhabitat features such as sandy rippled beds influencing the concentration of POM/food resources, with higher and more variable densities of this species in ripple troughs compared to crests (Ramey and Bodnar 2008). This small-scale distribution pattern is established by an interaction between the behavior of the worm and the effects of unidirectional, near-bottom, and Brinkman-layer flows on the distribution and concentration of POM within the sediments (Ramey and Bodnar 2008). Experiments under ambient flow conditions in a laboratory flume showed significant subsurface movement of this species to sediment patches containing higher amounts of POM in 48 hours. Although locating organic patches was not the consequence of a directed search, worms that located organically richer patches remained there and fed. The rate of movement in sediments indicated that *P. jouinae* could potentially travel the wavelength of a typical ripple (14–30 cm) in 35 to 75 minutes (Ramey and Bodnar 2008).

The population dynamics and life history traits of Polygordiidae have been studied in *P. lacteus* and *P. appendiculatus* Fraipont, 1887 in the North Sea (Nordheim 1984) and *P. jouinae* in the northwestern Atlantic (Ramey 2008a, b). Most Polygordiidae are gonochoristic; sexual dimorphism has not been observed. Reports of a single species, *P. triestinus* Hempelmann, 1906, as being hermaphroditic has been questioned (Westheide 2008). Compared to other interstitial polychaetes, *Polygordius* produces relatively large numbers of gametes, which develop in segments throughout the entire body, starting at segments 15 to 70 depending on the species and sex (Rota and Carchini 1999, Ramey 2008b). Sperm structure is consistent with external fertilization (Franzén 1977) via broadcast spawning. Swarming behavior has only been observed for *Polygordius epitocus* Dawydoff, 1905 off the coast of New Guinea (Dawydoff 1905). Some species reproduce once a year being monotelic, whereas others are polytelic and reproduce several times a year. Gametes are believed to be set free through rupture of the body wall, as gonoducts have not been observed (Hempelmann 1906, Ramey et al. 2006). *P. jouinae* and *P. appendiculatus* are generally thought to die after spawning, having a 1-year life span. Nonspawning individuals of *P. jouinae*, however, can potentially live longer than 1 year, with populations consisting of two generations for a short period of time, as sexually mature individuals kept alive in static laboratory cultures indicated that they can resorb their gametes (Ramey 2008a). In contrast, *P. lacteus* likely survives spawning, living for more than 1 year, as only the posterior segments are believed to rupture and then regenerate (Hempelmann 1906). A North Sea population of *P. lacteus* was found to contain multiple generations, exhibited by a wide range of body lengths (Nordheim 1984).

The development in Polygordiidae is indirect with a planktotrophic larval phase that can last for several weeks up to a month (Ramey-Balci and Ambler 2014). Depending on the species, a metatrochophore in the form of either an endolarva (e.g., *P. lacteus* and *P. appendiculatus*) (Fig. 7.11.1.1B, C) or an exolarva (e.g., *P. neapolitanus* Fraipont, 1887, *P. jouinae*, and *P. triestinus*) (Fig. 7.11.1.1D) is formed from a trochophore (Woltereck 1905, Schroeder and Hermans 1975). The structure and development of these larvae differ greatly. For example, in the endolarval form, the developing worm or trunk of the worm remains folded up inside the hyposphere until metamorphosis occurs (Lovén 1843, Woltereck 1902, Ramey-Balci and Ambler 2014), whereas in the exolarva the worm trunk is gradually elongated by the addition of new segments posterior to the hyposphere (Hatschek 1878, Ramey-Balci and Ambler 2014, Cañete et al. 2019). According to Hatschek (1878), who studied *Polygordius* larvae collected at Triest in early 1877, the metamorphosis of these can be divided into six phases: (1) young larva, (2) older larva, (3) beginning of morphological changes (tentacles become visible, unfolding of the worm trunk), (4) extension of the worm trunk, (5) transformation of the anterior end, and (6) young *Polygordius*. Whether metamorphosis is a gradual process of development or a "catastrophic" event caused a controversial debate between Söderstrom (1924a, b, 1925) and Woltereck (1924, 1925, 1926). Herrmann (1986) produced a film showing metamorphosis to be a gradual process interrupted by resting periods. The metamorphosis in *P. lacteus* and *P. appendiculatus* (both from Helgoland) lasts about 2 hours (Herrmann 1986). In temperate regions, the reproductive period of *Polygordius* usually begins in May and extends to August or as late as October depending on the species/location. Along the coast of New Jersey, sexually mature individuals of *P. jouinae* were 13 to 43 mm long, and

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the recruitment from the plankton to the benthos begins no later than July (Ramey 2008a). The smallest individual recorded was 2 mm long and 0.07 mm wide (fixed specimen) and provided the first estimate of size at initial recruitment. A combination of life history traits, such as high numbers of planktotrophic larvae and rapid development along with their dispersal ability and habitat selection, likely contribute to the widespread distribution and community dominance of *P. jouinae* (Ramey 2008a).

Because Polygordiidae exhibit such a strong habitat affinity, they may be an important indicator of changing environmental conditions. Changes in sediment composition and concomitant increases in organic loading have been shown to affect the abundance and distribution of *P. jouinae* (Ramey et al. 2006, Ramey 2008a, b, Ramey and Bodnar 2008). Moreover, temporal patterns of abundance of this species from two systems at the northern and southern ends of its known distribution along the northeastern United States reveal similar long-term trends. Preliminary analysis suggested that these trends are related to large-scale oceanographic processes and climate variability resulting from phenomena such as the North Atlantic Oscillation or the Atlantic Multidecadal Oscillation (Ramey 2008c, Schofield et al. 2008). At much smaller scales, these worms likely have a major impact on sediment biogeochemistry occupying the interstices of sandy sediments and being highly motile deposit feeders (Ramey and Bodnar 2008).

Taxonomy and phylogeny

Phylogeny

Current cladistic (Rouse and Fauchald 1997, reviewed by Rouse and Pleijel 2006) and molecular polygenetic (reviewed by McHugh 2005, Rousset et al. 2007) approaches have not specifically targeted *Polygordius* species in their annelid phylogenetic analyses, and the systematic placement of Polygordiidae within Annelida remained unresolved (Wilkens and Purschke 2009). However, later on, certain molecular phylogenetic evidence was provided (although no statistical support) that *Polygordius* diverged early relative to most other annelid lineages (Struck et al. 2002, 2014, Struck 2011). Since then, the first phylogenomic studies were conducted, revealing a more reliable picture of the evolutionary history of annelids (Andrade et al. 2015, Struck et al. 2015, Struck 2019). These studies constantly found a taxon, Protodriliformia comprising Polygordiidae and Protodrilida with Saccocirridae, Protodrilidae, and Protodriloididae being the sister group of Eunicida and Phyllodocida within Errantia (Struck et al. 2015). Thus, *Polygordius* may represent another important example of morphostasis (unchanging morphological features), such as what has recently been shown to be the case for *Stygocapitella* spp. (Parergodrilidae and Pleistoannelida) (Cerca et al. 2020a, b) and provide insights into the early stages of annelid evolution. Several gene sequences for a few *Polygordius* species are available in GenBank (Struck et al. 2002, 2015, Ramey et al. 2006, Rousset et al. 2007, Andrade et al. 2015, Ramey-Balci et al. 2018).

Based on morphological data, *Saccocirrus*, *Protodrilus*, and Opheliidae have been hypothesized as being the closest relatives or sister groups to Polygordiidae (Giard 1880, Fraipont 1887, Hatschek 1893, Goodrich 1901; see Hermans 1969). As in Opheliidae, Polygordiidae almost lack circular musculature (Fraipont 1887, Rota and Carchini 1999), which has been hypothesized to be a plesiomorphic or ancestral state for Annelida (Tzetlin et al. 2002, Tzetlin and Filippova 2005). Alternative views suggested that the absence of key polychaete characteristics is derived. In either case, *Polygordius* species are well adapted for interstitial life (Hermans 1969, Westheide 1985, 1987, Worsaae and Kristensen 2005). In the cladistic analyses of Rouse and Fauchald (1997), the paired palps at the tip of the prostomium of *Polygordius* species [sometimes referred to as antennae (e.g., Fauchald 1977, Rota and Carchini 1999, Ramey et al. 2006) or tentacles (e.g., Westheide 1990, Hartmann-Schröder 1996, Paxton 2000)] were interpreted as being grooved feeding palps, as in most polychaetes belonging to the clade Canalipalpata (Rouse and Fauchald 1997). Although these structures are indeed palps without any doubt, they are atypical for such palps because they are not grooved and do not comprise coelomic cavities or ciliary tracts (see Wilkens and Purschke 2009). The original scoring error by Rouse and Fauchald (1997) was later realized by Rouse (2001). However, *Polygordius* was still considered as unplaced in Canalipalpata by the latter author.

Since the rejection of the archiannelid concept (see Fauchald 1977), *Polygordius* has usually been regarded as a rather isolated taxon of uncertain affinity by most morphologists, whereas different phylogenetic hypotheses were provided for the remaining former archiannelid taxa (Westheide 2008). Similarities with Protodrilida have been regarded as homoplastic due to similar selection pressures in similar environments. This was supported by recent ultrastructural studies, which again did not reveal synapomorphies with Saccocirridae but structural similarities with Opheliidae; thus, a relationship with the latter cannot be excluded (see Wilkens and Purschke 2009). Interestingly, and in contrast to these observations, molecular data have not revealed a relationship with opheliids but instead reintroduced a Polygordiidae-Saccocirridae relationship (Struck et al. 2002, 2008, Struck and

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Purschke 2005, Zrzavy et al. 2009). However, statistical support for this relationship was low or even lacking; therefore, it was uncertain whether this grouping is artificial. Although none of these taxa were included in the first contribution based on phylogenomic data (Struck et al. 2011), *Polygordius* and *Saccocirrus* (as well as the remaining Protodrilida) might alternatively be part of the basal radiation in the annelid tree before the formation of Pleistoannelida comprising the majority of Annelida (Struck 2011). However, all current phylogenomic analyses, including data from Polygordiidae, Saccocirridae, Protodrilidae, and Protodriloididae, found them as monophyletic clade in a basal position within Errantia (Andrade et al. 2015, Struck et al. 2015, Struck 2019).

Taxonomy

Polygordius species are unique in their lack of defining polychaete characters, such as parapodia, and chaetae. Hatschek (1878) considered them to be primitive forms close to a common ancestor of the Annelida and created the taxon Archiannelida for them. The endolarva was described by Lovén (1843). Its earliest stage was later termed "Trochophora" by Hatschek (1878). Noting that several phyla had trochophore larvae, Hatschek proposed the "Trochozoon" as the hypothetical ancestor of many metazoan taxa with trochophore-like larvae. The first adult species, *P. lacteus*, was described by Schneider (1866), then attributed to the genus *Rhamphogordius* Rathke, 1843, for which Schneider proposed the new order Gymnotoma among the Nemathelminthes. In 1868, Schneider redescribed and moved the species to the newly erected genus *Polygordius*. By studying the larvae and their development, Schneider (1868) also realized that the larvae described by Lovén (1843) and Agassiz (1867) are in fact the larvae of *Polygordius*. The family name Polygordiidae was introduced by Czerniavsky (1881). Currently, 18 species and 2 subspecies are considered valid (Fig. 7.11.1.5). The validity of some species in this group has received much debate in the past, namely *P. neapolitanus*, *P. erythrophthalmus*, *Polygordius villoti* Perrier, 1875, and *Polygordius ponticus* Salensky, 1907. Recent work, including a phylogenetic analysis focusing on species of *Polygordius* from the Atlantic Ocean and Mediterranean Sea using two mitochondrial [i.e., cytochrome *c* oxidase (CO1) and 16S rDNA] and nuclear (ITS1/2) genes, combined with morphological data, has shown that *P. neapolitanus* is a valid species, whereas *P. erythrophthalmus* represents a junior synonym of *P. lacteus* (see Lehmacher et al. 2016, Ramey-Balci et al. 2018). The red pigment spots in the prostomium of *P. erythrophthalmus* considered as eyes and a distinguishing character of this species by Giard (1880) are pigment-containing coelomocytes that are highly variable in shape, size, and position (Lehmacher et al. 2016). *P. villoti* is also considered to be a junior synonym of *P. lacteus* (Ramey-Balci et al. 2018).

The taxonomic status of *P. ponticus* (type locality: Sewastopol, Black Sea) is uncertain. Some authors (e.g., Hempelmann 1906) regarded it also a junior synonym of *P. lacteus*. However, this is unlikely, as *P. lacteus* is restricted to the Northeast Atlantic and to date has not been found in the Mediterranean Sea (Ramey-Balci et al. 2018). Given that *P. neapolitanus* is morphologically similar to *P. lacteus* and its range extends into the eastern Mediterranean (Ramey-Balci et al. 2018), it is more likely that *P. ponticus* is a junior synonym of *P. neapolitanus*. *P. epitocus* is not considered to be valid, as its description by Dawydoff (1905) is not sufficiently detailed enough to allow subsequent identification.

According to Hartman (1959), the genera *Rhamphogordius* Rathke, 1843, *Linotrypane* McIntosh, 1875, and *Pseudogordius* Czerniavsky, 1881 are considered to be synonyms of *Polygordius*. Another genus in the family Polygordiidae was established for *Chaetogordius canaliculatus* described by Moore (1904). This species was characterized as having achaetous anterior segments, whereas the posterior 10 to 12 segments contained a pair of chaetae (i.e., a single chaeta in each segment on each side of the body) but without parapodia (Rouse 2001). However, the description was based on fragmented material collected off Cape Cod, USA, and this species has never been found again. It is generally regarded as an invalid taxon (Hermans 1969, Rota and Carchini 1999, Westheide 2008).

Species descriptions have traditionally relied on the comparison of only few morphological characters such as color, size, length of palps, shape of prostomium or pygidium, presence or absence of pygidial cirri and anal lobes, and arrangement of blood vessels. Some of these are of limited diagnostic value for assessing diversity within this group. More recent studies using SEM and TEM have found pygidial gland morphology (e.g., gland shape, number, and orientation), prostomial sense organs, and larval type to be especially useful in distinguishing among species (Fig. 7.11.1.4E–I) (Lehmacher et al. 2016, Ramey-Balci et al. 2018). In contrast, seemingly significant variation in the number and structure (i.e., forked vs. unforked) of pygidial cirri in a population of *P. appendiculatus* (Helgoland, Germany) was not diagnostic representing intraspecific variability not related to sex or size differences (Ramey-Balci et al. 2018). Thus, the view that Polygordiidae represents a relatively small, homogeneous group characterized by uniformity in external morphological features is less true than previously thought.

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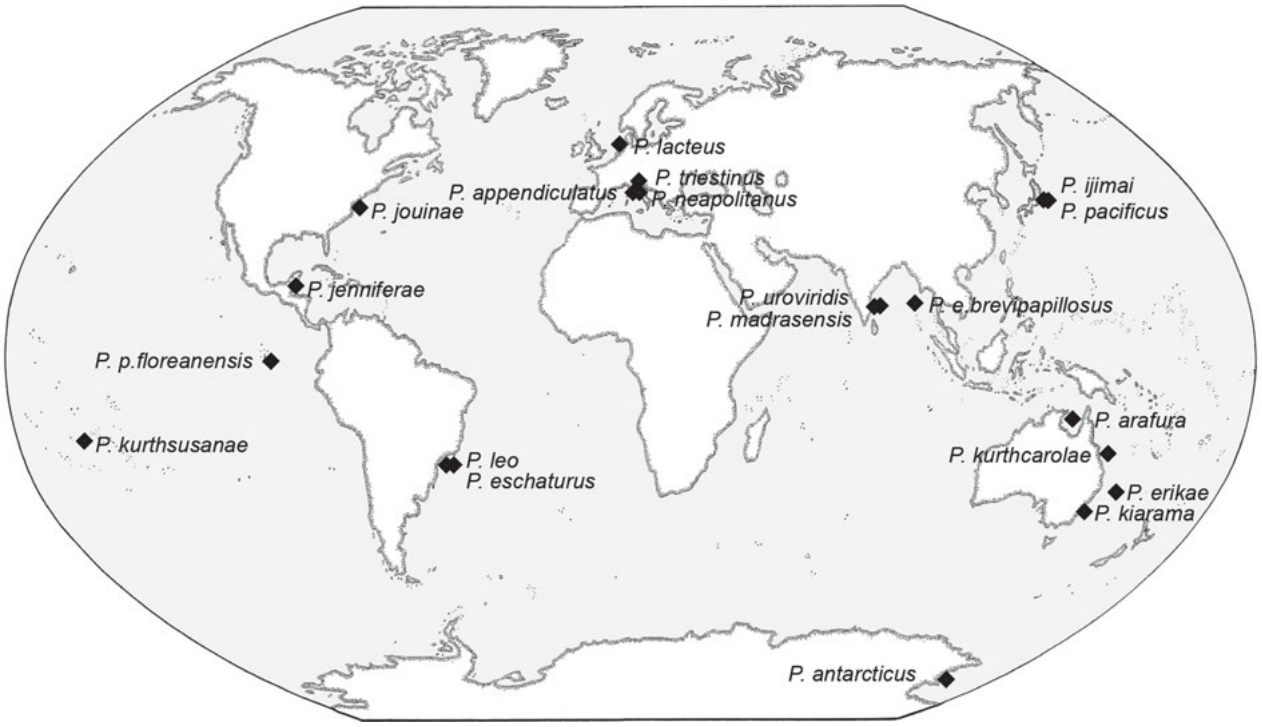


Fig. 7.11.1.5: Type localities of *Polygordius* species and subspecies considered valid.

Polygordiidae Czerniavsky, 1881
***Polygordius* Schneider, 1868**
Type species: *Polygordius lacteus* Schneider, 1868
Diagnosis: Thin, slender body with iridescent cuticle resembling nematodes. Segmentation present but often barely visible. Parapodia and chaetae absent. Prostomium rounded or conical with a pair of short palps. Pigmented eyes absent. Prostomium and peristomium separated by perpendicular head fold. Nuchal organs positioned dorsolaterally posteriorly on the prostomium. In most species, pygidium encircled by distinct ring of adhesive glands creating preterminal inflation: number, shape, and orientation of glands varying among species. Some species with pygidial or anal cirri. Anus often bordered by varying number of anal lobes. Live specimens colorless and partly transparent. Sexually mature individuals with reddish hue due to enlarged blood sinuses; females transparent to white, males milky white due to spermatozoa.

14 valid species and 2 subspecies (Fig. 7.11.1.5):
Polygordius antarcticus Rota & Carchini, 1999
Polygordius appendiculatus Fraipont, 1887
Polygordius arafura Avery, Ramey & Wilson, 2009
Polygordius erikae Tustison, Ramey-Balci & Rouse, 2020
Polygordius eschaturus Du Bois-Reymond Marcus, 1948
Polygordius eschaturus brevipapillosus Jouin & Rao, 1987
Polygordius ijimai Izuka, 1903
Polygordius jenniferae Tustison, Ramey-Balci & Rouse, 2020
Polygordius jouinae Ramey, Fiege & Leander, 2006
Polygordius kiarama Avery, Ramey & Wilson, 2009
Polygordius kurthcarolae Tustison, Ramey-Balci & Rouse, 2020
Polygordius kurthsusanae Tustison, Ramey-Balci & Rouse, 2020
Polygordius lacteus Schneider, 1868
Polygordius leo Du Bois-Reymond Marcus, 1955
Polygordius madrasensis Aiyar & Alikunhi, 1944
Polygordius neapolitanus Fraipont, 1887
Polygordius pacificus Uchida, 1935
Polygordius pacificus floreanensis Schmidt & Westheide, 1977
Polygordius triestinus Hempelmann, 1906
Polygordius uroviridis Aiyar & Alikunhi, 1944

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References

Agassiz, A. (1867): XXXIV. — On the young stages of a few annelids. *Annals of the Lyceum of Natural History of New York* 8: 303–343.

Aiyar, R.G. & Alikunhi, K.H. (1944): On some archiannelids of the Madras coast. *Proceedings of the National Institute of Sciences of India* 10: 113–140.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Avery, L., Ramey, P.A. & Wilson, R.S. (2009): New Polygordiidae (Polychaeta) from the Australian region. *Zootaxa* 2068: 59–68.

Brandenburger, J.L. & Eakin, R.M. (1981): Fine structure of ocelli in larvae of an archiannelid, *Polygordius* cf. *appendiculatus*. *Zoomorphology* 99: 23–36.

Cañete, J.I., Gallardo, C.S, Medina, A., Díaz-Ochoa, J., Olave, C. & Figueroa, T. (2019): Abundance and spatial distribution of *Polygordius* (Polychaeta: Polygordiidae) neustonic exolarvae in estuaries from southern Chile. *Anales Instituto Patagonia* 42: 19–33.

Cerca, J., Meyer, C., Stateczny, D., Siemon, D., Wegbrod, J., Purschke, G. , Dimitrov, D. & Struck, T.H. (2020a): Deceleration of morphological evolution in a cryptic species complex and its link to paleontological stasis. *Evolution* 74: 116–131.

Cerca, J., Meyer, C., Purschke, G. & Struck, T.H. (2020b): Delimitation of cryptic species drastically reduces the geographical ranges of marine interstitial ghost-worms (*Stygocapitella*; Annelida, Sedentaria). *Molecular Phylogenetics and Evolutio*n 143: 106663.

Clark, R.B. & Hermans C.O. (1976): Kinetics of swimming in some smooth-bodied polychaetes. *Journal of Zoology* 178: 147–159.

Czerniavsky, V. (1881): Materialia ad Zoographiam Ponticam Comparatam. Fasc. III Vermes. *Bulletin de la Société Impériale des Naturalistes de Moscou* 55: 211–363.

Dawydoff, C. (1905): III. On the morphology of the Archiannelida. Biological observations on the epitocus form of *Polygordius*. Scientific results of a travel to Java and other islands of the Malay Archipelago. *Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg* 22: 51–56. [in Russian]

Du Bois-Reymond Marcus, E. (1948): Further archiannelids from Brazil. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo* 48: 1–17.

Du Bois-Reymond Marcus, E. (1955): On Turbellaria and *Polygordius* from the Brazilian coast. *Boletim de Faculdade de Filosofia Ciencias e Letras. Universidade de Sao Paulo. Zoologia* 20: 19–53.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum Los Angeles County Science Series* 28: 1–188.

Fauchald, K., & Rouse, G.W. (1997): Polychaete systematics: past and present. *Zoologica Scripta* 26: 71–138.

Fewkes, J.W. (1883): On the development of certain worm larvae. *Bulletin of the Museum of Comparative Zoology* 11: 167–208.

Fraipont, J. (1884a): Le rein céphalique du *Polygordius*. *Archives de Biologie* 5: 103–109.

Fraipont, J. (1884b): Recherches sur le système nerveux central et périphérique des Archiannélides (*Protodrilus* et *Polygordius*) et du *Saccocirrus papillocercus*. *Archives de Biologie* 5: 243–304.

Fraipont, J. (1887): Le genre *Polygordius*. *Fauna und Flora des Golfes von Neapel* 14: 1–125.

Franzén, A. (1974): Sperm ultrastructure in some Polychaeta. In: Afzelius, B.A. (eds.), *The Functional Anatomy of the Spermatozoon*. Proceedings of the 2nd Wenner-Gren Symposium. Pergamon, Oxford: 267–278.

Franzén, A. (1977): Ultrastructure of sperm and spermatozoa in Archiannelida. *Zoon* 5: 97–105.

Giard, M.A. (1880): Sur les affinités du genre *Polygordius* avec les Annélides de la famille des Opheliidae. *Comptes Rendus des Séances de L'Académie des Sciences* 91: 715–718.

Goodrich, E.S. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science* 44: 413–428.

Grassle, J.F., Ramey, P.A., & Petrecca, R.F. (2009): Temporal and spatial variation in infaunal community structure in physically active continental shelf sediments at a long-term ecosystem observatory (LEO-15) off New Jersey, USA. *Journal of Marine Research* 67: 869–897.

Hagmeier, A. (1930): Die Besiedlung des Felsstrandes und der Klippen von Helgoland. I. Der Lebensraum. *Wissenschaftliche Meeresuntersuchungen (Abteilung Helgoland)* 15: 1–35.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Part II. *Allan Hancock Foundation Publications, Occasional Paper* 23: 353–628.

Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands. 58. Teil* (2. Aufl.). Fischer, Jena: 648 pp.

Hatschek, B. (1878): Studien über Entwicklungsgeschichte der Anneliden. *Arbeiten des Zoologischen Instituts der Universität Wien* 3: 277–404.

Hatschek, B. (1886): Zur Entwicklung des Kopfes von *Polygordius*. *Arbeiten aus dem Zoologischen Institut der Universität Wien* 6: 109–120.

Hatschek, B. (1893): System der Anneliden, ein vorläufiger Bericht. *Lotos* 13: 123–126.

Hausen, H. (2005): Comparative structure of the epidermis in polychaetes (Annelida). *Hydrobiologia* 535/536: 25–35.

Hay-Schmidt, A. (1995): The larval nervous system of *Polygordius lacteus* Scheinder [sic], 1868 (Polygordiidae, Polychaeta): Immunocytochemical data. *Acta Zoologica (Stockholm)* 76: 121–140.

Hempelmann, F. (1906): Zur Morphologie von *Polygordius lacteus* Schn. und *Polygordius triestinus* Wolterek, nov. spec. *Zeitschrift für wissenschaftliche Zoologie* 84: 527–618.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Herrmann, K. (1986): *Polygordius appendiculatus* (Archiannelida) — Metamorphose. *IWF, Göttingen. Publikationen zu Wissenschaftlichen Filmen, Sektion Biologie, Serie 18, Nr. 36 Film E* 2716: 1–15.

Izuka, A. (1903): On a new *Polygordius* from Misaki (*P. ijimai* n. sp.). *Annotationes Zoologicae Japonenses* 4: 137–139.

Jamieson, B.G.M. & Rouse, G.W. (1989): The spermatozoa of the Polychaeta (Annelida): An ultrastructural review. *Biological Reviews* 64: 93–157.

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Janowsky, R. (1905): Über die *Polygordius* Larve des Hafens von Triest. *Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 15: 197–212.

Jouin, C. (1970): Archiannélides interstitielles de Nouvelle Calédonie. In: Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie, 1960–1963. *Editions Fondation Singer-Polignac* 4: 149–157.

Jouin, C. & Rao, G.C. (1987): Morphological studies on some Polygordiidae and Saccocirridae (Polychaeta) from the Indian Ocean. *Cahiers de Biologie Marine* 28: 389–402.

Leander, B.C. & Ramey, P.A. (2006): Cellular identity of a novel small subunit rDNA sequence clade of apicomplexans. Description of the marine parasite *Rhytidocystis polygordiae* n. sp. (Host: *Polygordius* sp., Polychaeta). *Journal of Eukaryote Microbiology* 53: 280–291.

Lehmacher, C., Fiege, D. & Purschke, G. (2014): Immunohistochemical and ultrastructural analysis of the muscular and nervous systems in the interstitial polychaete *Polygordius appendiculatus* (Annelida). *Zoomorphology* 133: 21–41.

Lehmacher, C., Ramey-Balci, P.A., Wolff, L., Fiege, D. & Purschke, G. (2016): Ultrastructural differences in presumed photoreceptive organs and molecular data as a means for species discrimination in Polygordius (Annelida, Protodriliformia, Polygordiidae). *Organisms Diversity & Evolution* 16: 559–576.

Lovén, S. (1843): Observations on the metamorphosis of an Annelide. *The Annals and Magazine of Natural History, Series 1* 11: 43–45.

McHugh, D. (2005): Molecular systematics of polychaetes (Annelida). *Hydrobiologia* 535/536: 309–318.

McIntosh, W.C. (1875): On a new example of the Opheliidae (*Linotrypane apogon*) from Shetland. *Proceedings of the Royal Society of Edinburg* 8: 386–390.

Moore, J.P. (1904): A new generic type of Polygordiidae. *The American Naturalist* 38: 519–520.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.

Nordheim, H. von (1984): Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae, and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchungen* 38: 1–20.

Paxton, H. (2000): 1. Class Polychaeta, Family Polygordiidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies. The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 236.

Perrier, E. (1875): Sur un nouveau type intermédiaire du sous-embranchement des Vers (*Polygordius*?, Schneider). *Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences* 24: 1101–1105.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2002): On the ground pattern of Annelida. *Organisms, Diversity and Evolution* 2: 181–196.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 535/536: 53–78.

Purschke, G. & Tzetlin, A.B. (1995): Dorsolateral ciliary folds in the Polychaete foregut: Structure, prevalence and phylogenetic significance. *Acta Zoologica (Stockholm)* 77: 33–49.

Ramey, P.A. (2008a): Life history and population dynamics of a dominant polychaete, *Polygordius jouinae*, in inner continental shelf sands of the Mid-Atlantic Bight, USA. *Marine Biology* 154: 443–452.

Ramey, P.A. (2008b): *Processes affecting macrofaunal community structure in sandy sediments on the New Jersey inner continental shelf with a focus on the dominant polychaete, Polygordius jouinae.* Dissertation submitted to the Graduate School-New Brunswick, Rutgers, The State University of New Jersey, New Brunswick, New Jersey: 201 pp.

Ramey, P.A. (2008c): *Climate variability and temporal trends in abundance of a dominant polychaete on the Northwest Atlantic continental shelf.* ASLO 2008 Interactions on the Edge, St. John's, Newfoundland and Labrador, Canada June 8-13 (Abstract).

Ramey, P.A. & Bodnar, E. (2008): Selection by a deposit-feeding polychaete, *Polygordius jouinae*, for sands with relatively high organic content. *Limnology and Oceanography* 54: 1512–1520.

Ramey, P.A., Fiege, D. & Leander, B.S. (2006): A new species of *Polygordius* (Polychaeta: Polygordiidae): from the inner continental shelf and in bays and harbors of the north-eastern United States. *Journal of the Marine Biological Association of the United Kingdom* 86: 1025–1034.

Ramey, P.A., Grassle, J.P., Grassle, J.F., & Petrecca, R.F. (2009): Small-scale, patchy distributions of infauna in hydrodynamically mobile continental shelf sands: Do ripple crests and troughs support different communities? *Continental Shelf Research* 29: 2222–2233.

Ramey, P.A., Kennish, M.J., & Petrecca, R.F. (2011): Benthic index development: Assessment of ecological status of benthic communities in New Jersey marine coastal waters. *Technical Report to the U.S. Environmental Agency and New Jersey Department of Environmental Protection, Institute of Marine and Coastal Sciences, Rutgers University, New Jersey*: 192 pp.

Ramey-Balci, P.A. & Ambler, J.W. (2014): Distribution and seasonal abundance of *Polygordius* spp. (class: Polychaeta; family: Polygordiidae) exo- and endolarvae in the southern Mid-Atlantic Bight, USA. *Marine Biology* 161: 1565–1581.

Ramey-Balci, P., Fiege, D. & Struck, T.H. (2018): Molecular phylogeny, morphology, and distribution of *Polygordius* (Polychaeta: Polygordiidae) in the Atlantic and Mediterranean. *Molecular Phylogenetics and Evolution* 127: 919–930.

Rathke, H. (1843): Beiträge zur Fauna Norwegens. III. Würmer. *Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher* 12: 149–264.

Remane, A. (1932): VIa. Archiannelida. In: Grimpe, G. & Wagler, E. (eds.), *Die Tierwelt der Nord- und Ostsee*. Akademische Verlagsgesellschaft, Leipzig: 1–36.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the Spiralia. *Acta Zoologica (Stockholm)* 57: 53–68.

Ritter, W.E. (1892): Note on an abnormal *Polygordius* larva. *The American Naturalist* 26: 1047–1050.

Rota, E. & Carchini, G. (1999): A new *Polygordius* (Annelida: Polychaeta) from Terra Nova Bay, Ross Sea, Antarctica. *Polar Biology* 21: 201–213.

Rouse, G.W. (2001): 71. Polygordiidae Czerniavsky, 1881a. In: Rouse, G.W. & Pleijel, F. (eds.), *Polychaetes*. Oxford University Press, London: 279–281.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Pleijel, F. (2006): Annelid phylogeny and systematics. In: Rouse, G.W. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida. Reproductive Biology and Phylogeny* Vol. 4: 3–21.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Salensky, W. (1907): Morphogenetische Studien an Würmern. *Mémoires de l'Académie impériale des Sciences de St.-Petersbourg. Series 8*, 19: 1–349.

Schmidt, P. & Westheide, W. (1977): Interstitielle Fauna von Galapagos. XVII. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). *Mikrofauna des Meeresbodens* 62: 1–38.

Schneider, A. (1866): Monographie der Nematoden. Georg Reimer, Berlin: 357 pp.

Schneider, A. (1868): Über Bau und Entwickelung von *Polygordius*. *Archiv für Anatomie Physiologie und Wissenschaftliche Medicin* 10: 51–60.

Schofield, O., Chant, R., Cahill, B., Castelao, R., Gong, D., Kahl, A., Kohut, J., Montes-Hugo, M., Ramadurai, R., Ramey, P. A., Yi, X. & Glenn, S. (2008): The decadal view of the Mid-Atlantic Bight from the coolroom: Is our coastal system changing? Special Issue on Coastal Ocean Processes. Consequences of Seasonal Forcing. *Oceanography* 21: 108–117.

Schroeder, P.C. & Hermans, C.O., (1975): Annelids: Polychaeta. In Giese, A.C. & Pearse, J.S. (eds.), *Reproduction of Marine Invertebrates* Vol. III: *Annelids and Echiurans*. Academic Press, New York: 1–213.

Sensenbaugh, T. & Franzén, A. (1987): Fine structural observations of the apical organ in the larva of *Polygordius* (Annelida: Polychaeta). *Scanning Microscopy* 1: 181–189.

Shearer, C. (1908): IV. Studies on the development of larval nephridia. Part II. — *Polygordius*. *Philosophical Transactions of the Royal Society of London, Series B* 199: 199–230.

Smith, P.R. & Ruppert, E.E. (1988): The ultrastructure of Polychaeta. XIV. Nephridia. *Microfauna Marina* 4: 231–262.

Söderstrom, A. (1924a): Über die „Katastrophale Metamorphose" der *Polygordius*-Endolarve nebst Bemerkungen über die Spiralfurchung. *Uppsala Universitets Arsskrift* 1924. Almquist & Wiksells Boktryckeri-A.-B., Uppsala: 78 pp.

Söderstrom, A. (1924b): Das Problem der *Polygordius*-Endolarve. Eine Gegenantwort an Professor Richard Woltereck. Almquist & Wiksells Boktryckeri-A.-B., Uppsala: 168 pp.

Söderstrom, A. (1925): Kurze Bemerkungen zur "katastrophalen Metamorphose" der *Polygordius*-Larve. *Zoologischer Anzeiger* 64: 103–104.

Struck, T.H. (2011): Direction of evolution within Annelida and the definition of Pleistoannelida. *Journal of Zoological Systematics and Evolutionary Research* 49: 340–345.

Struck, T. (2019): Phylogeny. In G. Purschke, G., Böggemann, M., & Westheide, W. (eds.), *Handbook of Zoology* vol. 1: *Annelida*. De Gruyter, Berlin: 37–68.

Struck, T.H. & Purschke, G. (2005): The sister group relationship of Aeolosomatidae and Potamodrilidae (Annelida: 'Polychaeta') — A molecular phylogenetic approach based on 18S rDNA and cytochrome oxidase I. *Zoologischer Anzeiger* 243: 281–293.

Struck, T.H., Westheide, W. & Purschke, G. (2002): Progenesis in Eunicida ("Polychaeta", Annelida) — Separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution* 25: 190–199.

Struck, T.H., Nesnidal, M., Purschke, G. & Halanych, K.M. (2008): Detecting possible saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G., & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Struck, T.H., Purschke, G., Dordel, J., Hösel, C., Nesnidal, M.P., Diersing, F., Bleidorn, C., Paul, C., Hill, N., Tiedemann, R., Selbig, J., & Hartmann, S. (2014): Phylogeny and evolution of Annelida based on molecular data. In: Wägele, W. & Bartolomaeus, T. (eds.), *Deep Metazoan Phylogeny: The Backbone of the Tree of Life*. De Gruyter, Berlin: 143–160.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C., & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Tustison, C.A., Ramey-Balci, P.A., & Rouse, G.W. (2020): More knott worms: Four new *Polygordius* (Annelida) species from the Pacific and Caribbean. *Diversity* 12, 146:1–25.

Tzetlin, A.B. & Filippova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologia* 535/536: 113–126.

Tzetlin, A.B., Zhadan, A., Ivanov, I., Müller, M.C.M. & Purschke, G. (2002): On the absence of circular muscle elements in the body wall of *Dysponetus pygmaeus* (Chrysopetalidae, 'Polychaeta', Annelida). *Acta Zoologia* 83: 81–85.

Uchida, T. (1935): 36. Eine neue Urannelidenart, *Polygordius pacificus* n. sp. *Proceedings of the Imperial Academy Tokyo* 11: 119–120.

Westheide, W. (1984): The concept of reproduction in polychaetes with small body size: Adaptations in interstitial species. *Fortschritte der Zoologie* 29: 265–287.

Westheide, W. (1985): The systematic position of the Dinophilidae and the archiannelid problem. In: Morris, S.C., George, J.D., Gibson, R. & Platt, H.M. (eds.), *The Origins and Relationships of Lower Invertebrates*. Clarendon, Oxford: 310–326.

Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21: 843–854.

Westheide, W. (1990): *Polychaetes: Interstitial Families. Synopsis of the British Fauna (New Series) 44*. Backhuys, Oegstgeest: 152 pp.

Westheide, W. (2008): *Polychaetes: Interstitial Families. Synopses of the British Fauna 44 (New Series)*. 2nd ed. The Linnean Society of London, London: 169 pp.

Wilkens, V. & Purschke, G. (2009): Central nervous system and sense organs, with special reference to photoreceptor-like sensory elements, in *Polygordius appendiculatus* (Annelida), an interstitial polychaete with uncertain phylogenetic affinities. *Invertebrate Biology* 128: 46–64.

Woltereck, R. (1902): Trochophora-Studien I. Ueber die Histologie der Larve und die Entstehung des Annelids bei den *Polygordius*-Arten der Nordsee. *Zoologica* 34: 1–71.

Woltereck, R. (1905): Zur Kopffrage der Anneliden. *Verhandlungen der Deutschen Zoologischen Gesellschaft auf der fünfzehnten Jahrestagung zu Breslau, den 13. bis 16. Juni 1905*: 154–186.

Woltereck, R. (1924): Bemerkungen zur katastrophalen Metamorphose der *Polygordius*-Endolarve. In: Söderström, A. (ed.), *Das Problem der Polygordius-Endolarve. Eine Gegenantwort an Professor Richard Woltereck*. Almquist & Wiksells Boktryckeri-A.-B., Uppsala: 169–170.

Woltereck, R. (1925): Nochmals Dr. Söderström und die Polychaeten-Endolarve. *Zoologischer Anzeiger* 63: 8.

Woltereck, R. (1926): Neue und alte Beobachtungen zur Metamorphose der Endolarve von *Polygordius*. (Mit einem Zusatz, der die letzten Mitteilungen Dr. Söderströms betrifft.) *Zoologischer Anzeiger* 65: 49–69.

Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). *Hydrobiologia* 535/536: 319–340.

Zrzavy, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BioMed Central Evolutionary Biology* 9: 189.

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Maikon Di Domenico, Katrine Worsaae and Günter Purschke

7.11.2 Saccocirridae Czerniavsky, 1881

Introduction

The family Saccocirridae is marine and interstitial with body lengths ranging from 0.3 to 8 cm and comprising to up about 200 segments (Jouin 1971, Brown 1981, Jouin-Toulmond and Gambi 2007, Westheide 2008, Di Domenico et al. 2014a, b). Compared to most other interstitial animals, saccocirrids have a fairly large body width (up to 0.5 mm) and predominantly inhabit coarse sands. The animals are characterized by the presence of two long and highly flexible, muscular palps, small cylindrical uniramous parapodia with simple, retractable chaetae, and a bilobed adhesive pygidium (Figs. 7.11.2.1A, C, L, 7.11.2.2A–D). Usually, there are no other appendages besides the palps; only two species has been described possessing pygidial cirri (Aiyar and Alikunhi 1944 Baley-Brock et al. 2003). Until recently, the family was regarded to contain only one genus, although two distinct groups were recognized (Brown 1981, Purschke and Jouin 1988, Jouin-Toulmond and Gambi 2007). A combined phylogenetic analysis by Di Domenico et al. (2014a) using molecular and morphological data revealed that these groups in fact represent highly supported monophyletic groups finally leading to a separation of the currently 23 described species into two genera, namely *Saccocirrus* Brobretzky, 1872 and *Pharyngocirrus* Di Domenico, Martínez, Lana & Worsaae, 2014 (Figs. 7.11.2.1A–L, 7.11.2.2A–L).

Due to their seemingly simple morphology, from the last quarter of the nineteenth century until up to the eighties of the past century, Saccocirridae were regarded as part of the abandoned taxon Archiannelida (e.g., Brown 1981, but see Fauchald 1977). It has morphologically been grouped with Protodriloididae and Protodrilidae in the clade Protodrilida (Purschke and Jouin 1988, Westheide 2008), mainly based on the structure of the pharynx and palps (Purschke and Jouin 1988), which was left unresolved in the clade Canalipalpata in morphological phylogenies of Annelida (Rouse and Fauchald 1997, Rouse and Pleijel 2001). Unfortunately, the clade Protodrilida was never recovered in molecular analyses relying on single gene sequences, so the position of Saccocirridae within the annelid tree of life appeared to be unresolved over a long time (Rousset et al. 2007, Struck et al. 2007, 2008, Zrzavy et al. 2009). The problems of these early attempts were overcome by applying a phylogenomic approach and multigene analyses, which finally recovered the monophyly of Protodrilida (Andrade et al. 2015, Struck et al. 2015). Moreover, their systematic position within Annelida now seems to be resolved: Protodrilida plus Polygordiidae are united in a clade generally called Protodriliformia, which is the sister group of Phyllodocida and Eunicida within Errantia (Andrade et al. 2015, Struck et al. 2015, Weigert and Bleidorn 2016). Saccocirridae are thought to have evolved by gradual miniaturization rather than by progenesis as proposed for several other interstitial annelids, such as Dinophilidae (see Westheide 2019 for references), supported not only by their comparatively large size but also by certain other characters such as a life cycle including a trochophore larva and the presence of parapodia and chaetae (Struck et al. 2015).

Morphology

Head and palps

All Saccocirridae are long and slender worms and within Protodrilida somewhat resembling *Protodrilus* (Figs. 7.11.2.1A, 7.11.2.2A; see figs. 10, 11 in Protodrilidae chapter, Martinez et al. 2020a). The distinct head of Saccocirridae consists of a prostomium and a peristomium. The prostomium is rounded, relatively small, and distinctly set off from the following peristomium. It holds a pair of palps inserting

▸ **Fig. 7.11.2.1:** Morphology of *Saccocirrus*. A–C, E, I, J, Light micrographs; D, F, G, L, Scanning electron microscopy (SEM); H, K, M, Confocal laser scanning microscopy (CLSM); A, *Saccocirrus* sp. (Bermudas, Caribbean), dorsal view; B, *Saccocirrus pussicus* (Estaleiro Beach, Santa Catarina, Brazil), anterior view; C, *Saccocirrus* sp. (Giglio, Italy), ventral view of anterior end; D, *S. pussicus* (Barra Velha, Santa Catarina, Brazil), male, midbody view of seminal vesicule; E, *S. pussicus* (Estaleiro Beach, Santa Catarina, Brazil), lateral view; F, *Saccocirrus* sp. (Abades, Tenerife, Canary Islands); G, *Saccocirrus* sp. (Giglio, Italy), unequal longest setae; H, *Saccocirrus parvus* (La Marinella, Sorrento, Italy), depth-coded Z-stack projection of anti-α-tubulin immunoreactivity (IR), showing cilia, ciliation in epidermal glands and nephridia, nerves; I, *S. pussicus* (Barra Velha, Santa Catarina, Brazil), male, detailed view of seminal vesicule; J, *S. pussicus* (Barra Velha, Santa Catarina, Brazil), female, bilateral edges, midbody view; K, *S. parvus* (La Marinella, Sorrento, Italy), depth-coded Z-stack projection of anti-α-tubulin IR, ciliation, and nerves, anti-serotonin IR, nerves cells, DAPI staining; L, *Saccocirrus slateri* (Abades, Tenerife, Canary Islands), ventral of posterior end, pygidium, adhesive ridges, and epidermal adhesive glands; M, *S. parvus* (La Marinella, Sorrento, Italy), depth-coded Z-stack projection of anti-α-tubulin IR, ciliation, and nerves, green is F-actin staining showing musculature. an, anus; ar, adhesive ridges; br, brain; brm, bracing muscles; ci, ciliation; cn, palp connection; cpa, palp ciliation; cvp(mp), mouth ciliary patch; els, equal longest setae; epg, epidermal adhesive glands; ey, eye (ocellus); ess, esophagus start; ese, esophagus end; g, ganglia; lm, longitudinal muscle; lpg, long prong; ls, longest setae; mo, mouth opening; ms, medium setae; mvc, midventral ciliary band; nd, nephrydium (duct); no, nuchal organ; np, nephrydial (pore); oec, esophagus ciliation; oo, oocyte; oos, oocytes; p, penis; pa, palps; pc, palp internal canal; pe, peristomium; ph, pharynx; pi, palp insertion; pnc, palp neural cords; pnn, peripheral neural net; po, prostomium; pr, parapodium; py, pygidium; s, setae; se, setiger; spg, small prong; ss, shortes setae; sv, seminal vesicle; te, teeth; uls, unequal longest setae.

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ventrally, two dorsal pigmented eyes, and two nuchal organs behind the eyes at the border to the peristomium (Figs. 7.11.2.1A, C, 7.11.2.2A–C). The peristomium is twice as long as the prostomium and bears the ventral mouth (Figs. 7.11.2.1C, 7.11.2.2C). A pair of longitudinal bands or patches of motile cilia extending lateroventrally on the prostomium, from the palps to the peristomium, is present in species of *Pharyngocirrus* (Fig. 7.11.2.2C) (see Di Domenico et al. 2014a).

Depending on the species, the ventral palps are between 200 and 1500 µm long, supplied with an internal coelomic canal connected behind the brain. They are provided with a pair of basal sac-like structures (=ampullae) extending longitudinally up to the first or third segment. When oriented backward, the palps may extend to chaetiger 8 in certain species (e.g., *Pharyngocirrus tridentiger*). The wall of the ampullae and palp canals are formed by muscle fibers surrounded by a dense extracellular matrix (ECM); the muscle fibers are mainly arranged circularly in the ampullae, whereas both longitudinal and circular fibers are present in the canals (Figs. 7.11.2.2I, 7.11.2.3B, 7.11.2.6A–D, 7.11.2.7B) (Purschke 1993). In the palps, longitudinal fibers predominate and are arranged in a double helical pattern. An additional longitudinal bundle located outside the canal accompanies these fibers. The canals are densely filled with freely moveable coelenchyme-like cells (see Fransen 1980), which are poor in organelles and with electron-lucent cytoplasm. Each palp is supplied with a blind-ending blood vessel; both systems are connected by each other through podocyte-like cells forming part of the wall of the palp canals. It is thought that the basal ampullae aid to the stiffness control of the palps by varying the pressure within the canals (Purschke 1993). Thus, the palps are highly moveable structures proving the coarse sandy surroundings of the worms, which are pushed around in somewhat bustling movements. Mostly, palp ciliation is organized as individual tufts, uniformly scattered on the entire surface of the palp but often forming rows of tufts (Figs. 7.11.2.1C, 7.11.2.2C). Only in a *Saccocirrus* species (sp. 10, from Solomon Island in Di Domenico et al. 2014a), palp ciliation is arranged in longitudinal bands as in Protodrilidae (Martinez et al. 2020a) and Spionidae. It is suggested that ciliary tufts represent cilia of sensory cells, whereas ciliary bands are locomotory cilia generating water currents.

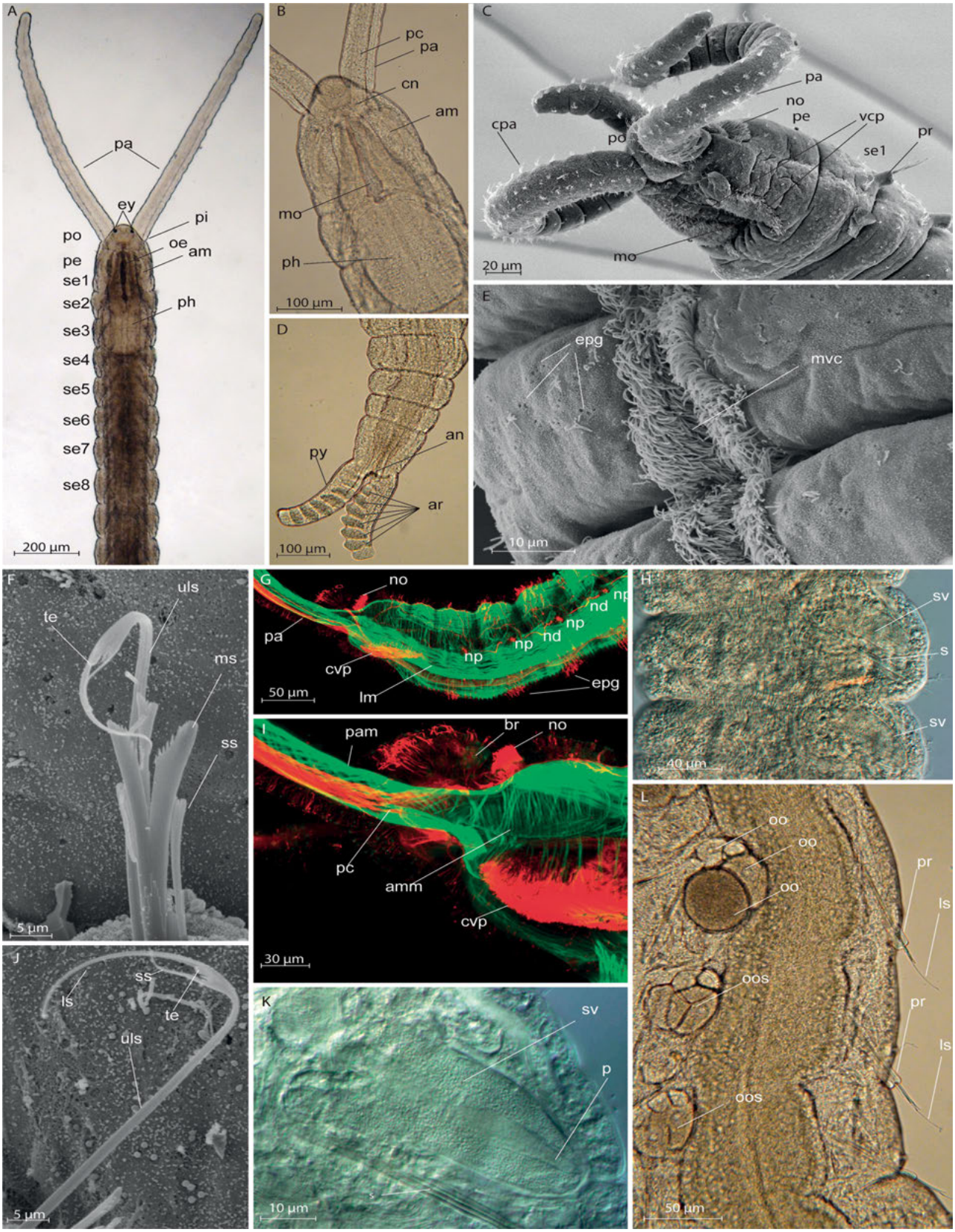
The nuchal organs are oval and elongated in Saccocirridae (Purschke 1988a, Westheide 2008, Di Domenico et al. 2014a). They are situated dorsally in shallow depressions, oriented transversally but never extend laterally around the peristomium (Fig. 7.11.2.3A, C). The size of the nuchal organs varies greatly among species. The eyes are situated anteriorly in the prostomium (Figs. 7.11.2.2A, 7.11.2.3B, C) (Eakin et al. 1977, Purschke 1992, Di Domenico et al. 2014a). Whereas the small pigmented eyes are easily seen under the light microscope, other, usually unpigmented photoreceptive sense organs may be present as well, which as, a rule, are invisible without electron microscopy. One exception is a pair of comparatively large sensory organs present in *Saccocirrus papillocercus* at the posterior end of the prostomium (Fig. 7.11.2.3C) (Purschke 1992). As this sense organ is absent in *Pharyngocirrus krusadensis*, this is another potential character of taxonomic importance in Saccocirridae.

Trunk and pygidium

Parapodia and chaetae. Fleshy small but distinct lateroventrally parapodia are present in Saccocirridae on all trunk segments, except for the posterior end (Figs. 7.11.2.2C, 7.11.2.3D, E). Here, a number of achaetigerous segments are present, being larger in juveniles than in adults (Figs. 7.11.2.1L, 7.11.2.2D). Parapodia are uniramous, cylindrical, without lobes or cirri, bearing 5 to 10 chaetae (Fig. 7.11.2.3D, E). Small ciliary tufts are present on the ventral side of the parapodia (Fig. 7.11.2.3D–F, 7.11.2.8B). Three types of chaetae are usually identified in all Saccocirridae: long, medium, and short (Figs. 7.11.2.1E–G, 7.11.2.2F, 7.11.2.3D, E) (Jouin-Toulmond and Gambi 2007). The longest chaetae in

▸ **Fig. 7.11.2.2:** Morphology of *Pharyngocirrus*. A, B, D, H, K, L, Light microscopy; C, E, F, J, SEM; G, I, CLSM; A, *Pharyngocirrus* sp. (Cariew Bow Cay, Belize), anterior view; B, Same specimen as A, anterior view, ventral pharyngeal bulbous; C, *Pharyngocirrus* sp. (Cariew Bow Cay, Belize), ventral view of anterior end, mouth ciliation; D, Same specimen as A, ventral view of posterior end, pygidium; E, *Pharyngocirrus* sp. (Nusa Anghana, Australia), ventral view, midventral ciliary band; F, *Pharyngocirrus* sp. (Nusa Anghana, Australia); G, *Pharyngocirrus goodrichi* (Napoli, Italy), depth-coded Z-stack projection of anti-α-tubulin IR, ciliation, and nerves, unequal longest setae, green is F-actin staining showing musculature; H, *Pharyngocirrus* sp. (Bocas del Toro, Panama), midbody of a male showing unilateral arrangement of seminal vesicles; I, Same specimen as G, lateral view showing musculature and nerves of palps; J, *Pharyngocirrus* sp. (Nusa Anghana, Australia); K, Same specimen as H; L, Same specimen as A, midbody of a female showing unilateral arrangement of oocytes. am, ampullae; an, anus; ar, adhesive ridges; br, brain; brm, bracing muscles; ci, ciliation; cn, palp connection; cpa, palp ciliation; cvp(mp), mouth ciliary patch; epg, epidermal adhesive glands; ey, eye (ocellus); ess, esophagus start; ese, esophagus end; g, ganglia; lm, longitudinal muscle; ls, longest setae; mo, mouth opening; ms, medium setae; mvc, midventral ciliary band; nd, nephrydium (duct); no, nuchal organ; np, nephrydial (pore); oec, esophagus ciliation; oo, oocyte; oos, oocytes; p, penis; pa, palps; pam, palp muscular fibers; pc, palp internal canal; pe, peristomium; ph, pharynx; pi, palp insertion; pnc, palp neural cords; pnm, peripheral neural net; po, prostomium; pr, parapodium; py, pygidium; s, setae; se, setiger; ss, shortes setae; sv, seminal vesicle; te, teeth; uls, unequal longest setae; vcp(mp), ventral (mouth) ciliary patch.

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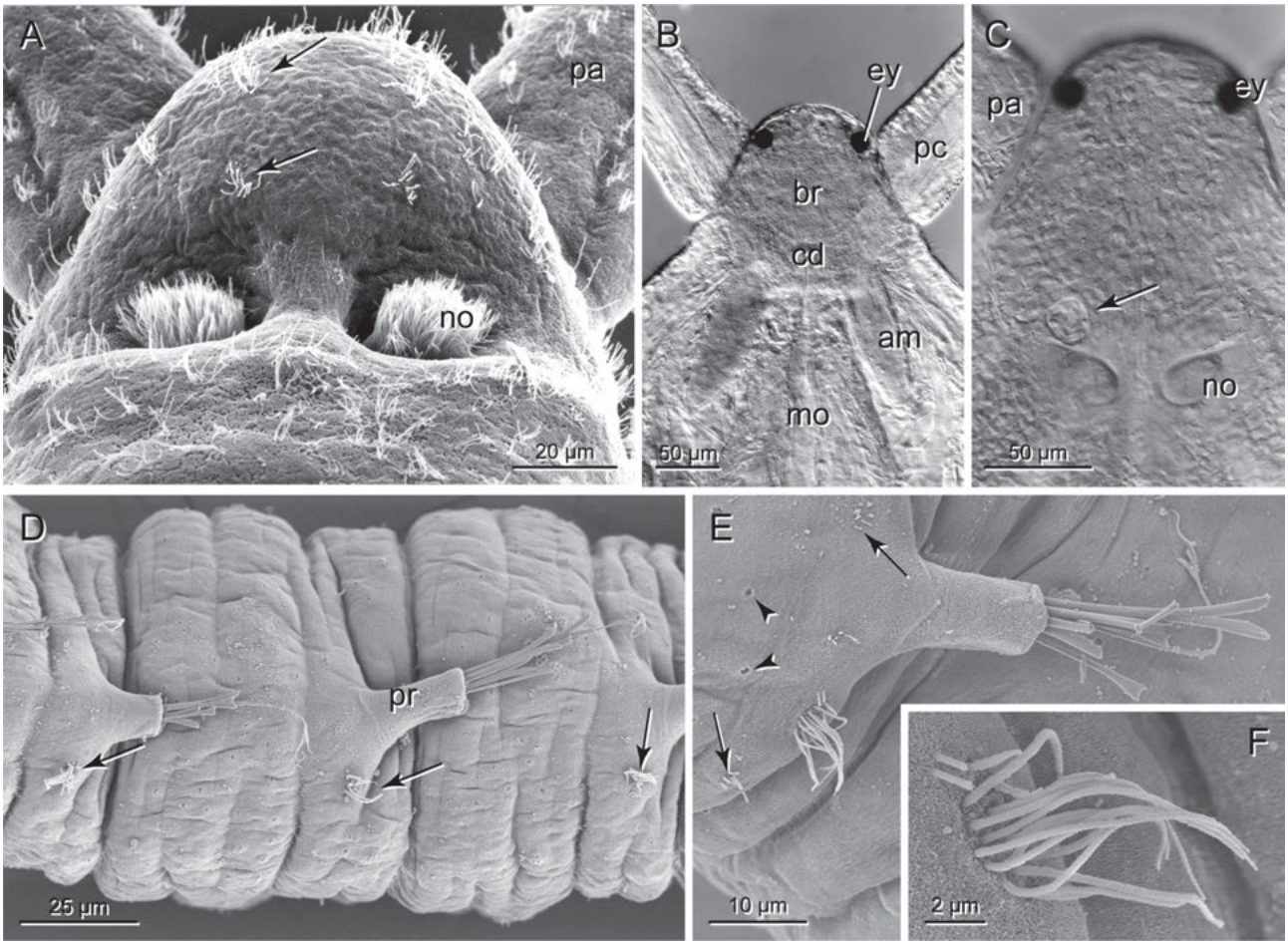


Fig. 7.11.2.3: Morphology and sense organs. *Saccocirrus papillocercus*. A, Prostomium with tufts of sensory cilia (arrows), nuchal organs (no) and palp bases (pa); B, Anterior end with pigmented eyes, palp bases, and coelomic cavities: palp canals (pc), ampullae (am), and connecting duct (cd); C, Enlargement of prostomium, focused on dorsal surface; multicellular photoreceptor organ visible as cavity with membranous content (arrow); D, Lateral view of two trunk segments with parapodia (pr), chaetae, and ventral ciliary tufts (arrows); E, Enlargement of parapodium with chaetae and ciliary tuft, arrows point to additional shorter sensory cilia, arrowheads point to openings of single gland cells; F, Close-up of the ciliary tuft shown in E, note different length of cilia. am, ampulla; br, brain; cd, connecting duct; ey, eye; no, nuchal organ; pa, palp; pc, palp canal. A, D–F, SEM micrographs; B, C, Interference contrast images of living animals.

Saccocirrus species are robust and forked (Fig. 7.11.2.1F, G), whereas *Pharyngocirrus* species have delicate fan-shaped lyrate chaetae (Fig. 7.11.2.2F, J) (Di Domenico et al. 2014a). The lyrate chaetae in *Pharyngocirrus* can be asymmetrical as in *P. krusadensis*, *P. jouinae*, and *P. tridentiger* or bilateral symmetric as in *P. gabriellae* and *P. sonomacus*. The medium length chaetae are spatulated to oar-shaped or with a smooth apex in *Saccocirrus* or bifid with two equally long prongs in *Pharyngocirrus* (Figs. 7.11.2.1F, 7.11.2.2F). The shortest (and thinnest) chaetae in *Pharyngocirrus* are bifid and bear a notched apex and spatulated with a smooth tip in *Saccocirrus* (Figs. 7.11.2.1E, F, 7.11.2.2F, 7.11.2.3E). In *Saccocirrus heterochaetus*, two additional types of hooks are present in a number of midbody and posterior segments: larger hooks, each with one curved tip, are present in both sexes, and tridentate hooks are restricted to penis-bearing segments in males (Jouin 1975).

Epidermal ciliation. Patterns of epidermal ciliation differ within the family. Whereas motile cilia are usually present in *Pharyngocirrus* as ciliary patches beside the mouth, species of *Saccocirrus* lack any motile epidermal ciliation. However, receptor cells with more or less short stiff cilia are quite abundant all over the body (Figs. 7.11.2.2C, E, 7.11.2.3A, D, E, 7.11.2.8C). The mouth ciliary patches consist of two short longitudinal bands at each side of the mouth

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(Fig. 7.11.2.2C) (Purschke and Jouin 1988). In contrast to previous assumptions, only in certain *Pharyngocirrus* species may these ciliary bands or patches unite posterior to the mouth and form a more or less long midventral ciliary band, which may reach chaetiger 8 or even further backward (Figs. 7.11.2.2E, 7.11.2.5A) (Brown 1981, Westheide 2008, Di Domenico et al. 2014a). Thus, the majority of Saccocirridae lack a ciliary midventral band, as found in many other interstitial annelids, and instead primarily use their muscular parapodia and the musculature of the body wall for locomotion.

Adhesive glands. Saccocirridae usually possess adhesive glands openings on the pygidial lobes and the trunk segments. These are generally well developed and most likely related to the turbulent environment most species live in, but in a few species the adhesive glands are less developed such as *Saccocirrus minor* or *Pharyngocirrus jouinae*. In the trunk region, adhesive glands open in transverse rows with usually three gland cells openings in a common small papilla (Figs. 7.11.2.1L, 7.11.2.4D, E). On the pygidium, gland cell openings are located on ventral ridges (Figs. 7.11.2.1L, 7.11.2.4A–C). In *S. minor*, pygidial lobes are comparatively small and do not possess adhesive ridges (Jouin and Rao 1987), whereas, in *P. jouinae*, segmental adhesive organs are less developed (Brown 1981). The adhesive glands present on several segments are composed of a series of mounds and encircle the trunk, except for a small gap on the midventral surface (Fig. 7.11.2.1H, M) (Martin 1978).

The two pygidial lobes are cylindrical with a few transverse ventral adhesive ridges (e.g., 7–12 in *Pharyngocirrus sonomacus*; their number appears to be age dependent besides a species-specific range), with the terminal anus located between them (Fig. 7.11.2.1L, M). Each pygidial ridge bears numerous openings of adhesive glands (Fig. 7.11.2.4B, C), whereas the corresponding cell bodies are located deeply in the body, which have been described in detail by Martin (1978). Because a microtubule system is involved in the secretion-releasing process, the glands are stained in LSM preparations with antibodies against tubulin (Fig. 7.11.2.1H, K, M, 7.11.2.2G). As described for other interstitial animals, these contribute to a duo-gland system regarded to represent viscid and releasing glands, but the ratio is not 1:1; instead, there are two to three times more viscid gland cells than releasing glands. When disturbed, the animals adhere immediately with their pygidium to the substrate, curl to form a ball, and attach sediment particles to increase the body weight/surface ratio (Martin 1978).

Digestive system

The digestive system of Saccocirridae comprises a ventral mouth, buccal cavity with or without muscular pharynx, long esophagus, intestine, and terminal anus (Fig. 7.11.2.5A–G) (Goodrich 1901, Salensky 1907, Purschke and Jouin 1988, Westheide 2008). *Saccocirrus papillocercus* has an I-shaped mouth opening with both anterior and posterior slits resulting in four lips (Purschke and Tzetlin 1996) in contrast to the slit-like mouth of *Pharyngocirrus eroticus* (see Gray 1969). The pharyngeal region of *S. papillocercus* and other *Saccocirrus* spp. bears dorsolateral ciliary folds ("Schlundtaschen" of Salensky 1907) and no muscular ventral pharynx (Fig. 7.11.2.5D, E, G), whereas, in *Pharyngocirrus* spp., such an organ is present (Fig. 7.11.2.3F) (Jouin 1971, Brown 1981, Purschke and Tzetlin 1996, Tzetlin and Purschke 2005, Jouin-Toulmond and Gambi 2007, Di Domenico et al. 2014a). These dorsolateral folds are supplied by a few loosely arranged muscle fibers that mainly follow the folds in the anteroposterior direction (Figs. 7.11.2.6E, 7.11.2.7D, E). This musculature is separate from the fibers surrounding the buccal cavity and esophagus.

The ventral pharynx consists of a ventral muscle bulb and a tongue-like organ connected and ventrally encircled by longitudinally arranged investing muscles (Fig. 7.11.2.5F). The bulb is made up of plate-like transverse muscle fibers and interstitial cells (Purschke 1988b, Purschke and Jouin 1988). In the interstitial cells, a well-developed system of intermediate filaments is present running perpendicular to the transversely oriented myofilaments. Thus, the bulb is a structure of more or less constant shape but varying elasticity. The ventral pharynx of Saccocirridae belongs to the most common type in annelids, which is also present in Protodrilidae and *Protodriloides* (Tzetlin and Purschke 2005). Dorsally, the ciliated mouth cavity leads into the esophagus, which is densely ciliated as well and may extend into chaetiger 8 or even further (Fig. 7.11.2.1K). At the transition between the buccal cavity and the esophagus, numerous salivary gland cells discharge their secretions into the foregut. Their cell bodies are located within the esophageal epithelium. *Saccocirrus* spp. lack a ventral pharynx, and the mouth cavity dorsally continues as a glandular esophagus (Fig. 7.11.2.5D, E, G). The esophagus leads to the intestine, which is not regionalized, except for the posterior part. Ciliation is almost absent from the intestine (or less dense), except for a ventral ciliated groove aiding the food particles through the gut. The hindgut is densely ciliated as well and may extend for a few segments and opens in the terminal anus between the pygidial lobes (Figs. 7.11.2.1M, L, 7.11.2.2D).

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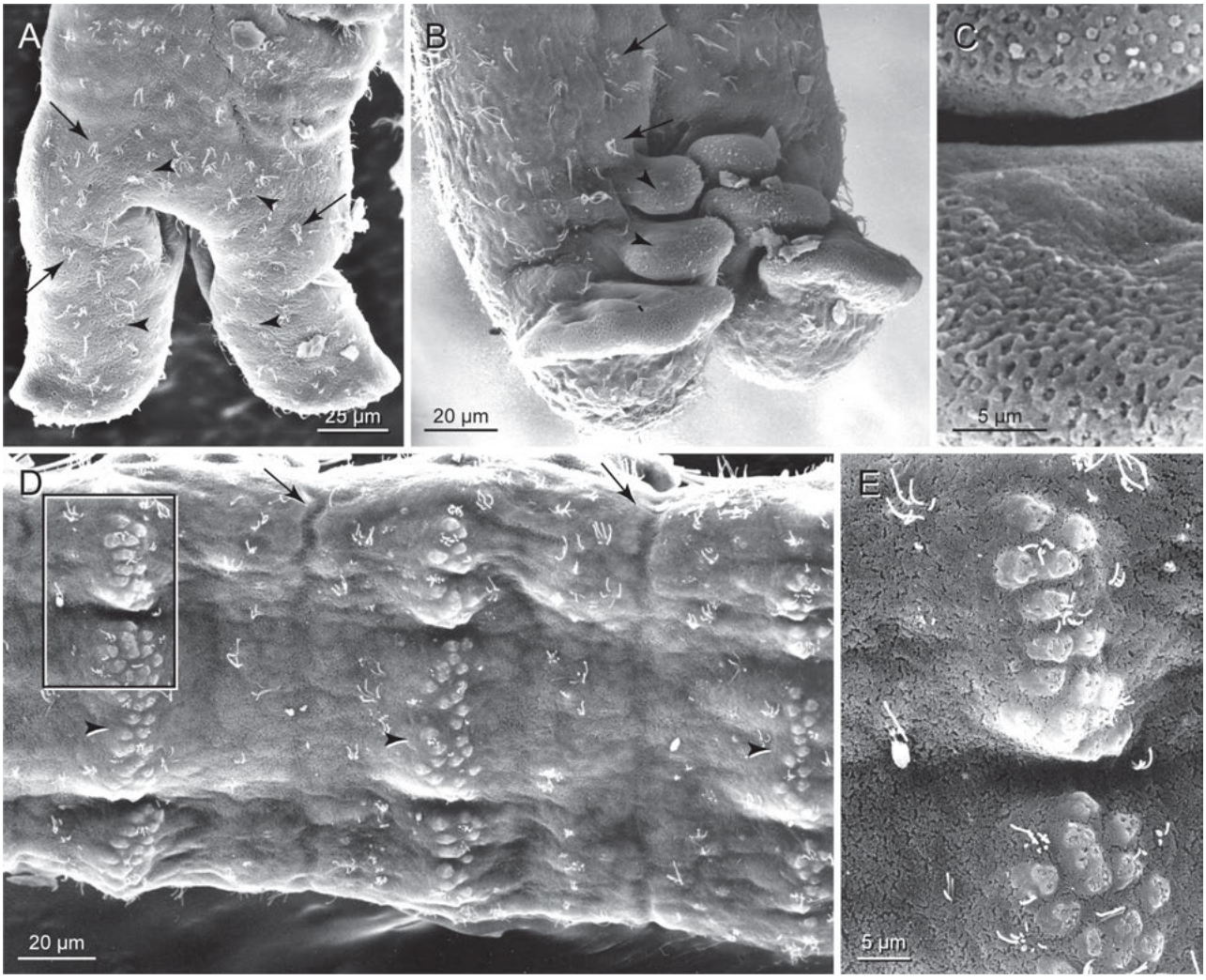


Fig. 7.11.2.4: Adhesive glands. *Saccocirrus papillocercus* SEM. A, Dorsal view of bilobed pygidium with numerous patches of sensory cilia (arrows) and single epidermal gland cell openings (arrowheads); B, Ventral view of pygidium with transverse ridges, each with numerous adhesive gland cell openings (arrowheads), arrows point to sensory cilia; C, Enlargement of adhesive gland cell openings; D, Ventral view of trunk region with three transverse rows of adhesive gland cell openings (arrowheads), arrows point to segmental borders, boxed area indicates enlarged part shown in E, cilia of sensory cells form indistinct transverse rows; E, Segmental adhesive glands, always three openings are close together forming a small papilla, note sensory cell cilia adjacent and between adhesive papillae.

Musculature

At first sight, the musculature of the trunk appears to be rather simple. It is dominated by longitudinal fibers, substituted by oblique, circular, and bracing muscle fibers (Figs. 7.11.2.6A–H, 7.11.2.7A–I). The longitudinal musculature is arranged in three pairs of fibers: dorsolateral and ventromedian forming a cylinder-like structure as well as ventrolateral (Figs. 7.11.2.6A–C, E–H, 7.11.2.7A, C, D, F–I) (Goodrich 1901, Salensky 1907, Aiyar and Alikunhi 1944, Silberbauer 1969). This arrangement reflects the triangular outline of cross-sections in the trunk region and is rather similar to that of Protodriloididae (see Martinez et al. 2020b, chapter Protodriloididae, pp. 338, this volume). The dorsolateral and ventrolateral bundles taper anteriorly and partly continue as longitudinal fibers of the palps, positioned laterally beside the coelomic canal (Fig. 7.11.2.6A, C, E, F, 7.11.2.7B, D, E). After a short distance, they form a single bundle. Most dorsolateral longitudinal fibers of the trunk terminate at the posterior border of the prostomium; just a small group of fibers enters the prostomium between the nuchal organs, tapers, and terminates anteriorly at the palp canal connection (Figs. 7.11.2.6B, F, 7.11.2.7A, C). The ventromedian bundle originates behind the mouth (Fig. 7.11.2.7D–E). Circular muscle fibers are present and comprise minute and inconspicuous isolated

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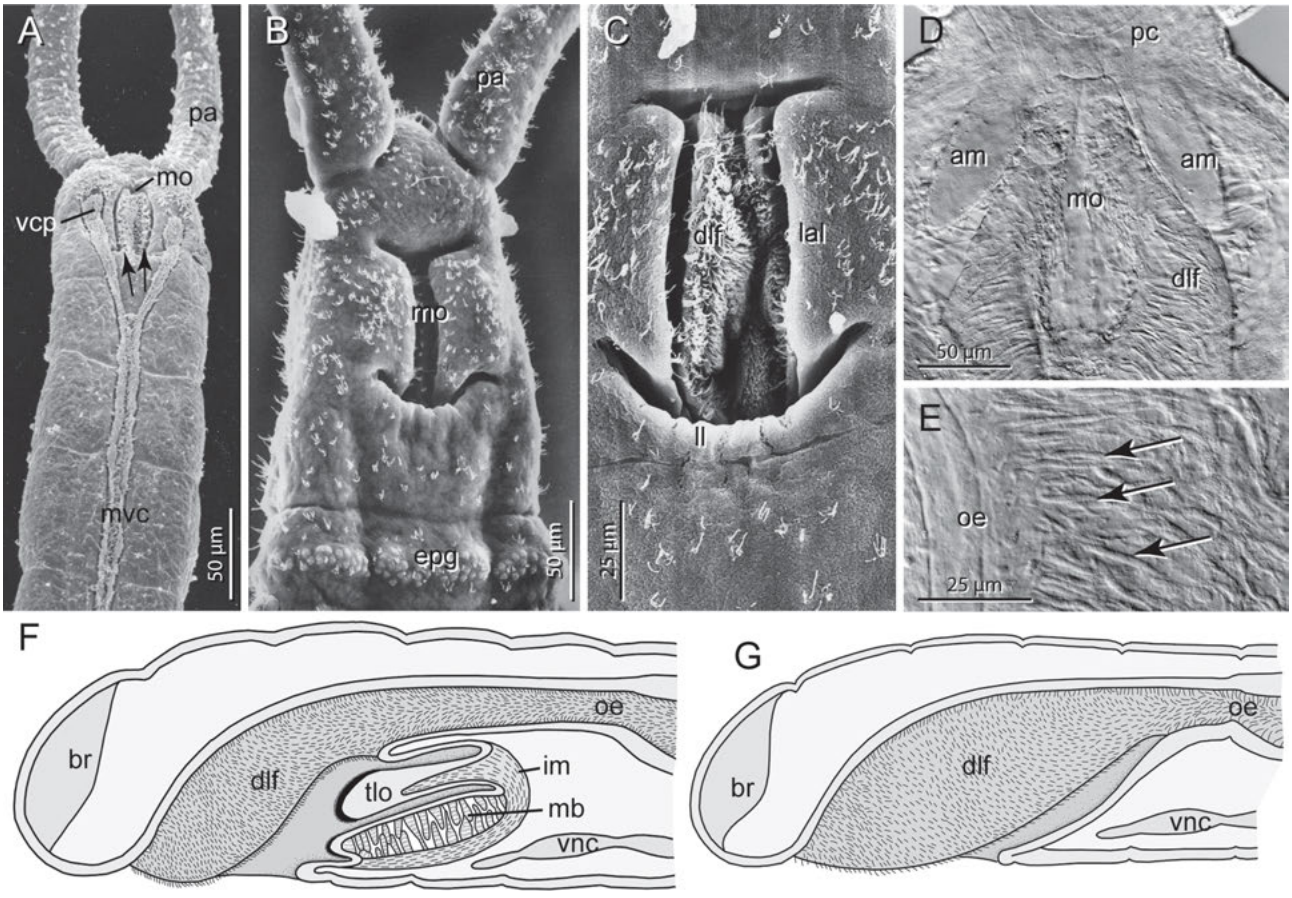


Fig. 7.11.2.5: Pharynx. A, *Pharyngocirrus* sp., ventral view with ciliary patches (vcp) beside mouth opening (mo) and midventral ciliary band (mvc), note somewhat protruded dorsolateral ciliary folds (arrows) inside buccal cavity, SEM; B–E, *Saccocirrus papillocercus*; B, Ventral view, dorsolateral folds fully inverted, SEM; C, Dorsolateral ciliary folds (arrows) partly everted and clearly visible between lateral lips (lal); D, Mouth (mo) and dorsolateral folds in living specimen; E, Enlargement of dorsolateral fold with numerous gland cell processes (arrows); F, *Pharyngocirrus* sp., schematic representation of ventral pharynx comprising tongue-like organ (tlo), muscle bulb (mb), and investing muscle (im) ventral to dorsolateral folds (dlf); G, *Saccocirrus* sp., schematic representation of foregut only comprising dorsolateral folds (dlf). A–C, SEM micrographs; D, E, interference contrast images of living specimen. am, ampulla; br, brain; dlf, dorsolateral fold; epg, epidermal adhesive glands; im, investing muscle; lal, lateral lip; ll, lower lip; mb, muscle bulb; mo, mouth; mvc, midventral ciliary band; pa, palp; pc, palp canal; tlo, tongue-like organ; vcp, ventral ciliary patch; vnc, ventral nerve cord.

fibers forming a regular pattern along the trunk (Figs. 7.11.2.6H, 7.11.2.7H–I). Oblique muscles are present in each segment and represented by separate bundles running from the ventrolateral nerve cords diagonally to the lateral furrow; as such, they separate the round bundle of ventrolateral longitudinal fibers from the rest of the musculature (Fig. 7.11.2.7B). In addition, so-called bracing muscles oriented at about 45° to the longitudinal axis are also present (Fig. 7.11.2.6A–C, F). These fibers form an outer double layer crossing at a right angle. Each chaetal sac is supplied with a specific musculature (Fig. 7.11.2.7D, G). In the posterior end, the longitudinal muscles taper and the number of fibers diminishes. Certain fibers from the dorsal and ventral bundles enter and supply the pygidial adhesive lobes (Fig. 7.11.2.7H–I). The entire digestive system is equipped with a dense net-like arrangement of circular and longitudinal fibers (Figs. 77.11.2.6E, 7.11.2.7D, E).

Nervous system and sensory organs

Nervous system. The nervous system in Saccocirridae is located basiepithelially and comprises a prostomial brain and a ventral nerve cord (Fig. 7.11.2.1K). The ventral nerve cord comprises two distinct, widely separated bundles of neurites, positioned in the distinct midventral gap formed where the two ventral longitudinal muscle systems converge. The ventral cord communicates via the circumesophageal connectives with the brain. The connectives split up into a thinner dorsal and a thicker ventral root anterior to the mouth. The brain and these roots give off the nerves innervating the palps; in *S. papillocercus*, five neurite bundles

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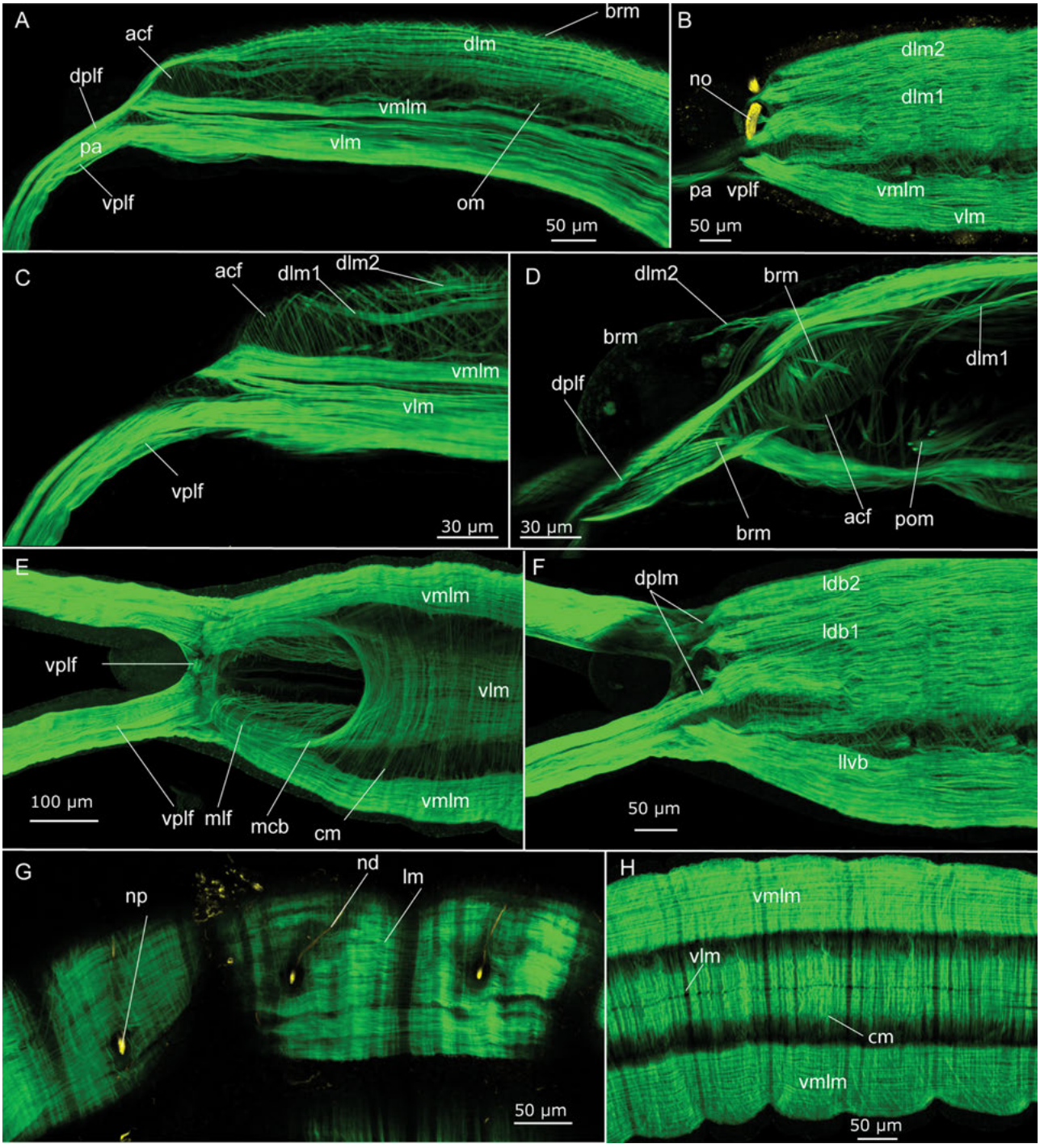


Fig. 7.11.2.6: Musculature of *Saccocirrus papillocercus* (Positano, Sorrento, Italy). CLSM, depth-coded Z-stack projection, yellow is anti-α-tubulin IR, ciliation, and nerves; green is F-actin staining showing musculature. A, Lateral view of anterior end, showing musculature of palps and body; B, Dorsal view of anterior end, showing nuchal organs; C, D, Same specimen as A, lateral view of anterior end, showing musculature of ampullae and palps; E, Ventral view of anterior end, mouth; F, Same specimen as B; G, Midbody showing arrangement of nephridium; H, Ventral view of midbody showing musculature arrangement. acf, ampullae circular fiber; brm, bracing muscle; cm, circular muscle; dlm, dorsal longitudinal muscle; dplf, dorsal palp longitudinal fibers; dplm, dorsal palp longitudinal muscles; ldb, longitudinal dorsal band; lm, longitudinal muscle; mcb, month circular band; mlf, mouth longitudinal folds; nd, nephridium (duct); np, nephridial (pore); om, oblique muscle; pa, palps; pfm, prostomium frontal muscle; plm, palp longitudinal muscle; pom, parapodial oblique muscle; pyl, pygidial lobe; vlm, ventral longitudinal muscle; vlm, ventral longitudinal muscle; vmlm, ventromedian longitudinal muscle; vplf, ventral palp longitudinal fibers.

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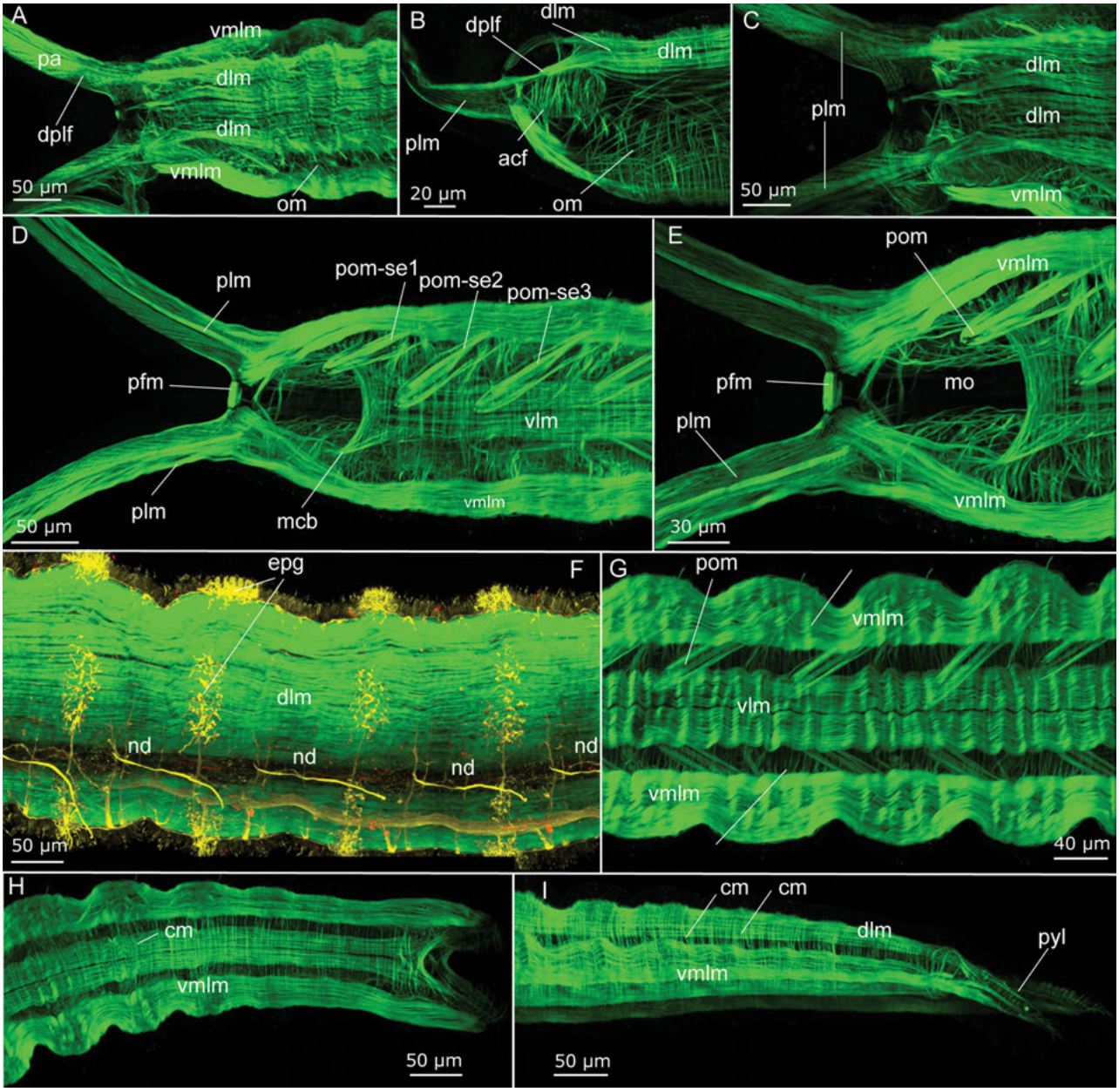


Fig. 7.11.2.7: Musculature of *Saccocirrus parvus* (La Marinella, Sorrento, Italy). CLSM, depth-coded Z-stack projection, yellow is anti-α-tubulin IR, ciliation, and nerves; green is F-actin staining showing musculature. A, Dorsal view of anterior end, showing musculature of palps and body; B, Lateral view of anterior end, showing nuchal organs; C, Same specimen as A, dorsal view of anterior end, showing musculature of palps; D, Ventral view of anterior end showing parapodium musculature arrangement; E, Same as D, ventral view of anterior end, showing musculature of mouth and palps; F, Midbody showing arrangement of nephridium and epidermal adhesive glands; G, Ventral view of midbody showing musculature arrangement; H, Ventral view of posterior end showing musculature arrangement, pygidium; I, Lateral view of posterior end showing musculature arrangement, pygidium. acf, ampullae circular fiber; cm, circular muscle; dlm, dorsal longitudinal muscle; dplf, dorsal palp longitudinal fibers; dplm, dorsal palp longitudinal muscles; ldb, longitudinal dorsal band; lm, longitudinal muscle; mcb, month circular band; nd, nephridium (duct); om, oblique muscle; pa, palps; pfm, prostomium frontal muscle; plm, palp longitudinal muscle; pom, parapodial oblique muscle; pyl, pygidial lobe; se, setiger; vlm, ventral longitudinal muscle; vmlm, ventromedian longitudinal muscle.

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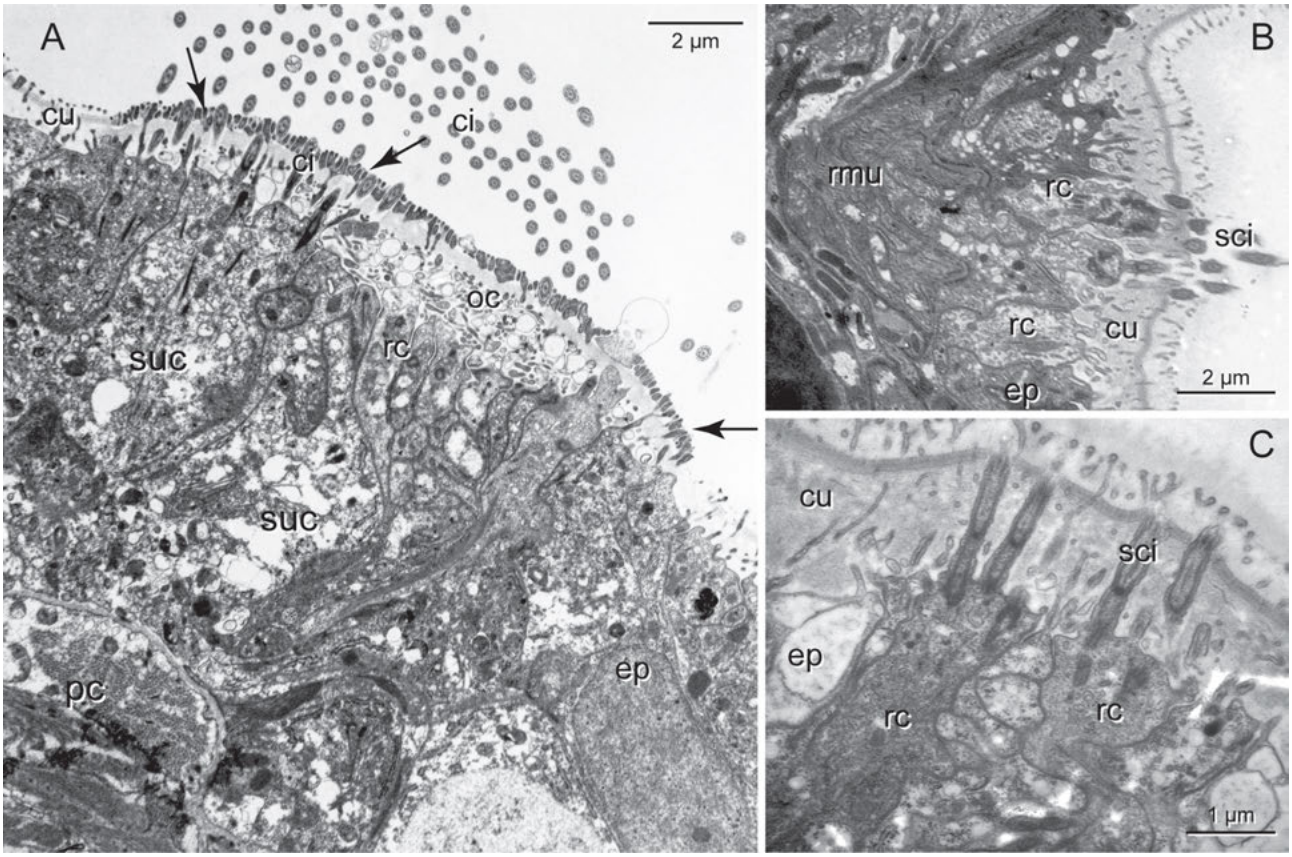


Fig. 7.11.2.8: Sense organs. TEM. A, *Pharyngocirrus krusadensis*, nuchal organ, multiciliated supportive cells (suc), monociliary receptor cells (rc), microvilli of supportive cells form specialized cover above nuchal organ (arrows), olfactory chamber (oc) with numerous sensory processes; B, *Saccocirrus papillocercus*, ciliary tuft associated with parapodia (see also Fig. 7.11.2.7D–F) formed by monociliary receptor cells (rc), a retractor muscle is attached to the base of the receptor cells; C, *S. papillocercus*, group of epidermal multiciliary receptor cells. ci, cilium; cu, cuticle; ep, epidermis; oc, olfactory chamber; pc, palp canal; rc, receptor cell; sci, sensory cilium; suc, supportive cell.

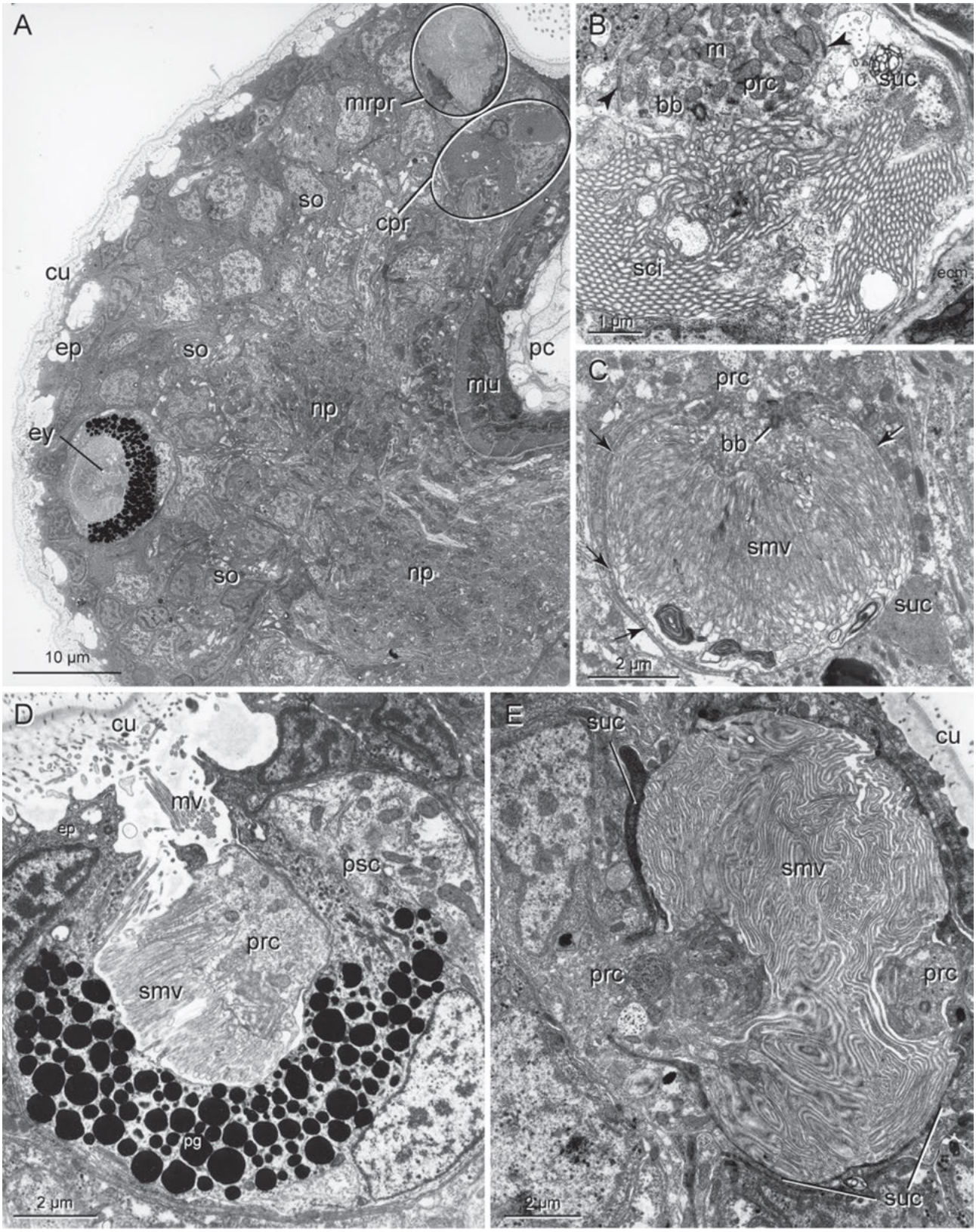
have been described, the median being by far the largest and emanates with two branches from the dorsal and ventral commissure in the brain (Purschke 1993). This pattern can be observed under the CLSM as well and may be present with some modifications in the entire group (Fig. 7.11.2.1K).

Other nerves originating from the brain are running posteriorly; these are the nuchal nerve, at least three dorsal or dorsolateral longitudinal nerves, and the stomatogastric nerves (Fig. 7.11.2.1K) (Purschke 1993, Müller 1999, Di Domenico et al. unpublished observation). The stomatogastric nerve has three roots emanating from the brain, which form a commissure just behind the neuropil. From here, it continues as two fiber bundles that form a loop behind the mouth and below the esophagus. From these loops, the pharyngeal region and the esophagus are innervated.

The ventral nerve cord is characterized by two comparatively widely separated main neurite bundles. Distinct

▸ **Fig. 7.11.2.9:** Photoreceptor-like sense organs. Transmission electron microscopy (TEM) micrographs. A, B, D, E, *Saccocirrus papillocercus*; C, *Pharyngocirrus krusadensis*; A, Low-power micrograph showing almost complete prostomium in longitudinal section with anterior pigmented eye (ey) embedded in somata of brain neurons (so) and ciliary photoreceptors (cpr) and multicellular rhabdomeric photoreceptor (mrpr) above palp canal (pc); B, Ciliary photoreceptor, receptor cell (prc) with numerous mitochondria (m) and basal body (bb), sensory processes represented by branches of cilia (sci) occupying cavity formed by receptor cell and supportive cell (suc), arrowheads point to junctional complexes between the two cells; C, Bicellular rhabdomeric photoreceptor, photoreceptor cell (prc) with numerous sensory microvilli (smv), the latter enveloped by thin supportive cell (arrows, suc); D, Pigmented eye, pigmented supportive cell (psc) with apical microvillar brush border (mv) and apical part of rhabdomeric photoreceptor cell (prc), note connection of eye cup to subcuticular space; E, Multicellular rhabdomeric photoreceptor with two receptor cells (prc), supportive cell (suc) forms thin envelope around sensory microvilli (smv). bb, basal body; cpr, ciliary photoreceptor; cu, cuticle; ecm, extracellular matrix; ep, epidermis; ey, pigmented eye; mrpr, multicellular rhabdomeric photoreceptor; mu, musculature; mv, microvilli; np, neuropil; pc, palp canal; pg, pigment granule; psc, pigmented supportive cell; m, mitochondria; sci, sensory cilia; so, soma; suc, supportive cell.

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ganglia do not exist; the somata are more or less evenly distributed along its length. In each segment, several smaller commissures are present, which exhibit a segmental pattern. The first commissure is formed behind the mouth and is the thickest. In *Saccocirrus papillocercus*, Müller (1999) found four transverse and two oblique commissures, which cross at the ventral midline. In *Saccocirrus parvus*, a comparable number of commissures is present (Di Domenico et al. unpublished observation). The main longitudinal nerves are complemented by a number of other longitudinal neurite bundles that are more or less evenly distributed around the body. In *Saccocirrus papillocercus*, 17 have been counted laterally and dorsally and another 2 bundles between the main trunks of the ventral cord (Müller 1999, Purschke 2016). These are regularly interconnected with each other and with the ventral cord by five circular neurite bundles. Thus, the entire nervous system has an orthogonal appearance. Neurites from the ventral cord and from dorsolateral nerves innervate the adhesive lobes in the pygidium (Fig. 7.11.2.1M).

Sensory organs. Sensory organs found in Saccocirridae include pigmented eyes, various types of unpigmented photoreceptive organs, palps, nuchal organs, various ciliary tufts, and segmentally arranged ciliated papillae or tufts associated with the parapodia (Figs. 7.11.2.3A–F, 7.11.2.4A, B, D, E, 7.11.2.8A–C, 7.11.2.9A–E). The latter are situated somewhat ventral and posterior to the parapodial lobes and were first described by Goodrich (1901) but most likely occur in every species (Di Domenico et al. 2014b). Compared to other tufts of sensory cilia on the trunk and palps, these cilia are considerably longer (Fig. 7.11.2.3D, E), but each bundle comprises cilia of different lengths throughout (Fig. 7.11.2.7F). Out of these, only the photoreceptors and nuchal organs have so far been studied with TEM (Eakin et al. 1977, Purschke 1988a, 1992, Arendt el al. 2009). Although the structure of the palps and that of the central nervous system were described together with a general outline of receptor cells in Protodrilida, the details of these cells are still missing for Saccocirridae (Purschke 1993). However, preliminary observations indicate that both multiciliary and monociliary receptor cells are present (Purschke unpublished observation). Among the latter, penetrative and nonpenetrative receptor cells occur (Fig. 7.11.2.8B, C). The ciliary tufts associated with the parapodia are exclusively composed of monociliary receptor cells (Purschke unpublished observation). The nuchal organs consist of ciliated supportive cells and bipolar receptor cells arranged in small bundles comprising 5 to 25 receptor cells (Fig. 7.11.2.8A) (Purschke 1988a). The receptor cells are monociliary with cilia extending into the subcuticular olfactory chamber as is typical for annelid nuchal organs (Purschke 1988a, 1997). The number of ciliary cells and receptor cells varies among species as does the size of the nuchal organs.

There are five types of photoreceptive organs present in Saccocirridae, some of which have potential of taxonomic significance (Purschke 1992). The pigmented eyes are structurally identical in all species investigated so far. The eyes are bicellular comprising a shading pigment cell and a rhabdomeric photoreceptor cell embedded in the epidermis (Fig. 7.11.2.9A, D). Both cells exhibit apical extensions with rhabdomer-like microvilli and one vestigial cilium (Eakin et al. 1977, Purschke 1992, 2005, Purschke et al. 2006, Arendt et al. 2009, Di Domenico et al. 2014b). Interestingly, the eye-cup formed by the two cells is not entirely closed but communicates with the subcuticular space. The occurrence of microvilli and an axon in the pigmented supportive cell has been suggested as being indicative for a still present sensory function of this cell (Arendt et al. 2009). In addition to these pigmented eyes, four different types of photoreceptor-like organs have been found in *Saccocirrus papillocercus* and *Pharyngocirrus krusadensis* (Purschke 1992). They comprise an inconspicuous supportive cell and one or a few photoreceptor cells of either rhabdomeric or ciliary design. In close association with the axons of the eye, a minute ciliated photoreceptor structure is present (Purschke 1992). A third, larger type of ciliary photoreceptor occurs at the posterior end of the prostomium (Fig. 7.11.2.9A, B). Several organs arranged in two groups may be found in the prostomium in the two species investigated. In addition to these organs, two further groups of six bicellular rhabdomeric photoreceptor organs each have been found in *P. krusadensis*, which were absent in *S. papillocercus* (Fig. 7.11.2.9C). In contrast to the latter, a multicellular photoreceptor organ was described at the posterior end of the prostomium above the ciliated ones (Figs. 7.11.2.3C, 7.11.2.9C). This latter organ may be visible under light microscopy if viewed with interference contrast (Fig. 7.11.2.3C). Because these latter two photoreceptive structures occur species specific, they are of potential taxonomic or phylogenetic importance in the family if studied at a broader scale. Only those organs employing ciliary photoreceptor cells can be visualized and counted after staining with antibodies against tubulin.

Coelom, blood vascular system, and nephridia

Saccocirridae have a well-developed coelom subdivided by septa and mesenteries (Westheide 2008). The coelom of the palps is separated from that of the body, completely filled with movable coelenchyme cells as already described (p. 282). A blood vascular system is present and comprises dorsal and ventral vessels (Goodrich 1901, Salensky 1907, Purschke 1993). These are connected by

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a loop surrounding the gut in each segment. The dorsal vessel divides anteriorly into two branches encircling the mouth and pharynx and then uniting and forming the ventral vessel. Laterally, each anterior branch gives off a blind-ending small vessel running into the palp. In the anterior region of the ampullae, there is a zone of close contact between blood space and palp coelom where the blood directly borders to the ECM surrounding the palp canal system. However, typical podocytes forming this part of the coelomic lining of the canals as described for Protodrilidae have not been found (Purschke 1993). Nephridia are of the metanephridia type and occur in all segments, except for the pharyngeal region and the posteriormost ones. As already observed by Goodrich (1901), their funnels are comparatively small. They can easily been visualized after staining with antibodies against tubulin (Fig. 7.11.2.1K, M).

Reproduction, development, and life cycles

The life history of saccocirrids may also be the determinant of their wide occurrence in shallow habitats, mainly sandy beaches. The species present internal fertilization, indirect development with planktotrophic larvae, a lifespan of 1 year, and seasonal reproductive events (Sasaki and Brown 1983, Westheide 1990, Giangrande 1997). Except for possessing pelagic larvae, several reproductive synapomorphies of the family are clear adaptations to interstitial life. Transverse pygidial adhesive ridges provide attachment and stability among the sand grains, and seminal vesicle and penis facilitate sperm transfer in these turbulent upper layers of the seafloor (Westheide 1984). Other reproductive adaptations to these environments are the genital hooks in *Saccocirrus heterochaetus* (see Jouin 1975) and *Saccocirrus slateri* (see Di Domenico et al. 2019) or the ovoviviparity in *Saccocirrus burchelli* (see Silberbauer 1969) and *Saccocirrus* sp. from Bocas del Toro, Panama (Di Domenico et al. 2014a).

Saccocirridae have a complex reproductive system differing in the arrangements of genital organs between genera and in numbers among species. The females have fertile segments in the median region of the body spanning up to 100 segments. Each fertile segment has its own reproductive system with paired or unpaired genital structures comprising spermathecae and ovaries. The number of oocytes present per segment varies from just 1 or 2 in *Pharyngocirrus goodrichi* to about 30 to 50 in *Saccocirrus uchidai* (see table 1 in Jouin-Toulmond and Gambi 2007). Usually, eggs are small (<100 µm in diameter) as typical in annelids with indirect development (Figs. 7.11.2.1J, 7.11.2.2L) (Westheide 1984). There is no obvious correlation between the number of eggs per segment and the genus. The development of sperm takes place in the coelomic cavity, and morulae of spermatids are formed (Brown 1981). Most likely, all males produce filiform sperm, and ultrastructural data are only available for an undetermined species (Purschke 2006). These comprise a simple acrosome, an elongated nucleus, and a long midpiece with thread-like mitochondria and stabilizing elements. Males have protractile penises situated in an epidermal pouch behind the parapodia and seminal vesicles with spermioducts (Figs. 7.11.2.1D, I, 7.11.2.2K) (Brown 1981, Purschke 2006). The copulatory organs consists of epithelial, glandular, and sensory cells. Stylet-like structures and genital chaetae have been described for certain species (Aiyar and Alikunhi 1944, Brown 1981, Jouin 1975). However, although internal fertilization seems inevitable, sperm transfer has not yet been observed.

The reproductive system is found unpaired in *Pharyngocirrus* species and paired among *Saccocirrus* species (Brown 1981, Di Domenico et al. 2014a). Within each genus, the species show a distinct number of fertile segments, presence or absence of ovaries, size of mature oocytes, number of segments with oocytes, and position of the testes (Brown 1981, Di Domenico et al. 2014a). Among *Pharyngocirrus*, females are described with ovaries on the left side in *P. uchidai*, *P. labilis*, *P. krusadensis*, and *P. goodrichi* and on the right side in *P. gabriellae*, *P. eroticus*, and *P. sonomacus*. The remaining species are reported unspecified as unilateral. The males present testes on the left side or are reported as unilateral. The number of fertile segments varies from 20 segments in *S. heterochaetus* to 175 segments in *Saccocirrus major* and 180 segments in *Pharyngocirrus burchelli*. Several details of the reproductive system remain unknown for *Saccocirrus waianaensis*, *Saccocirrus oahuensis*, *S. parvus*, *Pharyngocirrus alanhongi*, and *Pharyngocirrus archiboldi*.

Data on the development are restricted to a few species (*Saccocirrus uchidai*, *Pharyngocirrus krusadensis*, and *Pharyngociruus eroticus*) (Gray 1969, Sasaki and Brown 1983). Cleavage is spiral, and after 24 to 48 h, the trochophore is formed. In *S. uchidai*, the 48 h larva is characterized by two extensible oral arms used for collecting food. Midventral and mouth ciliation are at least present in the larva of *S. uchidai*, the only saccocirrid for which complete larval development is known (Sasaki and Brown 1983). Larvae swim by two ciliary rings or glide on the substratum using the midventral ciliary groove. Chaetae do not develop until the 10-segment stage is reached. In contrast, in *P. krusadensis*, the first chaetae are formed in the 3-segment stage. Mouth and midventral ciliation, and the prostomial longitudinal ciliary bands, may have evolved as retention of larval characters into the adult stage in *Pharyngocirrus*

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(underdevelopment, pedomorphosis) (Di Domenico et al. 2014a). During development of this species, the midventral ciliary band is progressively reduced and totally absent in most of the adults studied, whereas mouth ciliation is retained in all *Pharyngocirrus* species (Sasaki and Brown 1983). The retention of larval features is common in other interstitial groups (Westheide 1997, Worsaae and Kristensen 2005, Worsaae et al. 2012). The dispersal of these animals may be determined by their characteristics of grouping abundantly in a narrow strip of the mesolittoral (facilitating internal fertilization) and by the presence of planktotrophic larvae that are transported by littoral drift currents.

Biology and ecology

Distribution

Saccocirridae are found from medium to coarse sediments and gravel, from intertidal to subtidal regions. Records from the deeper sublittoral zone and the deep sea are lacking. Most records refer to only 3 of the 23 species: *Saccocirrus papillocerus*, *Saccocirrus parvus*, and *Pharyngocirrus krusadensis*. These species are usually recorded in sandy beach environments (Du Bois-Reymond Marcus 1946, 1948, Westheide 2008, Villora-Moreno et al. 1991, Di Domenico et al. 2009, 2019). A revision of the literature showed that *Pharyngocirrus* and *Saccocirrus* show different habitat preferences (Brown 1981, Di Domenico et al. 2014a). Species of *Pharyngocirrus* occur intertidally at sheltered beaches, bays, or coves, between rocks in tidal pools or subtidally. Generally, they occur in coarse sand with a well-defined redox layer. Species of *Saccocirrus* are found intertidally in well-oxygenated coarse sand of exposed beaches and can often be found in the surf zone where they are hunting for prey or animals damaged by wave action. These annelids cling to sand grains or shells using their posterior appendages and sticky skin due to mucous produced by adhesive glands particularly in high hydrodynamic environments (Du Bois-Reymond Marcus 1946, Martin 1978, Westheide 1990, Di Domenico et al. 2014b, 2019).

Both genera are usually found worldwide in tropical to temperate zones, but most species are described from warmer waters (Brown 1981, Di Domenico et al. 2014a), except *Pharyngocirrus eroticus* described from Orcas Island, West Coast of North America (Gray 1969). The deepest record of the family is *Saccocirrus waianaensis* found at 30 to 35 m in Oahu Island, Hawaii (Bailey-Brock et al. 2003). So far, records from boreal and polar latitudes are lacking. Geographic analyses yielded a well-supported diversity gradient of Saccocirridae, with a maximal diversity estimated at 20°N and with 95% of the diversity found between 0° and 30°N (Di Domenico et al. 2014b). In Europe, saccocirrids occur in the Mediterranean (three species) (Jouin-Toulmond and Gambi 2007) and up to the British Isles and Britany (*Saccocirrus papillocercus*), i.e., up to 50°N (Westheide 2008). These localities have been regarded to represent the northern limits in Europe so far. However, probably due to climate change and rising sea temperatures, this species extended its area into the North Sea and has repeatedly been found on the north Sea Island of Sylt (55°N, West Coast, surf zone) (Purschke unpublished observation). It remains to be seen whether the species is able to establish a stable population. In the Pacific region, the northern distribution limits are almost in the same range (American coastline: San Juan Island 48°40′N, Asian coastline: Possjet Bay, Russia, 43°N). *S. papillocercus*, the first species of Saccocirridae, was described in 1871 at Sebastopol Bay, Crimea Peninsula, Black Sea (Bobretzky 1871). Since then, *S. papillocercus* was reported by several authors along the Mediterranean Sea (Pierantoni 1906, 1907, Jouin-Toulmond and Gambi 2007) and North Atlantic (Boaden 1963, Núñez et al. 2005).

The distribution patterns of the described species of Saccocirridae have been summarized by Di Domenico et al. (2014a, table 3). *S. major* Pierantoni, 1907, *S. parvus* Gerlach, 1953, and *P. goodrichi* Jouin-Toulmond & Gambi, 2007 were reported from the Mediterranean Sea, but *S. parvus* was also reported from Canary Islands (Spain) (Di Domenico et al. 2019). *Saccocirrus archiboldi* Kirsteuer, 1967 and *S. pussicus* Du Bois-Reymond Marcus, 1948 have been described from the Atlantic region (Caribbean and Brazil, respectively). The other *Saccocirrus* species are known from the Indo-Pacific region, with records from India (*Saccocirrus orientalis* Alikunhi, 1946, *S. minor* Aiyar & Alikunhi, 1944, and *Saccocirrus cirratus* Aiyar & Alikunhi, 1944), Australia (*S. minor*), east coast of South Africa (*S. heterochaetus* Jouin, 1975 and *S. orientalis*), and Hawaii (*S. oahuensis* Bailey-Brock, Dreyer & Brock 2003 and *S. waianaensis* Bailey-Brock, Dreyer & Brock 2003). Within *Pharyngocirrus*, most records are known for *P. krusadensis* Alikunhi, 1942: South Africa, India, French Polynesia, and Australia. The following *Pharyngocirrus* species are reported from the Pacific: *P. eroticus* Gray, 1969, *P. labilis* Yamanishi, 1973, *P. sonomacus* Martin, 1977, *P. jouinae* Brown, 1981, *P. tridentiger* Brown, 1981, *P. uchidai* Saski, 1981, and *P. alanhongi* Bailey-Brock, Dreyer & Brock 2003, whereas *P. burchelli* Silberbauer, 1969 is only known from South Africa, Cape Agulhas, at the border between the Atlantic and Indian oceans. Only two species are known from the Atlantic (Mediterranean Sea and west Atlantic Ocean), *P. goodrichi* from Naples (Jouin-Toulmond and Gambi 2007) and *P. gabriellae* Du Bois-Reymond Marcus, 1946, which undoubtedly show that *Pharyngocirrus* has its distribution focus in the Indo-Pacific region, although disproving its restriction to this area (Jouin-Toulmond and Gambi 2007).

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Moreover, several yet undescribed species have been found in the Atlantic, possibly changing this view in the future (Di Domenico et al. 2014a).

Ecology

Data on the ecology and biology beyond distribution of Saccocirridae are still scarce. *Pharyngocirrus eroticus* and *P. krusadensis* are suggested to be suspension feeders using the ventral ciliation of the head to set up a strong water current drawing bacteria, diatoms, and algae from the shell gravel into the mouth (Gray 1969, Brown 1981, Jumars et al. 2015). The muscular pharynx appears to have a mechanical crushing and sorting function. The esophageal region is glandular, and absorption occurs in the intestine. Food is moved through the gut by the cilia of the ventral groove, as the gut does not have a well-developed muscle layer (Gray 1969).

Saccocirrus pussicus can be maintained in the laboratory feeding on *Skeletonema* sp. or on net plankton collected on the beaches from which worms were collected. *S. pussicus* used the waving motion of the palps to capture particles and transferred them to the mouth by helicoidal coiling of the palps, suggesting that a suspension feeding happened both at the sediment-water interface and interstitially (Di Domenico et al. 2014c). They also observed direct ingestion of particles by the mouth in a deposit-feeding mode. The feeding and motility strategies are well discussed by Jumars et al. (2015), and their guilds are inferred as "both morphotypes are small and rely on labile material." Both appear capable of surface deposit feeding with the palps or directly with the mouth or suspension feeding with coiled palps. It appears that *Pharyngocirrus* spp. are more herbivorous than *Saccocirrus* spp., being more carnivorous, but there is likely some overlap in food items. All are motile crawlers and ciliary gliders.

Saccocirrus species also displayed *in situ* ingestion of microfibers, rapidly egested with no apparent harm, inferring a potential indicator for trophic transfer studies into marine food webs through predation of *Saccocirrus* (Gusmao et al. 2016). The authors suggested that their nonselective microphagous suspension-feeding behavior makes *Saccocirrus* more prone to ingest microfibers (Gusmao et al. 2016).

Phylogeny and taxonomy

The monophyly of the family Saccocirridae was sustained by phylogenetic analyses (Di Domenico et al. 2014a) and the presence of palp canals with basal ampullae, transverse pygidial adhesive ridges, parapodial ciliary tufts, penis and seminal vesicles, as well as the presence of a specific type of long chaetae (Purschke and Jouin 1988, Di Domenico et al. 2014a).

Since the 1970s, it is obvious that two groups of species in Saccocirridae exist (Jouin 1971), and in certain older taxonomic and morphological studies, different species have been mixed under the name *Saccocirrus papillocercus* (e.g., Goodrich 1901, Salensky 1907). Within Saccocirridae, the monophyly of the genera *Pharyngocirrus* and *Saccocirrus* was supported by molecular and morphological synapomorphies. These two genera were previously called the "papillocercus" (=*Saccocirrus*) and "krusadensis" (=*Pharyngocirrus*) species complex in several studies (Brown 1981, Purschke and Jouin 1988, Purschke 1992, Jouin-Toulmond and Gambi 2007, Westheide 2008, Di Domenico et al. 2019). After phylogenetic analyses including four target genes (*18S + 16S + H3 + 28S*) and 34 morphological characters, these two genera have been formally described (Di Domenico et al. 2014a). The most striking morphological difference between *Pharyngocirrus* and *Saccocirrus* is the lack of a ventral pharyngeal bulbus muscle in *Saccocirrus* (Purschke and Jouin 1988, Purschke and Tzetlin 1996).

The monophyly of *Pharyngocirrus* was also supported by the presence of a prostomial transverse ciliary band, presence of a ventral pharyngeal apparatus with a tongue-like organ, presence of a mouth ciliation arranged as paired longitudinal bands, unilateral arrangement of the seminal vesicle (Fig. 7.11.2.1D), long chaetae lyrate (Fig. 7.11.2.1F, G), bifid medium chaetae, and notched apex short chaetae. The presence of asymmetrical lyrate chaetae and the presence of a midventral ciliary band up to segment 10 (Figs. 7.11.2.2E, 7.11.2.5A) are the synapomorphies supporting a clade with *P. tridentiger*, *P. jouinae*, and *P. krusadensis*. The presence of a ventral mouth ciliation arranged as paired longitudinal bands and the presence of a ventral pharynx are synapomorphies for *Pharyngocirrus* (Brown 1981, Jouin-Toulmond and Gambi 2007, Di Domenico et al. 2014a).

Because the clade comprising Protodrilidae and *Protodriloides* is the sister group of Saccocirridae (Andrade et al. 2015, Struck et al. 2015, Weigert and Bleidorn 2016), the absence of a prostomial transverse ciliary band, the ventral pharynx with its conspicuous muscle bulb, and the ciliary patches around the buccal area are coded as lacking for the genus *Saccocirrus*. However, the monophyly of the genus is supported by the presence of bilateral seminal vesicles, robust forked chaetae (Fig. 7.11.2.2F–H), and spatulated medium and short chaetae.

Genera diagnoses

Saccocirrus Brobretzky, 1872

Type species: *Saccocirrus papillocercus* Brobretzky, 1872 (Fig. 7.11.2.1A–L)

Diagnosis: Brown body. Prostomium with two pigmented eyes and long filiform palps. Ventral muscular pharynx, and ciliary patches absent. Uniramous parapodia with three types of chaetae: (1) one to two long chaetae, robust

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and forked with equal or unequal prongs; (2) two to three medium spatulated chaetae; and (3) two to three short spatulated chaetae, with notched apex. Females with bilateral ovaries. Males with bilateral seminal vesicles.

Species: *Saccocirrus papillocercus* Brobretzky, 1872. Type locality: Sebastopol Bay, Russia (Black Sea, Europe) (Brobretzky 1872, Repiachoff 1881, Goodrich 1901, Pierantoni 1906, 1907, Gusjewa 1929, Purschke 1988a, Mastepanova 2004, Abd-Elnaby 2009).

Saccocirrus major Pierantoni, 1907. Type locality: Resina, Italy (Mediterranean Sea) (Pierantoni 1907, Uchida 1933, Villora-Moreno 1997). Uchida and Okuda (1953) reported the species in the coast of Japan, Pacific Ocean (needs further investigation).

Saccocirrus orientalis Alikunhi, 1946. Type locality: Madras, India (Indian Ocean) (Alikunhi 1946, Jouin 1975, Jouin and Rao 1987).

Saccocirrus minor Aiyar & Alikunhi, 1944. Type locality: Madras Beach, India (Indian Ocean) (Aiyar and Alikunhi 1944, Jouin and Rao 1987, Rao and Ganapati 1968).

Saccocirrus pussicus Du Bois-Reymond Marcus, 1948. Type locality: São Sebastião Island, Brazil (Du Bois-Reymond Marcus 1948, Di Domenico et al. 2014a, b, Gusmao et al. 2016).

Saccocirrus heterochaetus Jouin, 1975. Type locality: Amanzimtoti (Natal), South Africa (Jouin 1975).

Saccocirrus parvus Gerlach, 1953. Type locality: Marina di Pisa, Italy (Mediterranean Sea) (Gerlach 1953, Villora-Moreno et al. 1991, Westheide 1972).

Saccocirrus oahuensis Bailey-Brock, Dreyer & Brock 2003. Type locality: Hanauma Bay, Oahu, Hawaii (Bailey-Brock et al. 2003).

Saccocirrus waianaensis Bailey-Brock, Dreyer & Brock 2003. Type locality: Barbers Point, Oahu, Hawaii (Bailey-Brock et al. 2003).

Saccocirrus cirratus Aiyar & Alikunhi, 1944. Type locality: Madras Beach, India (Indian Ocean) (Aiyar and Alikunhi 1944).

Saccocirrus slateri Di Domenico, Martínez & Worsaae 2019. Type locality: Tenerife Island, Canary Islands, Spain (Di Domenico et al. 2014a, 2019, Gusmao et al. 2016).

Pharyngocirrus Di Domenico, Martínez, Lana & Worsaae, 2014

Type species: *Pharyngocirrus gabriellae* (Du Bois-Reymond Marcus, 1946) (Fig. 7.11.2.2A–L).

Diagnosis: Brown body. Prostomium with two pigmented eyes and long filiform palps. Presence of prostomial transverse ciliary band. Mouth surrounded by ciliary patches consisting of paired longitudinal bands. Midventral ciliary band may be present. Ventral muscular pharynx present. Uniramous parapodia with three types of chaetae: (1) long capillary chaetae lyrate (equal or unequal sides) with a small median tooth, (2) medium bifid chaetae with equal lateral prongs, and (3) short chaetae with notched apex. Females with unilateral ovaries on the right or left side of the gut. Males with unilateral seminal vesicles on the right or left side of the gut.

Species: *Pharyngocirrus krusadensis* (Alikunhi, 1946). Type locality: Krusadai Island, India (Indian Ocean) (Alikunhi 1946, Brown 1981, Sasaki and Brown 1983, Purschke 1988a).

Pharyngocirrus gabriellae (Du Bois-Reymond Marcus, 1946). Type locality: Guarujá Beach, Brazil (Du Bois-Reymond Marcus 1946, Wu and Yang 1962, Di Domenico et al. 2014a, c).

Pharyngocirrus eroticus (Gray, 1969). Type locality: Orcas Island, Washington, USA (Pacific Ocean) (Gray 1969).

Pharyngocirrus labilis (Yamanishi, 1973). Type locality: Tanabe Bay, Wakayama, Japan (Yamanishi 1973).

Pharyngocirrus archiboldi (Kirsteuer, 1967). Type locality: Middle Bay, Dominica (Caribbean) (Kirsteuer 1967).

Pharyngocirrus sonomacus (Martin, 1977). Type locality: California, USA (Pacific Ocean) (Martin 1977, 1978, Schmidt and Westheide 1977, Di Domenico et al. 2014a).

Pharyngocirrus jouinae (Brown, 1981). Type locality: New South Wales, Australia (Pacific Ocean) (Brown 1981, Di Domenico et al. 2014a).

Pharyngocirrus tridentiger (Brown, 1981). Type locality: New South Wales, Australia (Pacific Ocean) (Brown 1981, Di Domenico et al. 2014a).

Pharyngocirrus uchidai (Sasaki, 1981). Type locality: Hokkaido, Japan (Pacific Ocean) (Sasaki 1981).

Pharyngocirrus goodrichi (Jouin-Toulmond & Gambi, 2007). Type locality: Ischia Island, Gulf of Naples, Italy (Mediterranean Sea) (Jouin-Toulmond and Gambi 2007).

Pharyngocirrus burchelli (Silberbauer, 1969). Type locality: Cape Agulhas, South Africa (Silberbauer 1969).

Pharyngocirrus alanhongi (Bailey-Brock, Dreyer & Brock 2003). Type locality: Wai'anae, O'ahu (Hawaii) (Bailey-Brock et al. 2003).

References

Abd-Elnaby, F.A. (2009): New records from the south part of Suez Canal, Egypt. *World Journal of Fisheries and Marine Science* 1: 7–19.

Aiyar, R.G. & Alikunhi, K.H. (1944): On some archiannelids of the Madras Coast. *Proceedings of the National Institute of Sciences of India* 10: 113–140.

Alikunhi, K.H. (1946): On a new species of *Saccocirrus* from the Madras Beach. *Current Science (Bangalore)* 15: 149.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids":

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Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Arendt, D., Hausen, H. & Purschke, G. (2009): The 'division of labour' model of eye evolution. *Philosophical Transactions of the Royal Society B Biological Sciences* 364: 2809–2817.

Bailey-Brock, J.H., Dreyer, J. & Brock, R.E. (2003): Three new species of *Saccocirrus* (Polychaeta: Saccocirridae) from Hawai'i. *Pacific Science* 57: 463–478.

Boaden, P.J.S. (1963): The interstitial fauna of some North Wales beaches. *Journal of the Marine Biological Association of the United Kingdom* 43: 79–96.

Bobretzky, N.V. (1872): *Saccocirrus papillocerus*, n. gen., n. sp. Tip' novago semeistra annelid. Sravmitel'no-Anatomichskii obcherk. *Kiev Odschestva Estest Zapisky* 2: 211–259. [in Russian]

Brown, R. (1981): Saccocirridae (Annelida: Archiannelida) from the central coast of New South Wales. *Australian Journal of Marine and Freshwater Research* 32: 439–456.

Di Domenico, M., Lana, P.C. & Garraffoni, A.R.S. (2009): Distribution patterns of interstitial polychaetes in sandy beaches of southern Brazil. *Marine Ecology* 30: 47–62.

Di Domenico, M., Martinez, A., Lana, P. & Worsaae, K. (2014a): Molecular and morphological phylogeny of Saccocirridae (Annelida) reveals two cosmopolitan clades with specific habitat preferences. *Molecular Phylogenetics and Evolution* 75: 202–218.

Di Domenico, M., Martinez, A., Amaral, A.C.Z., Lana, P.C. & Worsaae, K. (2014b): Saccocirridae (Annelida) from the southern and southeastern Brazilian coasts. *Marine Biodiversity* 44: 313–325.

Di Domenico, M., Martinez, A., Almeida, T.C.M., Martins, M.O., Worsaae, K. & Lana, P.d.C. (2014c): Response of the meiofaunal annelid *Saccocirrus pussicus* (Saccocirridae) to sandy beach morphodynamics. *Hydrobiologia* 734: 1–16.

Di Domenico, M., Martinez, A., & Worsaae, K. (2019): Saccocirridae (Annelida) from the Canary Islands with a description of *Saccocirrus slateri* sp. nov. *Marine Biodiversity* 49: 2125.

Du Bois-Reymond Marcus, E. (1946): On a new archiannelid, *Saccocirrus gabriellae*, from Brazil. *Comunicationes Zoologicas del Museo de Historia Natural de Montevideo* 37: 1–11.

Du Bois-Reymond Marcus, E. (1948): Further archiannelids from Brazil. *Comunicationes Zoologicas del Museo de Historia Natural de Montevideo* 48: 1–22.

Eakin, R.M., Martin, G.G. & Reed, C.T. (1977): Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphologie* 88: 1–18.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–188.

Fransen, M.E. (1980): Ultrastructure of coleomic lining in annelids. *Zoomorphologie* 95: 235–249.

Gerlach, S.A. (1953): Zur Kenntnis der Archianneliden des Mittelmeeres. *Kieler Meeresforschungen* 9: 248–251.

Giangrande, A. (1997): Reproductive patterns, life-cycle and life-history features of polychaetes: An overview. *Oceanography and Marine Biology, Annual Reviews* 35: 323–386.

Goodrich, E. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science* 44: 413–428.

Gray, J.S.A. (1969): A new species of *Saccocirrus* (Archiannelida) from the West Coast of North America. *Pacific Science* 23: 238–251.

Gusjewa, S. (1929): Zur Kenntnis von *Saccocirrus*. *Zoologischer Anzeiger* 84: 151–157.

Gusmao, F., Di Domenico, M., Amaral, A.C.Z., Martínez, A., Gonzalez, B.C., Worsaae, K., Ivar do Sul, J.A. & Lana, P.d.C. (2016): *In situ* ingestion of microfibres by meiofauna from sandy beaches. *Environmental Pollution* 216: 584–590.

Jouin, C. (1971): Status of the knowledge of the systematics and ecology of Archiannelida. *Smithsonian Contributions to Zoology* 76: 47–56.

Jouin, C. (1975): Étude de quelques Archiannélides des côtes d'Afrique du Sud: Description de *Saccocirrus heterochaetus* n. sp. (Archiannélide, Saccocirridae). *Cahiers de Biologie Marine* 16: 97–110.

Jouin, C. & Rao, G.C. (1987): Morphological studies on some Polygordiidae and Saccocirridae (Polychaeta) from the Indian Ocean. *Cahiers de Biologie Marine* 28: 389–402.

Jouin-Toulmond, C. & Gambi, C. (2007): Description of *Saccocirrus goodrichi* sp. nov. (Annelida: Polychaeta: Saccocirridae), a new Mediterranean species and new data on the chaetae of *S. papillocercus* and *S. major*. *Cahiers de Biologie Marine* 48: 381–390.

Jumars, P.A. Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Kirsteuer, E. (1967): Bredin-Archbold-Smithsonian biological survey of Dominica. 3. Marine archiannelids from Dominica. *Proceedings of the US National Museum* 123: 1–6.

Martin, G.G. (1977): *Saccocirrus sonomacus* sp. nov., a new archiannelid from California. *Transactions of the American Microscopical Society* 96: 97–103.

Martin, G.G. (1978): The duo-gland adhesive system of the archiannelids *Protodrilus* and *Saccocirrus* and the turbellarian *Monocelis*. *Zoomorphologie* 91: 63–75.

Martinez, A., Purschke, G. & Worsaae, K. (2020a): 7.11.3. Protodrilidae. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology. Annelida. Volume 3: Annelida, Pleistoannelida. Sedentaria III and Errantia I*. De Gruyter, Berlin: 299–337. Published online 2017.

Martinez, A., Worsaae, K. & Purschke, G. (2020b): 7.11.3. Protodriloididae. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology. Annelida. Volume 3: Annelida, Pleistoannelida. Sedentaria III and Errantia I*. De Gruyter, Berlin: 338–353. Published online 2018.

Mastepanova, E.A. (2004): Interstitial polychaetes of the seas of Russia. *Invertebrate Zoology* 1: 59–64. [in Russian]

Müller, M.C.M. (1999): *Das Nervensystem der Polychaeten: Immunhistochemische Untersuchungen an ausgewählten Taxa*. Ph.D. thesis, Osnabrück.

Núñez, J., Brito, M.C., & Docoito, J.R. (2005): Anélidos poliquetos de Canarias: Catálogo de especies, distribución y hábitats. *Vieraea*: 33, 297–321.

Pierantoni, U. (1906): Osservazioni suilo sviluppo embrionale e larvale del *Saccocirrus papillocercus* Bobr. *Mitteilungen aus der zoologischen Station zu Neapel* 18: 46–72.

Pierantoni, U. (1907): Il genere *Saccocirrus* Bobretzky e le sue specie. *Annuario dell'Instituto e Museo di Zoologia dell'Universita di Napoli* 2: 1–11.

Purschke, G. (1988a): Comparative electron microscopic investigation of the nuchal organs in *Protodriloides*, *Protodrilus* and *Saccocirrus* (Annelida, Polychaeta). *Canadian Journal of Zoology* 68: 325–338.

Purschke, G. (1988b): Pharynx. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of Polychaeta*. *Microfauna Marina* 4: 177–197.

Purschke, G. (1992): Ultrastructural investigation of presumed photoreceptive organs in two *Saccocirrus* species (Polychaeta, Saccocirridae). *Journal of Morphology* 211: 7-21.

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Purschke, G. (1993): Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology* 113: 1–20.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica* 78: 123–143.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 535/536: 53–78.

Purschke, G. (2006): Problematic annelid groups. In: Rouse, G. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida*. Science Publishers: Enfield: 638–667.

Purschke, G. (2016): Annelida: Basal groups and Pleistoannelida. In: Schmidt-Rhaesa, A. Harzsch, S. & Purschke, G. (eds.), *Structure and Function of Invertebrate Nervous Systems*. Oxford University Press, Oxford: 254–312.

Purschke, G. & Jouin, C. (1988): Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationships within the Protodrilida (Annelida: Polychaeta). *Journal of Zoology* 215: 405–432.

Purschke, G. & Tzetlin, A. (1996): Dorsolateral ciliary folds in the polychaete foregut: Structure, prevalence and phylogenetic significance. *Acta Zoologica* 77: 33–49.

Purschke, G., Arendt, D., Hausen, H. & Müller, M.C.M. (2006): Photoreceptor cells and eyes in Annelida. *Arthropod Structure and Development* 35: 211–230.

Rao, G.C. & Ganapati, P.N. (1968): On some archiannelids from the beach of Waltair Coast. *Proceedings of the National Academy of Sciences of India* 67B: 24–30.

Repiachoff, W. von (1881): Zur Entwickelungsgeschichte des *Polygordius flavocapitatus* Uljan. und *Saccocirrus papillocercus* Bobr. *Zoologischer Anzeiger* 4: 518–520.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, London.

Rousset, V., Pleijel, F., Rouse, G.W., Erseus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Salensky, W. (1907): Morphogenetische Studien an Würmern. *Memoires de l'Académie Impériale des Sciences de St. Pétersbourg. 8. Série Classe des Physico-Mathématique* 19: 1–349.

Sasaki, S. (1981): A new species of the genus *Saccocirrus* (Archiannelida) from Hokkaido, northern Japan. *Annotationes Zoololgicae Japonensis* 54: 259–266.

Sasaki, S. & Brown, R. (1983): Larval development of *Saccocirrus uchidai* from Hokkaido, Japan and *Saccocirrus krusadensis* from New South Wales, Australia (Archiannelida, Saccocirridae). *Annotationes Zoololgicae Japonensis* 56: 299–314.

Schmidt, P. & Westheide, W. (1977): Interstitielle Fauna von Galapagos. XVIII. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). *Mikrofauna des Meeresbodens* 62: 1–38.

Silberbauer, B.I. (1969): Archiannelids of the genus *Saccocirrus* from southern Africa. *Transactions of the Royal Society of South Africa* 38: 165–182.

Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7: 57.

Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535/536: 199–225.

Uchida, T. (1933): On the occurrence of the archiannelid, *Saccocirrus major* Pierantoni in Japan. *Proceedings of the Imperial Academy* 9: 128–129.

Uchida, T. & Okuda, S. (1953): Notes on an archiannelid, *Saccocirrus major*. *Journal of the Faculty of Sciences Hokkaido University Series VI. Zoology* 11: 175–181.

Villora-Moreno, S. (1997): Environmental heterogeneity and the biodiversity of interstitial Polychaeta. *Bulletin of Marine Science* 60: 494–501.

Villora-Moreno, S., Capaccioni-Azzati, R. & Garcia-Carrascosa, A.M. (1991): Meiobenthos of sandy beaches from the Gulf of Valencia (western Mediterranean): Ecology of interstitial polychaetes. *Bulletin of Marine Science* 48: 376–385.

Weigert, A. & Bleidorn, C. (2016): Current status of annelid phylogeny. *Organisms, Diversity & Evolution* 16: 345–362.

Westheide, W. (1972): Nouvelles récoltes d'annélides interstitielles dans les plages sableuses du Bassin d'Arcachon. *Vie et Milieu* 23: 365–370.

Westheide, W. (1984): The concept of reproduction in polychaetes with small body size: Adaptations in interstitial species. *Fortschritte der Zoologie* 29: 265–287.

Westheide, W. (1990): Polychaetes: Interstitial families. In: Kermack, D.M. & Barnes, R.S.K. (eds.), *Synopses of the British Fauna*. 1st ed. Universal Book Services/Dr. W. Backhuys, Oegstgeest: 1–152.

Westheide, W. (1997): The direction of evolution within the Polychaeta. *Journal of Natural History* 31: 1–15.

Westheide, W. (2008): Polychaetes: Interstitial families. In: Kermack, D.M., Barnes, R.S.K., Crothers, J.H. & Hayward, P.J. (eds.), *Synopses of the British Fauna*. 2nd ed. The Linnean Society of London, London: 1–169.

Westheide, W. (2019): Dinophilidae. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology. Annelida. Volume 3: Annelida Basal Groups and Pleistoannelida, Sedentaria III and Errantia I*. De Gruyter, Berlin: 217–234.

Worsaae, K., Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). Hydrobiologia 535 (536): 319–340.

Worsaae, K., Sterrer, W., Kaul-Strelow, S., Hay-Schmidt, A. & Giribet, G. (2012): An anatomical description of a miniaturized acorn worm (Hemichordata, Enteropneusta) with asexual reproduction by paratomy. *PLoS One* 7: 11, e48529.

Wu, B.L. & Yang, D.J. (1962): The taxonomy and distribution of the genus *Saccocirrus* Bobretzky (Archiannelida). *Oceanologica and Limnologia Sinica* 4: 169–179. [Chinese with Russian abstract]

Yamanishi, R. (1973): A new species of *Saccocirrus* (Archiannelida) in Japan. *Proceedings of the Seto Marine Biological Laboratory* 21: 73–76.

Zrzavy, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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7.11.3 Protodrilidae Hatschek, 1888

Introduction

Protodrilidae is a family of interstitial annelids lacking parapodia, chaetae, and appendages, except for two anterior palps. Their body ranges in length from 1 to 13 mm and comprises a rounded prostomium, a comparatively large peristomium, a cylindrical trunk with epidermal cilia and glands, and a pygidium with two adhesive lobes (Fig. 7.11.3.1A–C) (von Nordheim 1989a, Westheide 2008). The most conspicuous external characters of the family are their paired, filiform, ciliated palps arising anteroventrally at the prostomium provided with an internal coelomic channel connected behind the brain and their locomotion by ventral ciliary gliding. Protodrilidae currently consists of 36 described species, which are now grouped into six genera corresponding to monophyletic clades of a recent phylogenetic study employing molecular and morphological data (Martínez et al. 2015). These genera are *Protodrilus* Hatschek, 1881, being the type genus, *Meiodrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015, *Megadrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015, *Lindrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015, *Claudrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015, and *Astomus* Jouin, 1979. This last genus has been previously referred to as *Parenterodrilus* Jouin, 1979 (see remarks below) (Jouin 1992).

Early workers included Protodrilidae within the now disregarded group Archiannelida. Some of them interpreted the simple morphology of Protodrilidae as primitive and close to the annelid stem species (Czerniavsky 1881, Hatschek 1881, Pierantoni 1908), whereas others suggested that this apparent simplicity was rather the result of a secondary adaptation to interstitial life (Goodrich 1901, Remane 1932, Hermans 1969). More recent workers regarded Archiannelida as polyphyletic and placed Protodrilidae, Protodriloidae, and Saccocirridae in the taxon Protodrilida mainly based on the resemblance of the pharynx and palps among the three families (Purschke and Jouin 1988). This placement was supported by cladistic morphological analyses by Rouse and Fauchald (1997) and Parry et al. (2016), in which these three families were nested within the large clade Canalipalpata together with Spionida, Terebellida, and Sabellida. Despite this morphological support, Protodrilida was never recovered in any molecular analysis using single or a few genes (Rousset et al. 2007, Struck et al. 2007, Zrzavý et al. 2009), raising doubts on its monophyly. However, two recent phylogenomic analyses independently recovered Protodrilidae in a clade with Protodriloididae, Saccocirridae, and Polygordiidae, consistently as the first branch within Errantia (Andrade et al. 2015, Struck et al. 2015). With several large-sized annelid taxa branching off at deeper nodes than Protodrilidae (e.g., Weigert et al. 2014, Andrade et al. 2015, Struck et al. 2015, Parry et al. 2016), all phylogenetic studies support a secondary reduction in size and form, which in combination with the lack of larval-juvenile traits suggest that the slender elongate body and simple morphology is the result of gradual miniaturization rather than of progenesis (Westheide 1984, 1987, Worsaae and Kristensen 2005, Struck et al. 2015).

Morphology

Head and palps

All Protodrilidae have a distinct head consisting of a prostomium and peristomium (e.g., Figs. 7.11.3.1A–C, 7.11.3.10A, B, 7.11.3.11A, B). The prostomium is rounded and smaller than the peristomium and possesses a pair of palps as well as pigmented and unpigmented eyes depending on the species (e.g., Figs. 7.11.3.12A, 7.11.3.14G). The palps insert ventrolaterally in the prostomium and are easily lost when the animals are disturbed or fixed. The palps are filiform, ciliated, and provided with an internal coelomic canal, which runs longitudinally all along each palp connecting in the prostomium behind the neuropil of the brain (Figs 7.11.3.2A, 7.11.3.12B, 7.11.3.13A, 7.11.3.14C). The length of the palps varies among species, being longer and very motile in species of *Megadrilus*, *Protodrilus*, and *Lindrilus* and shorter and typically stiffer in species of *Meiodrilus* and *Claudrilus*, although with exceptions (Martínez et al. 2015). Palp ciliation typically consists of scattered compound and isolated cilia belonging to seven morphologically distinct cell types (Purschke 1993). In *Meiodrilus* and *Claudrilus*, palp ciliation is presumably solely sensory, whereas, in *Protodrilus*, *Megadrilus*, and *Lindrilus*, the palps possess additional dorsal and ventral ciliary bands, which can produce water currents (Figs. 7.11.3.11B, 7.11.3.16H) (Martínez et al. 2013, 2015). Rows of so-called bacillary glands (see below) are present on the palps of most species.

The palp canals are primarily made up of longitudinal muscle fibers with a few circular fibers interposed between them (Purschke 1993). In species possessing smaller palps such as *Meiodrilus adhaerens*, the lumen is filled with cell bodies of these muscle fibers, whereas additional coelenchyme cells are present in larger palps (e.g., *Protodrilus ciliatus*) (Fig. 7.11.3.2C). In none of the

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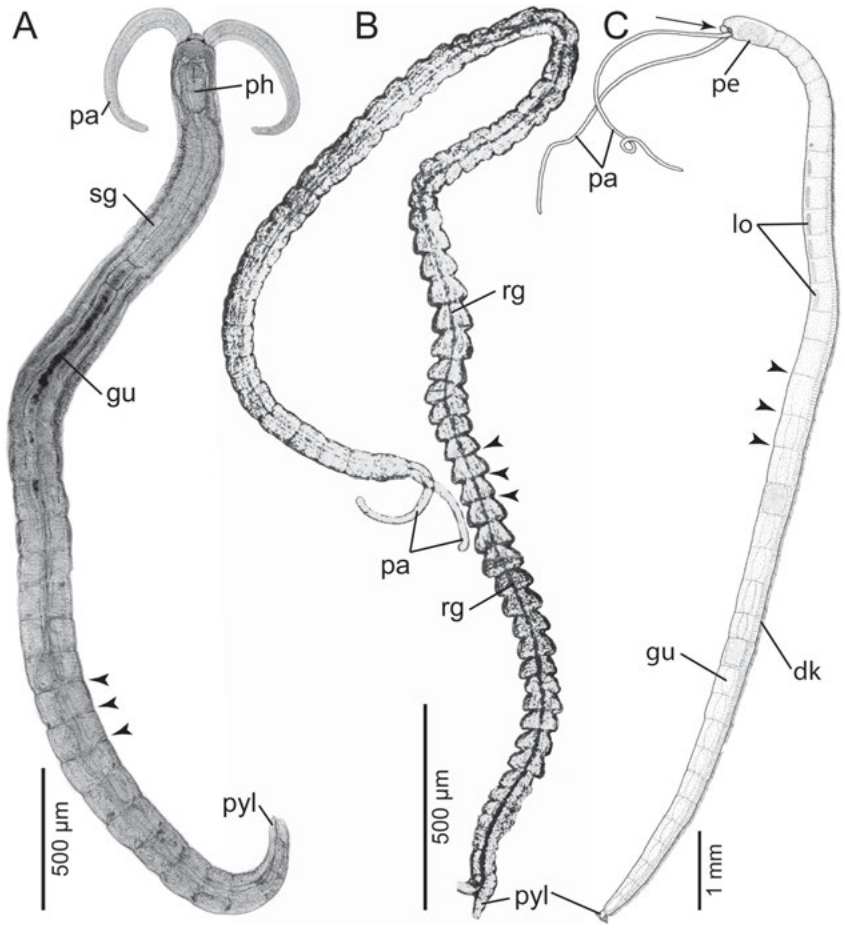


Fig. 7.11.3.1: General organization and habitus of Protodrilidae. Light microscopy (LM) images and drawings from living animals. Arrowheads point to segment borders. A, *Protodrilus oculifer*. mature male; B, *Astomus taenioides*. Adult, note the comparatively numerous segments and their unusal shape in the posterior part. C, *Megadrilus pelagicus*. Note the long palps. Animal normally moves in this J-shaped orientation with anterior end downward. Arrow points to prostomium. dk, dorsal ciliated keel; gu, gut; lo, lateral organ; pa, palp; pe, peristomium; ph, pharynx; pyl, pygidial lobe; rg, residual gut; sg, salivary gland. B, Modified from Jouin (1979); C, Redrawn from Martínez et al. (2017).

species studied so far, these canals are without cells and just fluid filled. Each palp is supplied with an additional bundle of longitudinal fibers, which is located outside the palp canal in an abfrontal position just opposite to the main palp nerve (Fig. 7.11.3.2A–C; $pn_{6,7}$). In addition, each palp is supplied with a blind-ending blood vessel arising from the anterior end of the blood vascular system (Fig. 7.11.3.2C). Podocytes situated at the proximal contact point between these two body compartments most likely transfer fluid to the palp canal from the blood vascular system (Purschke 1993). The palps are innervated by four neurite bundles originating on the dorsal and ventral roots of the circumesophageal connectives (Figs. 7.11.3.2C, 7.11.3.6A, C; $pn_{4,5,6\text{-}7,9}$).

On the prostomium, distinct ciliary patterns can be observed as well (Westheide 2008). These cilia may be grouped as tufts and rings on various positions of the head (Figs. 7.11.3.11B, C, 7.11.3.14H, 7.11.3.19A, 7.11.3.20H). Single and adjoined stiff sensory cilia are abundant (Figs. 7.11.3.14A, 7.11.3.20A–C). The respective receptor cells have been characterized and different types can be distinguished (Purschke 1993). In certain species, these long sensory cilia are important diagnostic features (Westheide 2008). Prostomial unpigmented ciliary and phaosomous photoreceptor-like receptor cells are present depending on the species (Figs. 7.11.3.6A, C, 7.11.3.10D, 7.11.3.12A–D, 7.11.3.14A, G, 7.11.3.15A, 7.11.3.20A, C), whereas pigmented eyes are present in the adults of only seven species and are restricted to *Lindrilus* spp. and a few *Protodrilus* spp. (Figs. 7.11.3.1A, 7.11.3.2A, 7.11.3.12A, 7.11.3.14G, and see below).

The nuchal organs, recognizable by their dense ciliation, are present dorsally or laterally on the posterior prostomium margin. The cilia in the nuchal organs beat continuously, producing a constant water flow. Large and oval nuchal organs are typically found in species of *Protodrilus* and *Megadrilus* (Figs. 7.11.3.11A–C, 7.11.3.16F). In *Megadrilus,* nuchal organs are particularly large and consist of a slightly depressed, dense ciliary band (Fig. 7.11.3.16J). In contrast, most species of *Claudrilus* and *Meiodrilus* have rounded nuchal organs, placed dorsally or dorsolaterally on the prostomium (Figs. 7.11.3.19A, 7.11.3.20B, J), except for a few species, such as *Claudrilus corderoi*, which have scarcely ciliated nuchal organs, best discernible under scanning electron microscopy (SEM) (Fig. 7.11.3.20J) (Di Domenico et al. 2013).

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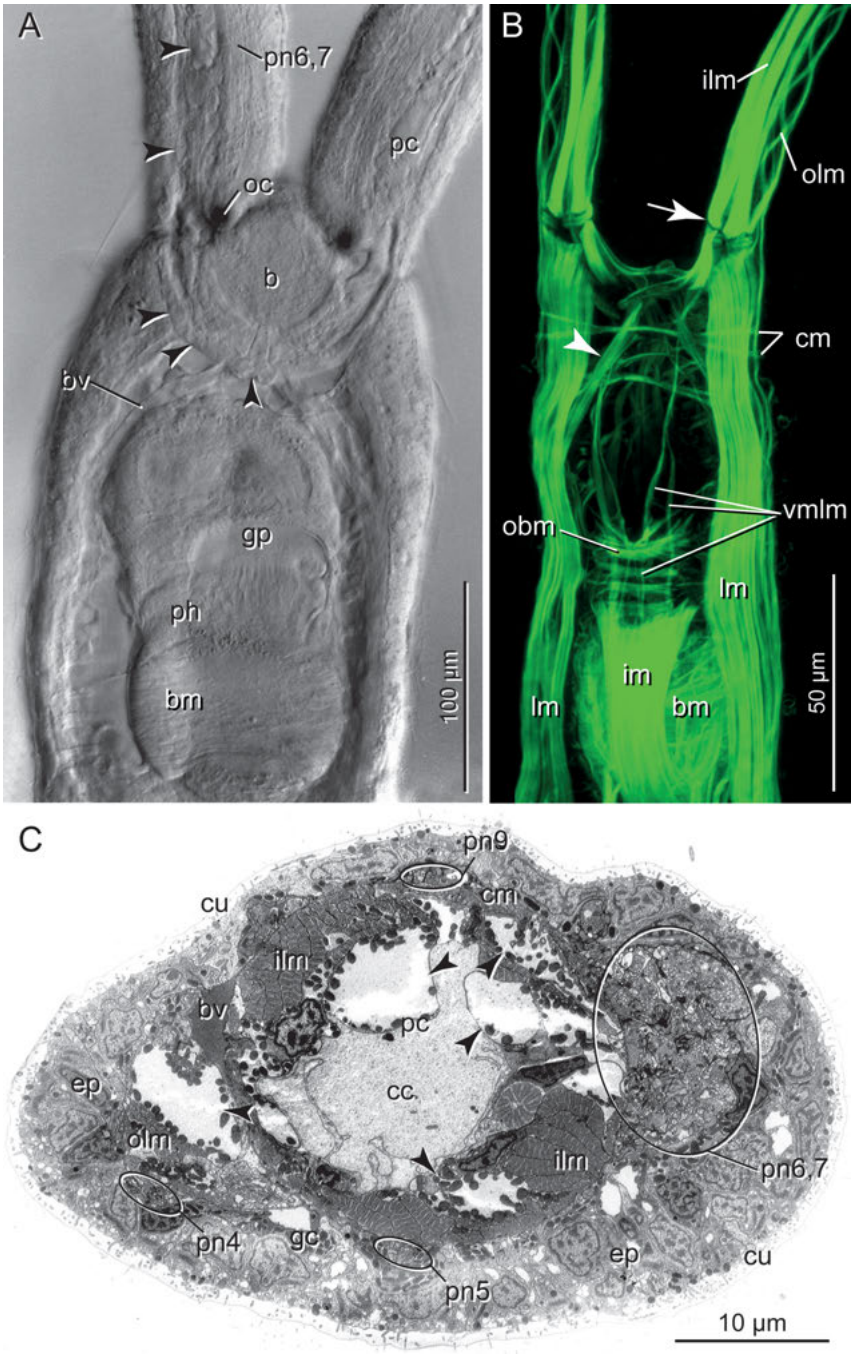


Fig. 7.11.3.2: Palp morphology. A, C, *Protodrilus oculifer*; B, *Claudrilus hypoleucus*. A, LM micrograph showing palp canals (pc, arrowheads) uniting behind the brain (b) and ventral pharynx (ph); B, Musculature of the anterior end after staining with phalloidin. Confocal laser scanning microscopy (CLSM) image. Note that the inner longitudinal muscles (ilm) of the palps are separated from the body wall musculature (lm) by a distinct gap (arrow); the outer longitudinal palp muscle fibers (olm) are a direct continuation of the longitudinal body wall muscles; these outer muscles are arranged in a spiral pattern. All longitudinal fibers are running into the head region and terminate at the palp bases or the palp canal (arrowhead); C, Transmission electron microscopy (TEM) cross-section of palp close to its base. Palp canal (pc) filled with cell bodies of muscle fibers (ilm, arrowheads) and coelenchyme cells (cc). Palp base supplied with a blind-ending blood vessel (bv) situated between intrinsic palp canal muscle (ilm) and outer (external) longitudinal musculature (olm). b, brain; bm, bulbus muscle; bv, blood vessel; cc, coelenchyme cell; cm, circular muscle; cu, cuticle; ep, epidermis; gc, glial cell; gp, grating plate; ilm, inner longitudinal muscle of palp; im, investing muscle; lm, longitudinal muscle (body wall); obm, oblique muscle; oc, ocellus; olm, outer longitudinal muscle of palp; pc, palp canal; ph, ventral pharynx; pn, palp nerve (labeling according to Orrhage and Müller 2005, Purschke 2016); vmlm, ventromedial longitudinal muscle.

The peristomium is approximately twice the length of the prostomium. It is elongated and bears the ventral ciliated mouth (Figs. 7.11.3.11C, 7.11.3.14K), except in *Astomus*, which has no mouth opening. Several members of *Protodrilus*, *Lindrilus*, and *Megadrilus* show a red, pink, or brownish pigmentation of the pharyngeal bulb and surrounding coelom (Figs. 7.11.3.10A, B, 7.11.3.14C, 7.11.3.15B, 7.11.3.16A, 7.11.3.17D) (Jägersten 1940, von Nordheim 1989a, Riser 1997). This coloration is difficult to observe in fixed or juvenile specimens and can be lost after keeping the specimens in culture (Riser 1997). A dark gray-colored spot can be found on the peristomium of large specimens of *Claudrilus helgolandicus* or *Claudrilus hypoleucus*. The peristomium is densely covered with cilia in species of *Lindrilus* and *Megadrilus* (Figs. 7.11.3.14H, 7.11.3.16F) or bearing a species-specific number of transverse ciliary bands in many species of *Protodrilus*, *Meiodrilus*, and *Claudrilus* (Figs. 7.11.3.11B, 7.11.3.19A, 7.11.3.20H).

Trunk

With a few exceptions, the trunk of most Protodrilidae consists of 20 to 50 cylindrical more or less distinct

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segments, morphologically identical and lacking chaetae or parapodia (Fig. 7.11.3.1A–C). The most conspicuous external feature is a midventral ciliary band that extends along the trunk from the mouth to the anus (Figs. 7.11.3.11C, 7.11.3.19E). It consists of a few longitudinal rows of multiciliated cells flanked by abundant mucous glands (Fig. 7.11.3.3A). Each multiciliated cell is provided with short continuously beating cilia, which in combination with mucus secretion generate the forward ciliary gliding locomotion of the animals (Martin 1978a). Additional single cilia and tufts of cilia are found elsewhere on the trunk, often in species-specific patterns (Figs. 7.11.3.11H, 7.11.3.19B). Dorsal and dorsolateral ciliary tufts are scarce or absent in most species of *Meiodrilus* and *Claudrilus*, which present only a few long stiff compound cilia, sometimes arranged as a midlateral longitudinal band (Fig. 7.11.3.19B). In opposite, most species of *Megadrilus, Lindrilus*, and *Protodrilus* have abundant tufts of cilia regularly covering the entire trunk (Figs. 7.11.3.14J, 7.11.3.16I). These ciliary tufts can sometimes be arranged as one to two rings on each trunk segment (Fig. 7.11.3.11H), which in some species, such as *Protodrilus ciliatus,* are involved in producing water currents (Fig. 7.11.3.11F). The males of *Protodrilus jagersteni*, *Protodrilus smithsoni*, and *Protodrilus pythonius* possess a dorsal ciliated area in the anterior segments consisting of bandlets of five to six short cilia (~1 μm long) arranged in larger rows (Fig. 7.11.3.11E) (Di Domenico et al. 2013, Martínez et al. 2013, 2015).

The trunk of *Astomus* consists of dorsoventrally flattened segments, deeply incised at the level of the septae, giving the animals a characteristic festooned appearance (Fig. 7.11.3.1B) (Jouin 1979). The number of segments is higher than in other Protodrilidae and may reach 135 in *A. taenioides*. On each side of the body, a pair of lateral ciliated furrows produces water currents ventilating the surface for gas exchange and nutrition (Jouin 1992).

Megadrilus pelagicus is laterally compressed in part due to the presence of a dorsal keel running longitudinally from segment six to the pygidium (Fig. 7.11.3.1C) (Martínez et al. 2017). This keel is constituted by an enlargement of the dorsal epidermis; it is ciliated and bears several rows of bacillary glands.

Segmental adhesive glands are present in the middle and posterior trunk segments of all species of *Meiodrilus* and *Claudrilus corderoi*. They consist of paired structures located at each side of the midventral ciliary band, slightly raised from the epidermis and provided with several terminal pores (Figs. 7.11.3.18E, F, 7.11.3.19E, F). Animals with segmental adhesive glands are very sticky and typically roll their bodies into a more or less irregular spiral or ball upon disturbance. The segmental glands consist of two rows of four to six adhesive glands in *Meiodrilus adhaerens* and six to eight in *Meiodrilus gracilis*. The secretion products of the gland are synthetized in the basal pole of the cells and are contained in large ovoid vacuoles, with a light gray mantle of filamentous material and darker granules.

Pygidium

Protodrilids possess two paddle-shaped pygidial lobes with terminal adhesive glands (von Nordheim 1989a). The gland cells necks are visible in LM as longitudinal striations (Figs. 7.11.3.14B, 7.11.3.16B, 7.11.3.20F) (Martin 1978b) and open up in two parallel rows of pores only visible under SEM or TEM along the posterior margin of the pygidial lobes, where adhesion occurs. Adhesion depends on a dual-gland system, similar to what has been described for other interstitial animals such as Saccocirridae or Protodriloididae (Giere 2009, Di Domenico et al. 2014), with two types of glands cells: a dorsal row of presumed releasing glands and a ventral row of viscid glands (Martin 1978b). Each gland cell consists of a basal synthetic zone and a long apical neck lined by microtubules, which give the striated appearance to the pygidium. The terminal pores are surrounded by a circle of microvilli arranged in a chimney-like pattern (Martin 1978b). The basal synthetic zones contain abundant large and ovoid granules in the presumed viscid glands and smaller, more abundant, and spheroidal in the presumed releasing glands.

An additional dorsal and leaf-shaped pygidial lobe is present in all species of *Megadrilus* (Fig. 7.11.3.16B). The function of this lobe is not yet clear. According to Westheide (2008), it is provided with terminal secretive gland cells that produce mucous secretions and apparently lack any adhesive function.

Epidermis

The epidermis consists of a monolayered epithelium with nearly cylindrical cells, lined by an extracellular matrix (ECM) and underlined by a few circular and diagonal bracing muscles. Depending on the species, different types of gland cells occur in the epidermis (Fig. 7.11.3.3A). The entire nervous system is located basiepithelial (Fig. 7.11.3.3A) (Salensky 1907, Pierantoni 1908).

The cuticle is 0.5 to 2.5 μm thick depending on the species and consists of a basal layer of irregularly oriented fine collagen fibers bordered by an irregular festooned, electron dense epicuticle consisting of interconnected, branching collagen fibers (Rieger and Rieger 1976). The epicuticle is covered by a glycocalyx consisting of a single layer of dark, loose fibrous material. Cuticle and glycocalyx are penetrated by numerous microvilli from the supporting cells of the epidermis, which strengthen the cuticle and might play a role in the formation of both the cuticle and the glycocalyx. Their density varies between

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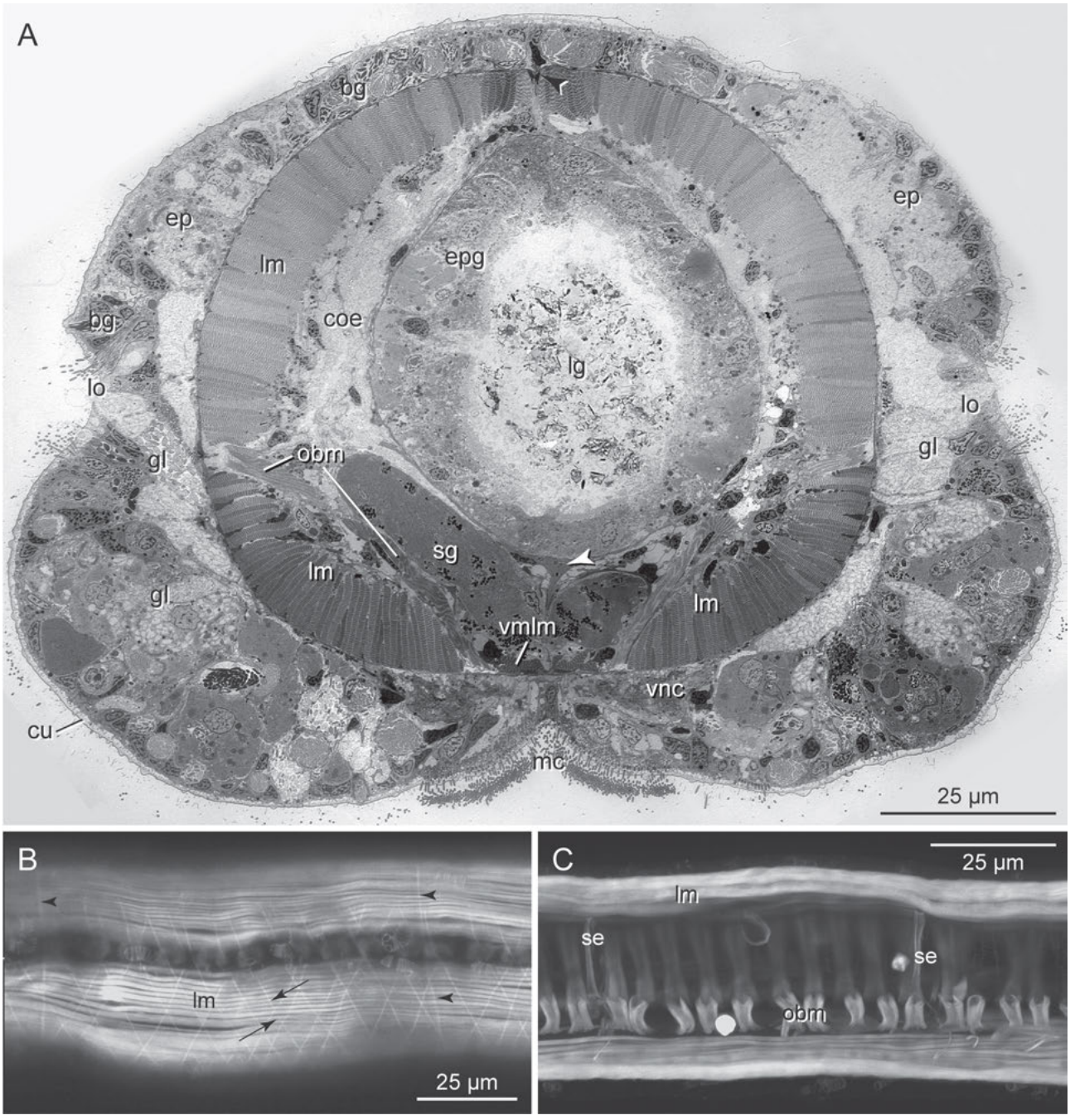


Fig. 7.11.3.3: Internal morphology and organization of trunk musculature. A, *Protodrilus ciliatus*. Cross-section of the trunk of a male at the level of the lateral organs anterior to the fertile region. Body cavity occupied by spacious gut (epg, lg), cell bodies of muscle fibers obliterating coelom (coe); longitudinal muscles (lm) almost form a complete cylinder interrupted by oblique muscle (obm) and ventromedial longitudinal muscle (vmlm); epidermis rich in gland cells (bg, gl); arrowheads point to ventral and dorsal blood vessels; B, C, *Claudrilus hypoleucus*. Musculature of the body wall after staining with phalloidin, CLSM images. B, Dorsal view, strong longitudinal fibers (lm) overlain by fine bracing muscle fibers (arrows). Circular fibers restricted to segment borders (arrowheads); C, Internal view showing oblique muscles (obm) and musculature of the septa (se) in addition to longitudinal fibers. bg, bacillary gland; coe, coelom; cu, cuticle; ep, epidermis; epg, epithelium of gut; gl, gland cell; lg, lumen of gut; lm, longitudinal muscle; lo, lateral organ; mc, midventral ciliary band; obm, oblique muscle; se, septum; sg, salivary gland; vmlm, ventromedial longitudinal muscle; vnc, ventral nerve cord. Micrograph A, Isabel Dykstra, Osnabrück.

species and is, for example, between 10 microvilli/µm^2 in *Protodrilus ciliatus* and 30 microvilli/µm^2 in *Astomus taenioides* (Purschke et al., unpublished observations).

The single-layered epithelium consists of supporting, glandular, and sensory cells (Fig. 7.11.3.3A), which are interconnected via zonulae adhaerentes followed

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by septate junctions. In *A. taenioides*, the supporting cells bear numerous microvilli and exhibit a significant endocytic activity, visible as numerous endocytic invaginations (i.e., coated pits and coated vesicles) and abundant primary and secondary lysosomes (Jouin 1992). This endocytic activity, much less developed in the anterior region of the body, is a peculiarity of the genus *Astomus*. Together with the supporting cells, cells with large vacuoles, bacillary gland cells, and mucous gland cells are found in the epidermis; these last along the longitudinal ciliary bands. The epithelium is underlined by a well-delineated basal lamina formed by a lattice of fibers, connected to the epithelium by hemidesmosomes followed by a basal-apical tonofilament system. The nervous tissue is located between the epithelial cells and the basal lamina (basiepithelial position of nervous system), whereas myoepithelial cells have not been confirmed by TEM so far.

Epidermal gland cells are found in several types across different species. The most conspicuous type is the so-called bacillary glands, which is present in all Protodrilidae, although with different arrangement depending on the species; thus, this represents a diagnostic feature (Figs. 7.11.3.3, 7.11.3.10C, 7.11.3.14E, 7.11.3.16E, 7.11.3.18C) (von Nordheim 1989a, Martínez et al. 2015). Each bacillary gland cell exhibits a more or less banana-shaped structure with rod-like content and an opening as a small pore raised few micrometers above the epidermis (Martin 1978c). Bacillary gland cells tend to be oval in certain species (e.g., *Protodrilus submersus*) or very elongated in others (e.g., *Protodrilus ciliatus*). Species of *Protodrilus*, *Lindrilus*, and *Megadrilus* can possess more than 100 gland cells per segment covering the entire epidermis in certain species (Figs. 7.11.3.10C, 7.11.3.14E, 7.11.3.16E) (Jouin 1970c). Gland cells are typically less abundant in *Meiodrilus*, which have only 10 to 20 gland cells per trunk segment, clearly separated from each other (Fig. 7.11.3.18C) (Jägersten 1952). In some species of *Claudrilus*, such as *C. hypoleucus* or *C. helgolandicus*, bacillary gland cells are practically absent and substituted by abundant flask-shaped vacuolar epidermal gland cells only found in this genus (Fig. 7.11.3.20C, D, F). Vacuolar gland cells are embedded in the external part of the epidermis and contain numerous apical vacuoles of different shapes and sizes with black secretion products in different stages of condensation. The presence of these glands gives many species of *Claudrilus* a characteristic white color under the dissecting microscope (Fig. 7.11.3.20C).

Digestive system, salivary glands, and ventral pharynx

Except for *Astomus*, most Protodrilidae possess a tubular alimentary canal, which consists of the mouth and mouth cavity, a ventral pharyngeal organ followed by a short esophagus, a midgut, and a hindgut opening between the pygidial lobes in a terminal anus (Figs. 7.11.3.1A, 7.11.3.2A, 7.11.3.10A, B, 7.11.3.14B, E, 7.11.3.16D). Most of the gut is surrounded by a regular grid of thin longitudinal and circular muscle fibers.

The mouth, absent in *Astomus*, is a slit-like opening, densely ciliated and situated ventrally in the peristomium. The mouth is laterally lined by two rows of short cilia, which continue into the midventral ciliary band, and an anterior ciliary band extending transversally along the anterior margin of the mouth (Figs. 7.11.3.11C, 7.11.3.14K, 7.11.3.16G). Some species, such as *Protodrilus brevis*, *Meiodrilus adhaerens*, and *Meiodrilus gracilis*, possess paired anterolateral tufts of long cilia, which perform occasional flicks and are involved in feeding (Fig. 7.11.3.20B). The ciliated epithelium of the mouth cavity is lined by abundant thin circular muscles, some of them delineating the mouth opening.

The mouth cavity continues into the ciliated esophagus, which tightly runs above the dorsal grating plate and the muscular bulb, before widening into the midgut in the first segment (Fig. 7.11.3.4C). The midgut extends along a variable number of segments and consists of a straight tube lined by a single layer of nonciliated supporting cells and a few gland cells interspersed between them (Fig. 7.11.3.3A). At the level of the end of the salivary glands, a ciliated gutter may be present ventrally in *Protodrilus ciliatus* (see Purschke et al. unpublished observations). It consists of two phalanxes of straight microvilli with cilia in between. More posteriorly, the intestine gradually transforms into the hindgut following a gradually decrease in microvilli-bearing absorptive cells and gland cells combined with an increase in ciliated cells. The midgut is lined ventrally and laterally by salivary glands, stainable with Shirla stain or hematoxylin (Pierantoni 1906a, Jägersten 1952), and extending through a species-specific number of anterior trunk segments (Figs. 7.11.3.10B, 7.11.3.18B). They extend up to segment 5 in *Meiodrilus* (Fig. 7.11.3.20D) and segment 6 in *Megadrilus* (except for *Megadrilus hochbergi*) (Fig. 7.11.3.17E) and are more variable in *Lindrilus*, *Protodrilus*, and *Claudrilus*, typically extending along around 15 segments (Figs. 7.11.3.12E, 7.11.3.15C, 7.11.3.22E). In *Astomus*, the salivary glands are retained in some anterior segments but are not visible with LM (Fig. 7.11.3.13B). They extend through the first three segments and are located on both sides of the residual gut, and due to the absence of an open stomodeum, they open ventrally on the body surface at the border between the prostomium and the peristomium (Jouin 1992). In the other genera, the salivary glands consist of rounded cell bodies located beside the gut system and, depending on the species and position of the

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cell bodies, a more or less long neck opening in the buccal cavity opposite the grating plate (Figs. 7.11.3.3A, 7.11.3.4C). The gland cell necks of each body side are united to form bundles of nerve-like processes. Secretion apparently is under nervous control, as synapses have been described at the salivary gland cell necks (Jouin 1992). These cells produce mostly mucous secretion and hydrolytic enzymes (Pierantoni 1906a). The hindgut extends from the midbody to the anus and consists of a straight ciliated tube, which is often constrained at the level of the septa.

The ventral pharyngeal apparatus is a prominent structure, clearly visible with LM, which occupies the entirely posterior half of the peristomium, between the mouth cavity and the first septum (Figs. 7.11.3.1A, 7.11.3.2A, B, 7.11.3.4A–C, 7.11.3.10A, 7.11.3.14C, 7.11.3.16A, 7.11.3.18A, B, 7.11.3.21C). It is very similar across all known protodrilids and only absent in the species of the genus *Astomus*. The fine structure has been described in *Claudrilus hypoleucus* by Jouin (1978a, 1978b). The ventral pharynx mainly consists of two antagonistic muscle systems, the bulbus muscle and the investing or sagittal muscle, which dorsally attaches to the tongue-like organ (Figs. 7.11.3.2B, 7.11.3.4A–C). The tongue-like organ is positioned between the muscle bulb and the esophagus (Fig. 7.11.3.4C). It consists of epithelial cells, an intrinsic longitudinal musculature, and the cuticular grating plate (Figs. 7.11.3.2A, 7.11.3.4B, C). The bulbus muscle is a conspicuous, rounded structure consisting of plate-shaped transverse muscular fibers with a few interstitial cells interposed between them (Figs. 7.11.3.2A, B, 7.11.3.4A–C). The processes of these interstitial cells extend dorsoventrally and contain prominent bundles of tonofilaments arranged perpendicular to the myofilaments of the muscle bulb. Due to the presence of a perpendicular tonofilament system, the contraction of the bulbus muscle fibers is more or less isodiametric, as it prevents a shortening of these muscle fibers. The entire structure thus ensures that the bulb mainly changes in stiffness or flexibility when the bulbus muscles contract. The investing muscle consists only of longitudinal fibers, which surround the bulb semicircularly and insert ventrally at the lower lip as well as supplying dorsolaterally the tongue-like organ with the grating plate (Figs. 7.11.3.2B, 7.11.3.4A–C). A median invagination of the pharyngeal organ separates the muscle bulb from the tongue-like organ. The grating plate is a thick cuticular structure at the dorsoposterior part of the buccal cavity, opposite to the salivary gland cell openings, probably involved in dislodging food particles from the substratum. Behind and above the grating plate, there is a cluster of large secretory cells. All muscle fibers of the pharynx are obliquely striated and possess a central core of sarcoplasm containing mitochondria and nuclei, except for the investing muscle, in which the nuclei are located in a posterior sac-like extension of the muscle. The ventral pharynx is supplied by several groups of retractor muscles, which insert dorsally and ventrally in the body wall after surrounding the esophagus (Fig. 7.11.3.4B, C).

Musculature of the trunk

Except for the anterior end, the trunk musculature is relatively simple and is dominated by longitudinal fibers, substituted by oblique, circular, and outer bracing muscles (Figs. 7.11.3.2B, 7.11.3.3A–C, 7.11.3.4A) (Martínez et al. 2017). In the prostomium and peristomium, additional muscle fibers are present, which are arranged in a more complex pattern (Figs. 7.11.3.2B, 7.11.3.4A, B). The longitudinal muscles consist of paired dorsolateral and ventrolateral conspicuous muscle blocks as well as a pair of smaller midventral muscles situated above the nerve cord (Figs. 7.11.3.2B, 7.11.3.3A–C, 7.11.3.4A, B). The dorsolateral and ventrolateral muscles originate near the palp insertions and extend along the trunk (Figs. 7.11.3.2B, 7.11.3.4A), with the exception of a few outer fibers that continue as the lateral muscle fibers of the palps (Fig. 7.11.3.2B, C). The dorsolateral muscles insert dorsally in the pygidium, and the ventrolateral muscles diverge, supplying the ventral pygidial lobes. Each longitudinal muscle is interrupted at the level of each septum, acquiring a segmented appearance (Fig. 7.11.3.3B, C). In transverse section, the muscular fibers in each longitudinal group are elongated, flattened, and arranged in a single layer, projecting toward the body cavity with their cell bodies (Fig. 7.11.3.3A). The myofilament containing parts of the fibers are attached to the ECM separating the epidermis and mesodermal tissues. The muscle fibers almost form a complete cylinder in cross-section, except for a small ventral gap above the ventral ciliary band, a separation in the dorsolateral groups where the oblique muscles attach to the body wall (Fig. 7.11.3.3A), as well as a dorsal separation by the dorsal mesenterium (Fig. 7.11.3.3B). The midventral longitudinal muscles originate at the posterior end of the peristomium behind the palp canals (Fig. 7.11.3.2B), extend underneath the midventral ciliary band between the main trunks of the ventral nerve cord and the ventrolateral longitudinal muscles (Fig. 7.11.3.3A), and insert ventrally in the pygidium. This muscle comprises only three pairs of flattened fibers that are attached to the ECM above the ventral epidermis and those forming the basal part of the ventral mesenterium.

The oblique muscles of the trunk consist of two paired groups of fibers originating ventrally between the midventral and the ventrolateral muscle and inserting laterally

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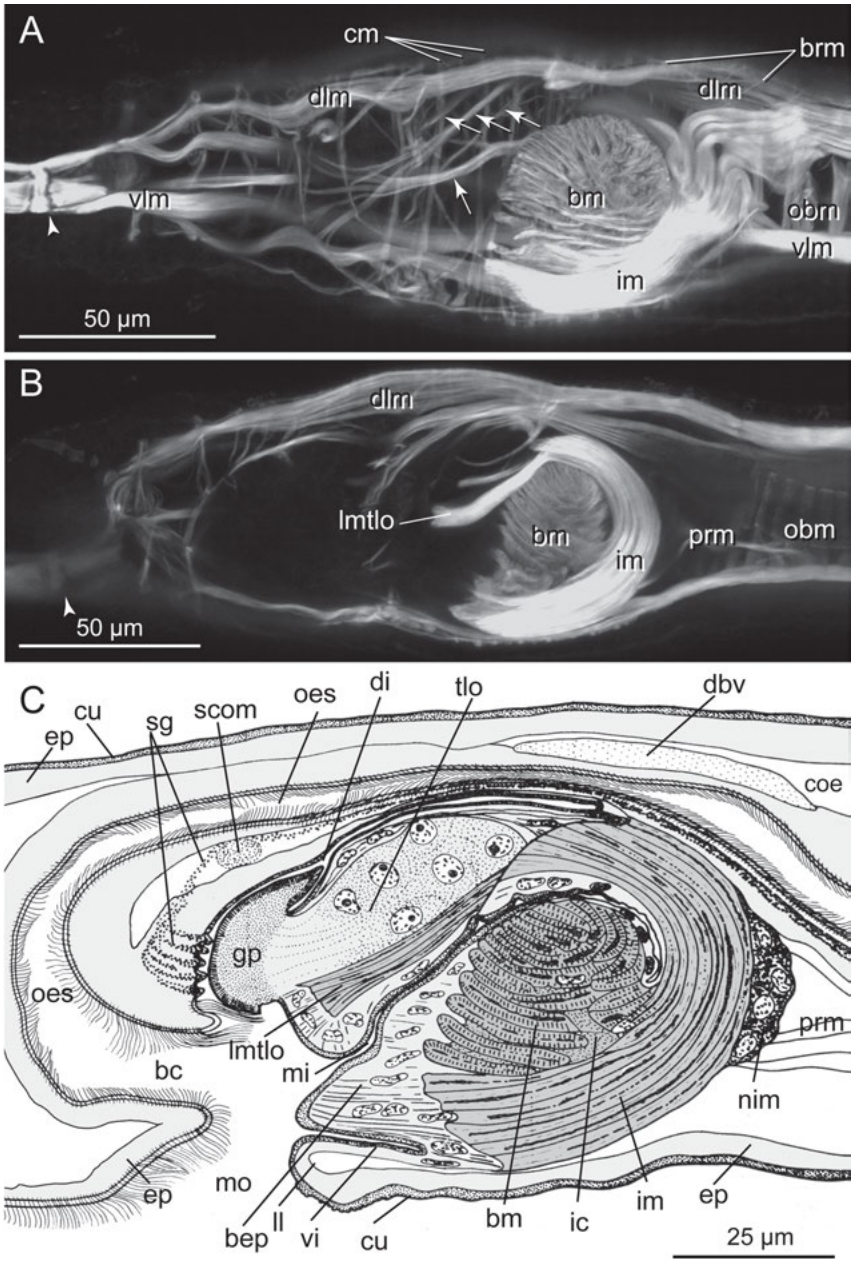


Fig. 7.11.3.4: *Claudrilus hypoleucus*. Musculature of the anterior end and ventral pharynx. A, B, Lateral view of anterior end after staining with phalloidin, CLSM images; arrowheads point to insertion of palp; A, Musculature of the body wall and pharynx; B, Sagittal section showing the musculature of the ventral pharynx comprising bulbus muscle (bm), investing muscle (im), and longitudinal muscle of tongue-like organ (lmtlo); C, Sagittal section of ventral pharynx; reconstruction from TEM observations. Three invaginations (vi, mi, and di) separate the different parts: lower lip (ll), bulbus muscle (bm), and tongue-like organ (tlo) surrounded and connected by investing muscle (im). Bulbus muscle comprises transverse fibers and interstitial cell (ic), tongue-like organ (tlo) with strong epithelium, muscle fibers, and cuticular grating plate (gp). Salivary gland cells (sg) open into the buccal cavity (bc) opposite to the grating plate. Redrawn from Jouin (1978a). bc, buccal cavity; bep, bulbus epithelium; bm, bulbus muscle; brm, bracing muscle; cm, circular muscle; coe, coelom; cu, cuticle; dbv, dorsal blood vessel; di, dorsal invagination; dlm, dorsal longitudinal muscle; ep, epidermis; gp, grating plate; ic, interstitial cell; im, investing muscle; ll, lower lip; lmtlo, longitudinal muscle of tlo; mi, median invagination; mo, mouth; nim, nuclei of investing muscle fibers; obm, oblique muscle; oes, esophagus; prm, pharynx retractor muscle; scom, subesophageal commissure; sg, salivary gland cell processes; tlo, tongue-like organ; vi, ventral invagination; vlm, ventral longitudinal muscle.

between the dorsolateral and ventrolateral longitudinal muscles (Figs. 7.11.3.3A, C, 7.11.3.4A). Typically, there are 10 to 30 pairs of oblique muscle fibers in each trunk segment (Fig. 7.11.3.3C), although the number can vary among individuals and trunk regions. Trunk circular muscle cells are arranged as rings around the longitudinal musculature at the level of each septum (Fig. 7.11.3.3B, C). The trunk outer bracing musculature consists of thin fibers arranged in a lattice-like pattern dorsally on the trunk covering the dorsolateral muscles (Figs. 7.11.3.3B, 7.11.3.4A). Circular and bracing muscles are inconspicuous and have been largely overlooked in LM and TEM sections, although they are clearly visible under CLSM investigations. In the anterior end, circular muscle fibers are more prominent (Figs. 7.11.3.2B, 7.11.3.4A).

Coelom, blood vascular system, and nephridia

It has been extensively discussed whether or not Protodrilidae have a true coelom and whether their nephridia are protonephridia or metanephridia (Salensky 1907, Pierantoni 1908, Goodrich 1931, Jägersten 1952, Fransen 1980, 1988, von Nordheim and Schrader 1994). Although a coelom with septa and mesenteries is present (Fig. 7.11.3.3C), the coelomic cavities are partly filled with cell bodies of muscle fibers, nephridia, or gametes as well as cell bodies of the salivary glands (Fig. 7.11.3.3A) (Fransen 1980, Worsaae and Kristensen 2005). The septa are composed of double layer of thin peritoneal cells facing with their apical parts toward the body cavity and separated by an ECM to which their basal sides are attached (Fransen 1980, 1988, von Nordheim and Schrader 1994). Thus, at

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higher magnification, they appear as double layered in CLSM (Fig. 7.11.3.3C). According to Fransen (1980), a complete splanchnic peritoneum does not exist and is represented by the monolayer of plate-shaped longitudinal muscle cells. In contrast, the intestine is covered by a thin peritoneum followed by the likewise thin splanchnic musculature. The peritoneal cells may be between 60 and 100 nm thin.

As typical for invertebrates, the lumen of the blood vessels is situated within the ECM at the basal surfaces of adjacent epithelia. Compared to larger polychaete species, the blood vascular system appears somewhat reduced and less complex (von Nordheim and Schrader 1994), but unlike other small annelids it comprises the main dorsal and ventral longitudinal vessels of a typical annelid blood vascular system, although branching vessels are less developed (Fig. 7.11.3.3A) (Worsaae and Kristensen 2005). The anterior blood vascular system comprises a dorsal blood vessel, two ventral vessels, and two palp vessels. The dorsal vessel leads to a larger cavity anterior to the mouth. Here, the ventral vessels branch; one branch extends posteriorly surrounding the pharynx and one runs anteriorly into the dorsal side of the palps between the palp canal and the lateral bundle of muscle cells. The outline of the blood vessels is irregular, with the ECM being continuous with those between the epithelium and the musculature. Two specialized zones of contact between the palp canal system and the blood vessels are found in the prostomium. In these zones, the wall of the palp canals is formed by podocytes with numerous pedicels, close together throughout their lengths and containing small vesicles. This special zone is absent in *A. taenioides*. In the trunk, blood lacunae are formed ventrally where the septa are close to the gut (von Nordheim and Schrader 1994).

Usually, a pair of nephridia is present in the ventrolateral coelomic chamber below the oblique muscle in each segment, except for the fertile region (Jouin 1970c, Fransen 1980, von Nordheim and Schrader 1994). These nephridia may be stained by antibodies against tubulin and thus become visible in CLSM (Fig. 7.11.3.6D). The terminal parts are located preseptally in the anterior segment, then the septum is traversed, and the nephridial duct is mainly located in the following segment. It may comprise several loops and finally opens ventrolaterally near the septum to the outside (*Lindrilus rubropharyngeus*), but in other species the nephridioduct is shorter and does not form loops and opens in the midsegmental region (e.g., *Protodrilus leuckartii*) (Jägersten 1952, Jouin 1970c, von Nordheim and Schrader 1994). The nephridia have been investigated by TEM in *L. rubropharyngeus* by von Nordheim and Schrader (1994) and can be classified as protonephridia. These nephridia end with a multiciliated terminal cell comprising numerous pores through which

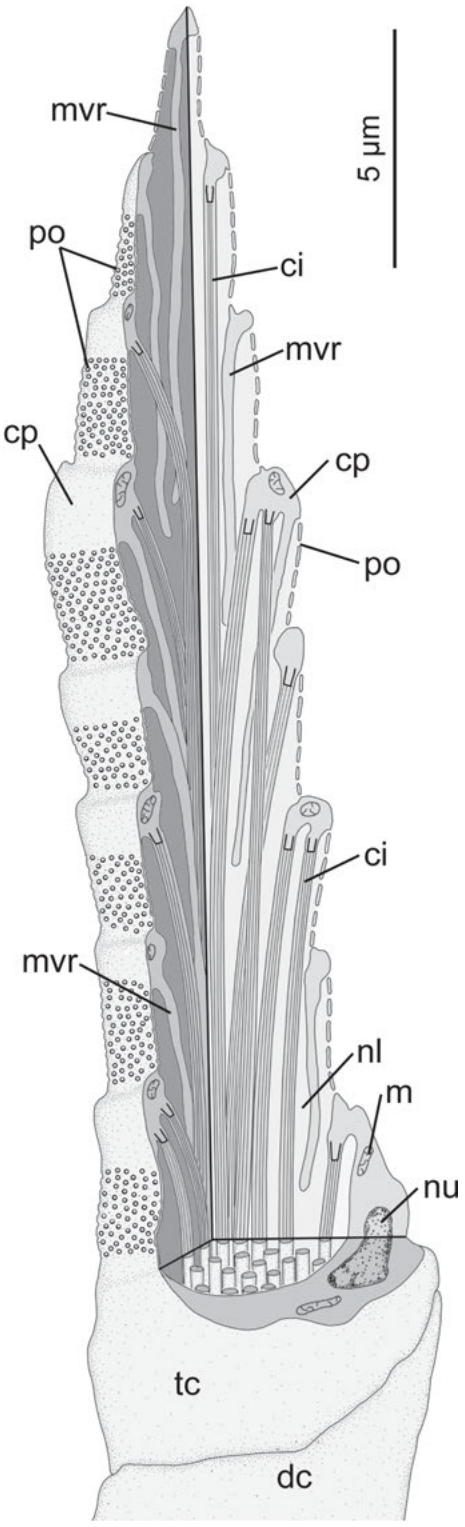


Fig. 7.11.3.5: *Lindrilus rubropharyngeus*. Terminal cell (tc) of protonephridium. Reconstruction from electron microscopic observations. Terminal cell bears numerous cilia (ci) and microvillar rods (mvr) projecting into the nephridial lumen (nl). Terminal cell tapers distally and forms cytoplasmic protrusions (cp), which give rise to cilia and microvilli interrupted by thin area perforated by spherical pores (po) through which the primary urine enters the nephridium. ci, cilium; cp, cytoplasmic protrusion; dc, duct cell; m, mitochondrion; mvr, microvillar rod; nu, nucleus; nl, nephridial lumen; po, pore; tc, terminal cell. Redrawn after von Nordheim and Schrader (1994).

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the primary urine enters the nephridium (Fig. 7.11.3.5). In addition, a second filtration structure in the form of typical podocytes lining blood vessels is present at the segmental blood lacunae described above. The terminal cell and a few proximal ducts cells make up the preseptal part of the nephridia.

Nervous system

The nervous system in Protodrilidae has been studied by Salensky (1907) and Pierantoni (1908) and more recently by Merker and Vaupel-von Harnack (1967), Orrhage (1974), Bubko (1981), Purschke (1993), Purschke and Jouin-Toulmond (1994), and Müller (1999) using different methods. As mentioned above, the entire nervous system has a basiepithelial position (Fig. 7.11.3.3A). It consists of a conspicuous brain, situated in the prostomium, and the ventral nerve cord extending toward the pygidium (Fig. 7.11.3.6A, C). These give rise to several main nerves, including the four pairs of palp nerves, three ventral and one dorsal, running anteriorly, and two pairs of dorsal nerves, one pair of nuchal nerves, two stomatogastric nerves, running posteriorly, and numerous segmental nerves innervating the periphery of each segment (Fig. 7.11.3.6A–D).

The neuropil of the brain is situated between the anterior prostomium margin and the curve formed by the palp canal system (Fig. 7.11.3.6A, C). Dorsally, the neuropil covers half of the palp canal. Most somata are positioned anteriorly and dorsally with only a few lying ventrally in all species studied, except for *Astomus taenioides*, which possesses two pairs of posterior ganglionic extensions containing most of the somata (Purschke and Jouin-Toulmond 1994). These extensions might be an adaptation related to the comparatively small prostomium in this species. Ventrolaterally, the brain gives rise to the strong ventral roots of the circumesophageal connectives, whereas the smaller dorsal roots originate somewhat more posteriorly and dorsally. They form a loop around the palp canal and unite to form the pair of single connectives surrounding the mouth opening. The palp nerves emanate from these roots: the largest palp nerve ($pn_{6\text{-}7}$ in Figs. 7.11.3.2A, C, 7.11.3.6A, C) (vpn4 after Purschke 1993 or nos. 06, 07 following the nomenclature of Orrhage and Müller 2005) originates close to the neuropil and most likely belongs to both roots of the circumesophageal connectives, the two smaller ventral palp nerves ($pn_{4,5}$ in Figs. 7.11.3.2C, 7.11.3.6A) (vpn1, vpn2 in Purschke 1993 or nos. 04, 05 in Orrhage and Müller 2005) stem from the ventral root, and the dorsal palp nerve (pn_9 in Figs. 7.11.3.2, 7.11.3.6) (dpn or no. 09) comes from the dorsal root (Fig. 7.11.3.6A). A network of groups of a few neurites expands among the longitudinal nerves, surrounding the lateral muscles and the palp canals. The size of the palp nerves depends on the number of fibers included in each nerve, which varies greatly between species, ranging from 230 to 600 in the main nerve, in *Meiodrilus adhaerens* and *Protodrilus ciliatus*, respectively, and from 5 to 60 in the other nerves. The main palp nerve is mainly sensory and comprises the axons of the receptor cells present on the palps (Fig. 7.11.3.6C).

Two nerves arise together from the posterior edge of the brain and run posteriorly: the nuchal organ nerve and the second dorsal nerve. The former comprises the axons of the receptor cells of the nuchal organ, and the latter innervates the dorsal part of the trunk. These dorsal nerves unite somewhat behind the prostomium to form an unpaired dorsomedial nerve. Another dorsal nerve arises from the dorsal root of the circumesophageal connective running posteriorly. In addition, it comprises the efferent innervation of the nuchal organs. The axons of the unpigmented prostomial photoreceptor-like organ (so-called statocysts, see below) enter the neuropil separately, near the origin of the main palp nerve. The stomatogastric nerves arise ventrally from the posterior edge of the brain, running posteriorly and forming a plexus around the digestive canal. These nerves are connected to the ventral root of the circumesophageal connective by a commissure near the brain, which connects the stomatogastric nerves with the ventral nerve cord.

The ventral nerve cord comprises two main neurite bundles commonly called main ventral nerves (see Orrhage and Müller 2005, Purschke 2016), each of which is accompanied by a smaller paramedian neurite bundle situated medially (Fig. 7.11.3.6B). A median nerve is lacking so that the ventral nerve cord may be characterized as a tetra-neuralian cord. These nerves are interconnected by numerous commissures, which do not show a clear segmental repetitive pattern (Fig. 7.11.3.6B). Moreover, typical ganglia are absent, but certain specific neurons such as serotonin-like immunoreactive somata show a segmental pattern (Purschke et al. unpublished observations). In each segment, the ventral nerve cord gives rise to numerous segmental lateral nerves in a hardly discernable segmental pattern (Fig. 7.11.3.6B, D). According to Müller (1999), only one of these forms a complete ring connecting the ventral nerve cord with the other longitudinal nerves. Thus, the paired and unpaired dorsal longitudinal nerves as well as the ventral nerve cord and their ring-shaped segmental lateral connections form a more or less well-defined orthogonal nervous system. In *Protodrilus ciliatus*, each half of the ventral cord comprises between 700 and 850 neurites (Purschke et al. unpublished observations). Finally, the ventral nerve cord forms a thin loop in the pygidium and thereby innervates the adhesive lobes.

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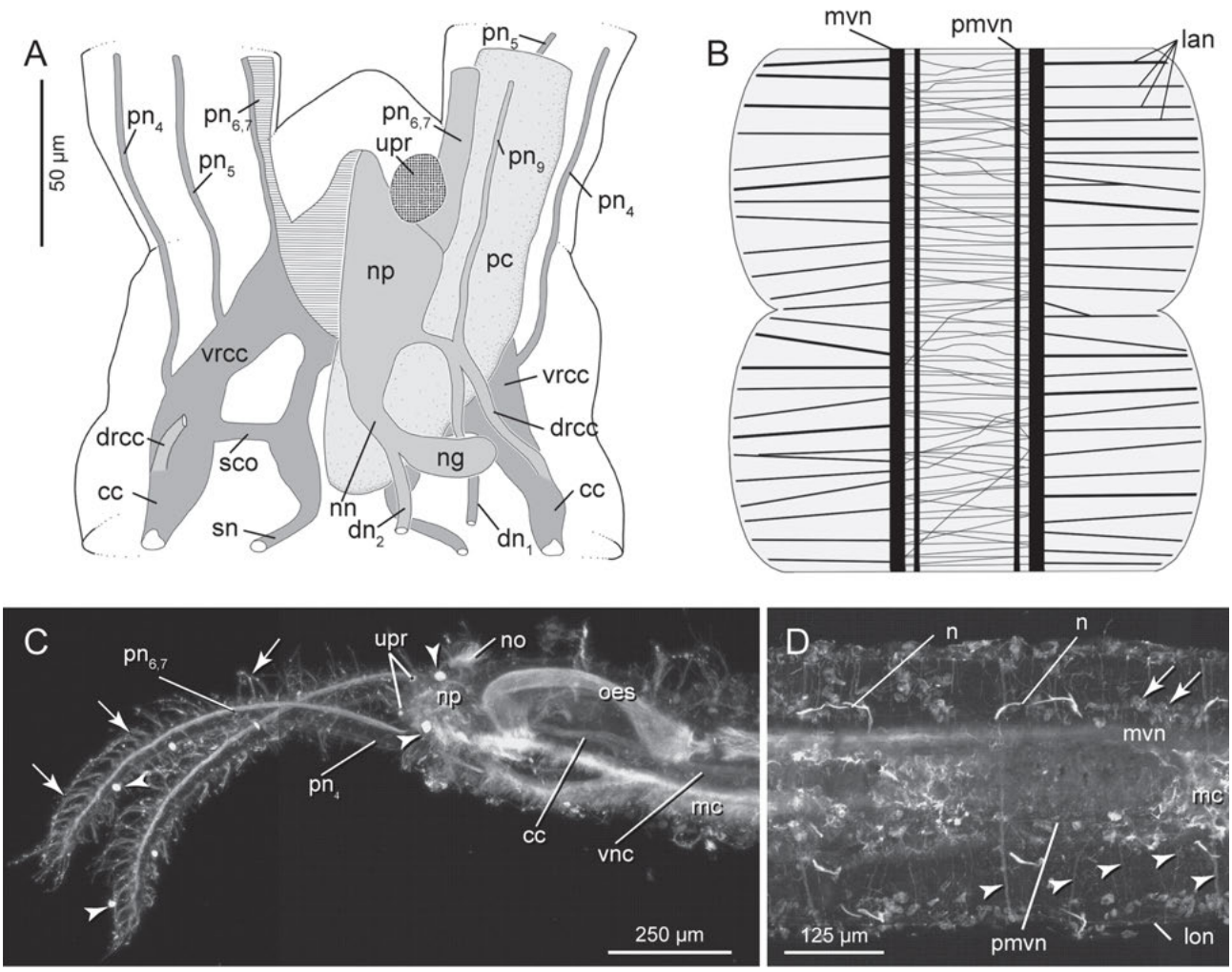


Fig. 7.11.3.6: Nervous system. A, *Protodrilus ciliatus*. Neuropil of the brain (np) and associated nerves. On the left, only ventral parts are shown. Reconstruction from TEM observations; B, Schematic representation of the ventral nervous system in two trunk segments showing two strong median cords (mvn) accompanied by two smaller paramedian nerve cords (pmvn); C, D, *Meiodrilus adhaerens*. Nervous system after staining against acetylated α-tubulin; C, Nervous system of anterior end and palps. Note main palp nerve ($pn_{6,7}$) giving off numerous branches representing dendritic processes or receptor cells (arrows). In the palps and the prostomium, ciliary phaosomes are labeled (arrowheads) as well as minute unpigmented photoreceptor-like organs (upr); in the trunk, nervous structures are partly masked by midventral ciliary band (mc) and cilia of the esophagus (oes); D, Ventral view of two trunk segments. Note numerous segmental nerves (arrowheads), paramedian (pmvn), and lateral nerve (ln). Nephridia (n), epidermal glands (arrows), and midventral ciliary band (mc) also stained. cc, circumesophageal connective; dn_n, dorsal nerve (index refers to number); drcc, dorsal root of cc; lan, lateral nerve; lon, longitudinal nerve; mc, midventral ciliary band; mvn, median ventral nerve; n, nephridium; ng, nuchal ganglion; nn, nuchal nerve; no, nuchal organ; np, neuropil of brain; oes, esophagus; pc, palp canal; pmvn, paramedian median ventral nerve; pnr_n, palp nerve root number (numbers after Orrhage and Müller 2005); sco, commissure of sn; sn, stomatogastric nerve; upr, unpigmented photoreceptor-like organ; vnc, ventral nerve cord; vrcc, ventral root of cc. A, Redrawn from Purschke (1993); B, Redrawn from Müller (1999); Micrographs C, D, Corinna Stühmeier, Osnabrück.

Sensory structures

Species of Protodrilidae possess the entire range of sensory structures as described for annelids in general (Purschke 2005, 2016). These comprise several types of sensory cells differing by the number and length of their sensory cilia and whether these penetrate the cuticle or not (Purschke 1993). These cells are especially abundant on the palps and the prostomium but may be found elsewhere on the body as well. Sense organs are comparatively simple and comprise pigmented eyes, unpigmented photoreceptive structures (formerly known as statocysts), and nuchal organs (Purschke 1988, 1990a, b, 1997). Lateral organs, which are present in many sedentary polychaetes, are absent in Protodrilidae, and the homonymous organs occurring in the males are not sensory but part of the reproductive system (see below).

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Protodrilidae present several types of photoreceptor sensory structures, including pigmented rhabdomeric eyes, unpigmented ciliary eyes and phaosomous receptors (Fig. 7.11.3.7A, C). Pigmented prostomial eyes are present in all known protodrilid larvae, but they are lost during metamorphosis to the adults in most species. In adults, pigmented prostomial eyes are only reported in species of the genus *Lindrilus* as well as in *Protodrilus huanghaiensis* and *Protodrilus oculifer* (see Wu et al. 1980, von Nordheim 1989a). In *Lindrilus,* adult eyes are dorsal and appear during the late larval stage, not being uncommon to find juveniles bearing two pairs of eyes, larval and adult eyes. In opposite, eyes in *P. oculifer* are ventral and smaller than those in *Lindrilus* spp. and more likely represent retention of the larval eyes in the adult. Electron microscopic studies on the eyes of *P. oculifer* (see Purschke 2006) and an undetermined other protodrilid species (Eakin et al. 1977) have shown that they consist of only two cells: a supportive cell, cup-shaped and pigmented by the presence of many granules with black pigment, and a sensory cell that lies into the cavity of the former. Both cells are situated just below the epidermis and the cuticle. The sensory cell contains a photosensitive array of microvilli or rhabdomere, which is projecting from the inner surface of the receptive part of the receptor cell away from the light entering the eye cup and thus may be called inverse. Although probably representing adult eyes, the structure of the eyes in *Lindrilus rubropharyngeus* and *Lindrilus haurakiensis* is the same (Merker and Vaupel-von Harnack 1967, Purschke unpublished observations). A decision whether these eyes represent adult or retained larval eyes can only be done with certainty if the genes involved in the formation of these eyes have been determined (see Arendt et al. 2009). Additionally, dorsal prostomial pigmented spots have been described in *Protodrilus brevis*, which do not represent eyes (Jouin 1970c).

Unpigmented ciliary eyes (previously termed as "statocyst") (e.g., Jägersten 1952, Jouin 1970c) consist of a rounded to ovoid cavity, just below the epidermis, completely filled with membranous structure, either paracrystalline or microvillus-like (Fig. 7.11.3.7C) (Purschke 1990a, b, Purschke and Jouin-Toulmond 1993); they have been studied by electron microscopy in *Lindrilus haurakiensis*, *Protodrilus ciliatus*, *Protodrilus oculifer*, *Claudrilus helgolandicus*, and *Meiodrilus adhaerens* by these authors. This cavity is formed by four cells: one cup-shaped supportive cell, one large biciliated or multiciliated sensory cell, and two small uniciliated or biciliated sensory cells. The axon of the large sensory cell enters the dorsal part of the neuropil of the brain, closely behind the sensory organ. These unpigmented ciliary eyes in *Lindrilus* and *Protodrilus* are situated terminally in the prostomium, visible as rounded structures containing a comparatively high volume of paracrystals, whereas in *C. helgolandicus* and *M. adhaerens* they are inconspicuous and mostly filled with microvillous-like material. In *M. adhaerens*, unpigmented receptors are situated terminally in the prostomium (Fig. 7.11.3.6C), whereas in *C. helgolandicus* they occur at the base of the palp, are oval, and contain comparatively low volume of paracrystals. In *Astomus taenioides*, three types of unpigmented photoreceptor-like sense organs have been found. One of these somewhat resembles the "statocysts" of other protodrilids, but with respect to their different position in the posterior extensions of the brain, their higher number, and their cellular composition, these were not regarded as homologous with ciliary unpigmented eyes by Purschke and Jouin-Toulmond (1993). In *P. ciliatus,* these unpigmented ciliary eyes are associated with a small, phaosomous structure (Fig. 7.11.3.7C and see below).

Phaosomous receptors consist of one single, ovoid cell with an internal cavity filled with microvillous-like structures that originated from two ramified cilia in protodrilids. Therefore, these receptor cells are labeled with antibodies against tubulin (Fig. 7.11.3.6C). This type of receptors has been described at the base of the palps in *Meiodrilus adhaerens* (in other literature referred to as "statocyst") (Purschke 1990a), in the posterior part of the prostomium in *Astomus taenioides*, as well as in the palps of *Protodrilus ciliatus* and *A. taenioides* (Purschke 1993, Purschke and Jouin-Toulmond 1993) approximately half-way between the base and the tip of the palp (Fig. 7.11.3.6C).

The nuchal organs consist of supportive ciliated and bipolar sensory cells (Fig. 7.11.3.7B) (Purschke 1988). The ciliated cells rest upon an ECM and are arranged as a single layer with basal interdigitating processes. The bipolar sensory cells occur in clusters immediately below the anterior ciliated supportive cells, forming the olfactory chambers. Two olfactory chambers containing approximately 50 sensory cells are found in *Protodrilus ciliatus*, whereas only one chamber with less than 10 receptor cells are described in *Meiodrilus adhaerens* and *Astomus taenioides* (Purschke 1988, Purschke and Jouin-Toulmond 1993). The somata of the bipolar sensory cells form the nuchal ganglia, and their axons constitute the nuchal nerve, which enters the neuropil of the brain dorsally and medially to the dorsal root of the circumesophageal connective (Fig. 7.11.3.6A). Each nuchal organ is supported by a retractor muscle, which attaches to the ECM opposite to the ciliated cells and inserts near the longitudinal muscles in the prostomium (Fig. 7.11.3.7B).

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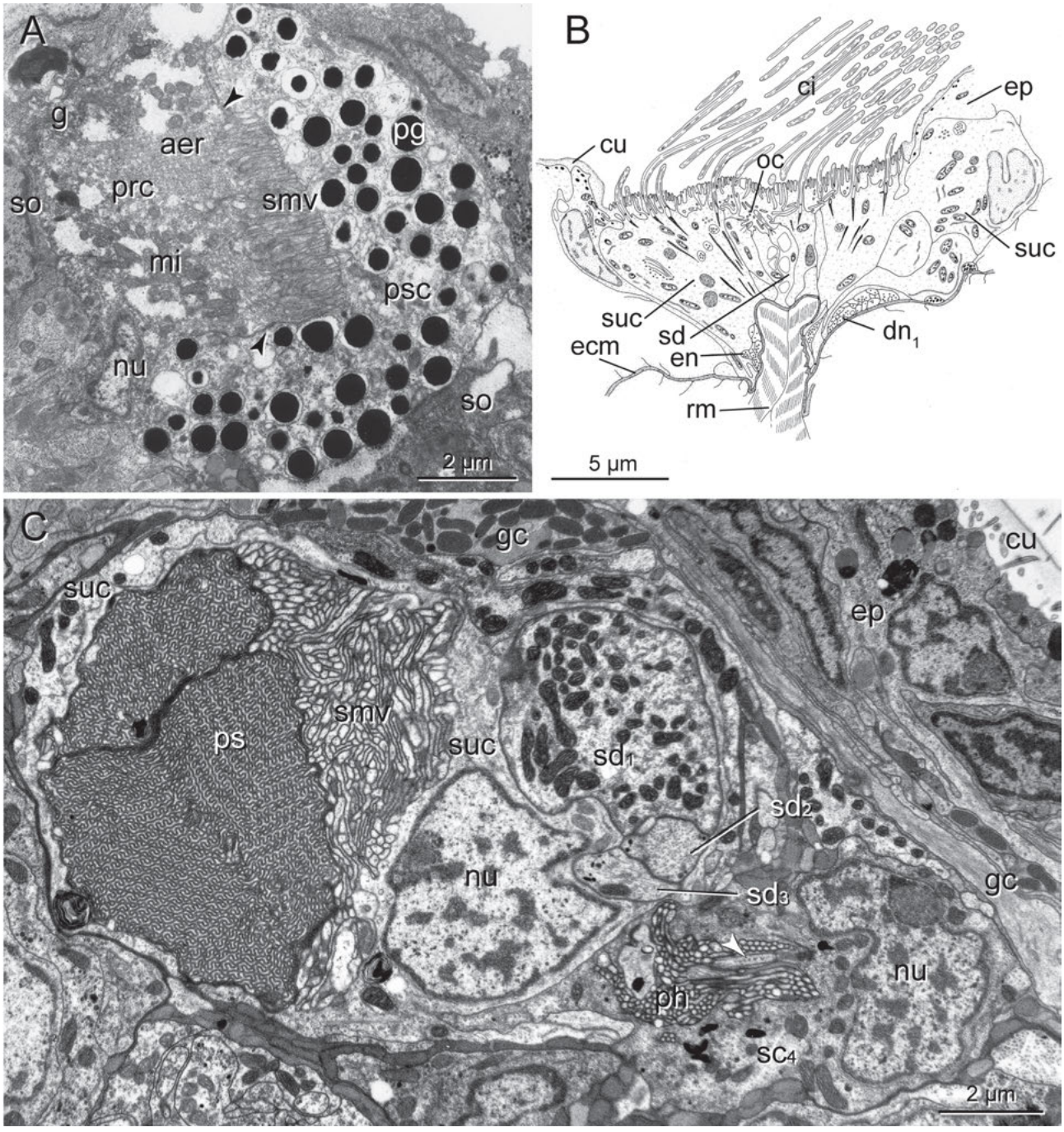


Fig. 7.11.3.7: Sense organs. TEM observations. A, *Protodrilus oculifer*. Pigmented eye embedded in the somata (so) of the brain and comprising one pigmented supportive cell (psc) and one rhabdomeric photoreceptor cell (prc) forming an extracellular cavity into which the sensory microvilli (smv) project; arrowheads point to zonula adhaerens; B, *Meiodrilus adhaerens*. Nuchal organ. Organ composed of a few ciliated supportive cells (suc), surrounding a few sensory dendrites (sd) of primary sensory cells; their sensory processes lie within the olfactory chamber (oc) below the modified cuticle (cu); C, *Protodrilus ciliatus;* unpigmented photoreceptor organ ("statocyst") embedded in the brain tissues and separated from the epidermis (ep) by glial cell processes (gc). Paracrystals (ps) made up of ciliary membranes constitute a refractive body, and microvillar sensory processes (smv) of three sensory cells (scd_{1-3}) project into an extracellular cavity formed by these cells and a supportive cell (suc); a ciliary phaosome (ph) of a fourth sensory cell (sc_4) is found in close vicinity; arrowhead points to sensory cilium. aer, agranular endoplasmic reticulum; ci, cilium; cu, cuticle; dn_1, dorsal nerve 1; ecm, ECM; en, efferent innervation; ep, epidermis; g, Golgi apparatus; gc, glial cell; mi, mitochondrion; n, nucleus; oc, olfactory chamber; pg, pigment granule; ph, phaosome; prc, photoreceptor cell; ps, paracrystal; psc, pigmented supportive cell; rm, retractor muscle; sc_4, sensory cell 4; sd_{1-3}, sensory dendrites 1 to 3; smv, sensory microvilli; so, soma (of neuron); suc, supportive cell. B, Redrawn from Purschke (1988).

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Reproduction, development, and life cycles

In Protodrilidae, sexes are separate; usually, the fertile region follows the salivary glands region and the number of fertile segments is large (Jägersten 1952, Jouin 1970b, c, von Nordheim 1989a, Purschke 2006, Westheide 2008). The structure and arrangement of genital organs are species specific in both sexes but is not sufficiently known for every species described. In females, the fertile region may extend from segment 10 and backward (except for *Protodrilus gelderi*); in males, fertile segments normally start between segments 9 and 13 and backward. In these segments, developing spermatids, spermatozoa, or oocytes finally occupy most of the coelomic spaces at the end of gamete maturation. Fertilization in Protodrilidae is internal, and sperm transfer is achieved via spermatophores. In contrast to many other interstitial annelids, the development includes a trochophore; accordingly, the number of oocytes produced usually is comparatively high in many species (Westheide 2008). This later phenomenon is in accordance with the hypothesis that Protodrilida have evolved by miniaturization rather than by progenesis as suggested by Struck et al. (2015).

Males

Mature males of Protodrilidae possess paired lateral organs, which are involved in the production of spermatophores (von Nordheim 1991b). The lateral organs are invaginations of the epidermis, which form a wide furrow into which numerous gland cells open and numerous cilia project (Figs. 7.11.3.3A, 7.11.3.8A, 7.11.3.11D, 7.11.3.14H, 7.11.3.16I, 7.11.3.18C, 7.11.3.19C, 7.11.3.20K) (von Nordheim 1991b, Westheide 2008). These furrows can be continuous and extend over several segments (Fig. 7.11.3.11D) or be segmentally separated (e.g., Figs. 7.11.3.14H, 7.11.3.19C). The first pair of lateral organs is reduced to a small, rounded ciliated pit in some species (Figs. 7.11.3.11D, 7.11.3.19C), whereas in others it is morphologically identical or slightly shorter than the subsequent lateral organs (Fig. 7.11.3.14H). Lateral organs are generally limited to a species-specific number of anterior segments and have been traditionally used as a character for species delineation (e.g., Figs. 7.11.3.12E, 7.11.3.13C, 7.11.3.15C, 7.11.3.17E, 7.11.3.20D, 7.11.3.22D) (Jägersten 1952, Jouin 1970c, von Nordheim 1989a, Westheide 2008). One exception is found in *Claudrilus tenuis*, for which the extension of the lateral organs depends on the degree of maturation (Jouin 1970c, Jouin-Toulmond and Purschke 2004). The ultrastructure of lateral organs is similar in all species investigated, only differing in the number and types of surrounding gland cells (Fig. 7.11.3.8A). They comprise exocrine merocrine gland cells positioned dorsally or ventrally relative to the lateral organs, as well as supporting cells, large vacuolated cells (probably representing a special type of supporting cells called “sponge cells” by von Nordheim 1991a), a few sensory cells, and several multiciliated cells. An irregular layer of glia-like cells and nervous tissue containing vesicles of neuropeptides lies just above the basal lamina.

The spermioducts occur in a species-specific number and run along two consecutive trunk segments before opening into the lateral organs (Jouin 1970c, von Nordheim 1989a, Westheide 2008, Martínez et al. 2017). They consist of a fully ciliated tube, which opens to the coelom as a comparatively wide fully ciliated funnel (von Nordheim 1991b). Directly behind the funnel, the diameter of the spermioduct is abruptly reduced to a tube that penetrates the posterior septum and runs beneath the transverse muscles to the lateral organs. Terminally, the diameter of the spermioduct tube diminishes, penetrates the epidermal basal lamina a little below the lateral organ, and opens into the anterior area of the organ. The spermioducts are not surrounded by muscular tissue, and ciliary movement seems to facilitate the transportation of the spermatozoa along the spermioducts. The spermatophores are elaborated by a secretion around the bundle of spermatozoa, which is formed at the gland pore openings in the lateral organs.

All male protodrilids have two types of slender and filiform spermatozoa: euspermatozoa and paraspermatozoa (Fig. 7.11.3.8B, C). First reported from LM observations by Pierantoni (1908), their ultrastructure has been completely described by von Nordheim (1989b). So far, ultrastructural data for 14 different species from all genera, including *Astomus*, are available (Franzén 1977, von Nordheim 1989b, Jouin-Toulmond and Purschke 2004). Euspermatozoa are involved in the fertilization of the oocytes, whereas the paraspermatozoa are considered to play a role in the enzymatic opening of the spermatophore and the female epidermis during sperm transfer. The morphology of the euspermatozoa is complex and shows a species-specific variation, potentially containing phylogenetic information for the family, differing in the size of the different sperm regions, the structure of acrosome and nucleus, the presence or absence of an axial rod, as well as the number, shape, and size of supporting elements in the midpiece and the tail. In contrast, the paraspermatozoa are very similar across species, and supporting structures in the midpiece and tail region are lacking (Fig. 7.11.3.8B, C).

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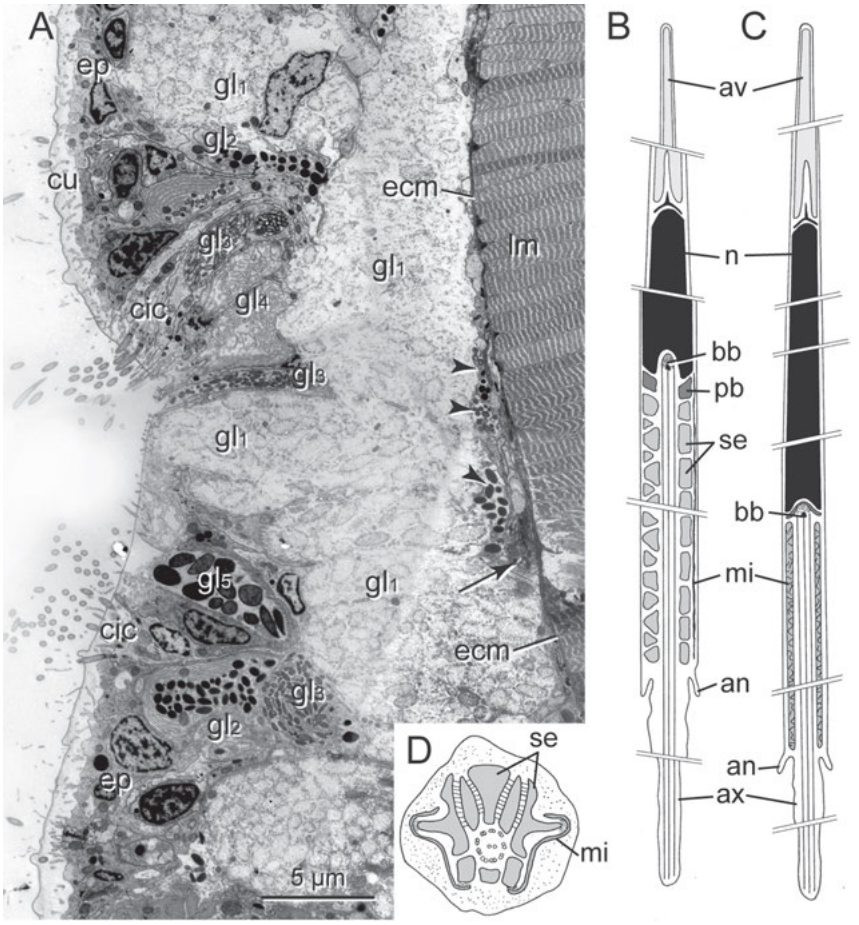


Fig. 7.11.3.8: Male genital organs and spermatozoa. A, *Protodrilus ciliatus*. Anterior lateral organ comprising five types of gland cells (gl1-5) and ciliated cells (cic), arrowheads point to gland cell necks, arrow points to neurite bundle, TEM; B, D, *Astomus taenioides*. Spermatozoa. Reconstructions from TEM observations; B, Euspermatozoon; C, Paraspermatozoon; D, Cross-section of euspermatozoon below basal body showing arrangement and different sizes of supporting elements (se) around axoneme (ax). an, annulus; av, acrosomal vesicle; ax, axoneme; bb, basal body; cic, ciliated cell; cu, cuticle; ecm, ECM; ep, epidermis; gl1-5, gland cells 1 to 5; lm, longitudinal musculature; mi, mitochondrion; n, nucleus; pb, parabasal body; se, supporting element. B–D, Modified after Jouin-Toulmond and Purschke (2004).

Females

The females of most protodrilids lack any conspicuous external reproductive structures, except for ciliary furrows (Fig. 7.11.3.11F) and the dorsal organs (Fig. 7.11.3.14F, I, J), which are present in a few species (von Nordheim 1989a, Westheide 2008). Dorsal organs are segmentally arranged structures, extending backward from segments 19 to 22. They are found in the females of *Lindrilus rubropharyngeus* and *Lindrilus flavocapitatus* (see von Nordheim 1989a) and are involved in the sperm transfer (von Nordheim 1991a). Each dorsal organ consists of rosette-shaped ciliary pits (Fig. 7.11.3.14I), which continues internally through the epidermis and the basal lamina as a narrow tube toward the longitudinal muscle layer, with the ventral section of the organ bordering directly on the epithelium of the dorsal blood vessel (Fig. 7.11.3.14F). The rosette-like structure consists of several supportive cells as well as the internal and external gland cells. Ciliary furrows are only known from females of *Protodrilus leuckartii* and *Protodrilus ciliatus* (see Jouin 1970c); extending along several anterior trunk segments (Fig. 7.11.3.11F), they consist of fully ciliated continuous furrows, very similar to lateral organs of males but lacking exocrine glands. Oviducts are described only in a few species of Protodrilidae, including *Lindrilus rubropharyngeus*, *Lindrilus flavocapitatus*, *Lindrilus haurakiensis*, *Protodrilus brevis*, *Megadrilus pelagicus*, and *Megadrilus purpureus* (see Jägersten 1952, Jouin 1970c, von Nordheim 1991a, Martínez et al. 2017). They consist of fully ciliated tubes extending along two consecutive posterior segments. They open in the body cavity as a wide, fully ciliated funnel near the posterior septum. In *L. rubropharyngeus* and *M. purpureus*, the funnel is sealed by a muscular diaphragm. The diameter of the oviducts depends on the size of the eggs, being larger in those species with larger eggs. Irrespective of the species and the size of the females, oocytes generally measure between 25 and 65 µm in Protodrilidae (reviewed by von Nordheim 1989a, own unpublished observations). Abundant oocytes are present in *Lindrilus* and *Megadrilus* (Figs. 7.11.3.10E, 7.11.3.16D), where usually 20 to 50 oocytes per segment can be found, but in certain species such as *L. rubropharyngeus* or *L. haurakiensis* there may be up to 100 or even 160 per segment (von Nordheim 1989a). In contrast, species of *Meiodrilus* and *Claudrilus* have only a few oocytes per segment, usually 4 to 6, whereas *Protodrilus* shows a

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somewhat intermediate number with 6 to 14 oocytes per segment. At least in species of *Meiodrilus* and *Claudrilus*, often, sole gregarines may be found in the coelom pretending large oocytes (Figs. 7.11.3.18G, 7.11.3.21G). However, as a rule, these parasites do not occur in every (fertile) segment and also outside the breeding season as well.

Reproductive strategies

The reproduction of Protodrilidae remained unknown until first Langerhans (1880) then Pierantoni (1906a, b, c, 1908) correctly described the gametogenesis and the early development in the family and Jägersten (1952) correctly described the sperm transfer strategies. For example, early workers confused the salivary glands, present in the anterior trunk segments, with gonads and considered all species as hermaphroditic (Schneider 1868, Uljanin 1878, Hatschek 1881), whereas Goodrich (1931) proposed that the opening section of the lateral organ in *Lindrilus flavocapitatus* could be evaginated like a penis involved in fertilization.

However, all following investigations have shown that all protodrilids are gonochoristic and bear the gonads in the body cavity of the middle and posterior trunk segments. Sperm transfer occurs via spermatophores, which the males deposit on sand grains (Jägersten 1952, Jouin 1970c, von Nordheim 1991a). The spermatophore is produced in the lateral organs, where the sperm is released through the spermioducts and surrounded by glandular secretions of the lateral organs, which form the sheath of the spermatophore (Jouin 1970c, von Nordheim 1989b, 1991b). The secretions from different types of glands might possibly represent different functions, serving as a nutrient for the spermatozoa or attracting the females (Pierantoni 1908). The shape of the spermatophore varies across species, being rounded in *Lindrilus rubropharyngeus* and elongated in *Claudrilus helgolandicus* (see Jägersten 1952).

The females collect the spermatophores from the sand grains by gliding over it. The spermatophore attaches to a random spot on the female body in most species (von Nordheim 1991b). After the attachment of the spermatophore, the sperm penetrates the female epidermis (Jägersten 1952, von Nordheim 1991a) supposedly opened histolytically by substances in the spermatophore or in the acrosome of the paraspermatozoa, which gets completely lost or reduced after penetration. Exceptionally, in the females of *Lindrilus rubropharyngeus* and *Lindrilus flavocapitatus*, the balloon-shaped spermatophores always attach to the dorsal organs before sperm penetrate through its tube and gather in the ventral section of the organ. It has also been suggested that in some species the spermatozoa might enter the body cavity through the nephridia, as spermatozoa have been found in the ducts of the protonephridia of *L. rubropharyngeus* (von Nordheim and Schrader 1994). The females of *Protodrilus leuckartii* and *Protodrilus ciliatus* possess ciliary furrows, which are possibly involved in sperm transfer, although their exact role remains unknown.

After fertilization, which involves the euspermatozoa and takes place in the body cavity of the female, oviposition occurs in a number of different ways. Fertilized eggs are released through oviducts in *Lindrilus*, *Megadrilus*, and *Protodrilus brevis*. In other species, oviposition occurs by rupture of the body wall or by shedding some posterior segments, as suggested by Pierantoni (1908), who frequently found females with regenerating posterior body segments at the end of the reproduction period. *Claudrilus helgolandicus* sheds the eggs after lateral rupture of the body wall in the posterior segments, which heals rapidly after oviposition (von Nordheim 1983). Oviposition combined with partial rupture of the hindmost body wall was also observed in *Protodrilus litoralis* (see von Nordheim 1989a) and very likely occurs similarly in *Protodrilus submersus*. Finally, some species (e.g., *Meiodrilus adhaerens*) might release the eggs using the nephridial ducts and openings, as supported by the presence of thicker nephridia in fertile specimens *M. adhaerens* as well as the lack of injuries in the epidermis of the females of several species after oviposition.

Most protodrilids deposit grouped eggs individually on the surface of sand grains. Species of *Meiodrilus* have special glands to produce cocoons that attach to sand grains (Swedmark 1964, von Nordheim 1989a, Giere 2009) and host the first developmental stages. In *Protodrilus albicans*, segmentation and gastrulation take place within the coelomic cavity of the females and small trochophores are released into the water column.

Development

The larval development has been studied in *Megadrilus purpureus*, *Lindrilus rubropharyngeus*, *Meiodrilus adhaerens*, and *Protodrilus ciliatus* and certain other species (Pierantoni 1906c, 1908, Jägersten 1940, 1952, Jouin 1970b). All species studied so far possess planktonic developmental stages. According to Jägersten (1952), in all species, development comprises a trochophore stage followed by two larval stages (metatrochophores), so-called immature and mature larval stages, distinguishable by their body size and the number of ciliary rings (two to four in the immature stage and more than four in the mature stage) (Fig. 7.11.3.9A–E).

The young trochophores are spherical, generally about 50 µm in diameter, and possess well-developed germ layers and a prototroch consisting of a double row of cilia (Fig. 7.11.3.9A, B). Internally, the yolk occupies the prospective gut and the foregut is visible as a rudiment.

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In all protodrilid species studied, the trochophore is characterized by an eversible stomodeal funnel that is ciliated and allows the capture of suspended particles (Fig. 7.11.3.9C, D). The shape, position, and ciliation of this stomodeal funnel are species specific (Jägersten 1952, Jouin 1970b). In *Protodrilus ciliatus* and *Lindrilus rubropharyngeus*, this organ is oriented ventroposteriorly and densely ciliated, collecting food particles by ciliary water currents (Fig. 7.11.3.9C), whereas in *Meiodrilus adhaerens* and *Protodrilus oculifer* it is ventrally oriented and possesses a long, motile, finger-like appendage with a few terminal motile cilia and abundant glands (Fig. 7.11.3.9C), which intercept food particles by producing mucous secretions. A muscular and ciliated valve separates the funnel organ from the midgut (Fig. 7.11.3.9C, D).

Progressively, the body enlarges and becomes oval and the mouth, foregut, and midgut start to differentiate, although in different positions depending on the species. In *Meiodrilus adhaerens*, the mouth opens just behind the prototroch in the gut and extends toward the posterior end. In contrast, in *Lindrilus rubropharyngeus*, the mouth opens in the posterior half of the body followed by the foregut running upward and midgut extending forward forming a 90° angle. At the end of this embryonic stage, some species possess two pigmented anterior eyes (normally one appears earlier than the other) as well as sensory ciliary tufts anteriorly and posteriorly. A few bacillary glands and chromophile granules are already visible in the epidermis. The telotroch develops at the end of that stage in *M. adhaerens*.

The first metatrochophore larval stage is planktonic as well. During that stage, the digestive system becomes fully functional, the epidermal ciliation develops further, and the anlagen of the pygidial lobes appear in the posterior end (Fig. 7.11.3.9E). The midgut becomes fully ciliated and its epithelium contains brownish granules in all species. The anus opens at the posterior end, terminally in *Meiodrilus adhaerens* and dorsally in *Protodrilus ciliatus* and *Lindrilus rubropharyngeus*. At the end of the first metatrochophore larval stage, two additional rings appear in the larva between the second ring and the telotroch, and the larva grows up to approximately 200 to 300 µm by adding more metameres at the posterior end.

The second metatrochophore larval stage is the last larval stage before metamorphosis and is characterized by the presence of four ciliary rings. These larvae are 70 to 270 µm long in *Meiodrilus adhaerens*. The midventral ciliary band appears as a small ciliary tuft between the second and third rings after the development of the fourth

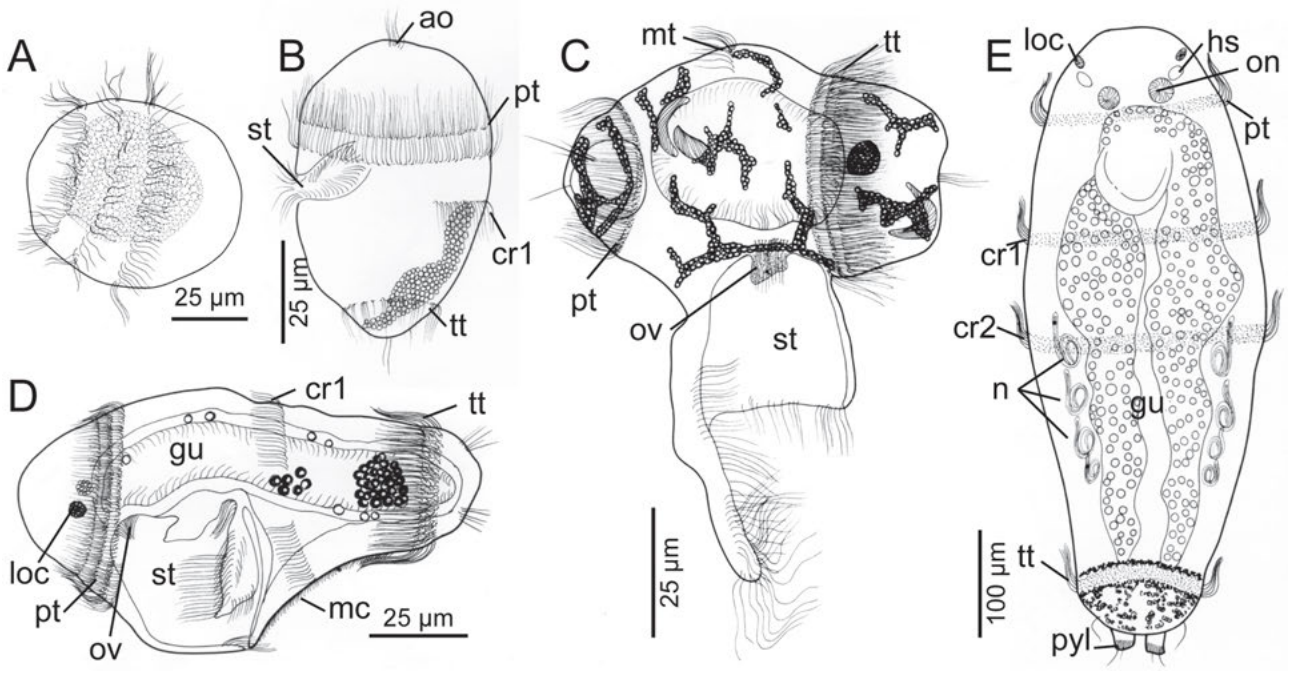


Fig. 7.11.3.9: Development. A, *Megadrilus purpureus*. Swimming gastrula/early trochophore, three ciliary rings differentiated; B, *Claudrilus hypoleucus*. 1d early trochophore, stomodaeum (st) begins to develop, prototroch (pt) by double ring of cilia, telotroch (tt) and first ciliary ring (cr1) present; C, *Protodrilus oculifer*. 4d trochophore with pigment pattern, ciliated funnel fully everted; D, *Protodrilus ciliatus*. Late trochophore, ciliated funnel retracted and closed, development of midventral ciliary band (mc) begins; E, *P. oculifer*. Metatrochophore ("immature larva"), pygidial lobes begin to develop, first four pairs of nephridia have been formed, larval eyes (ocelli, loc) still present and adult eyes not formed yet. ao, apical organ; cr1, 2, ciliary ring 1, 2; gu, gut; hs, hyaline structure; loc, larval ocellus; mc, midventral ciliary ring; n, nephridium; no, nuchal organ; ov, esophageal valve; pt, prototroch; pyl, pygidial lobe; st, stomodaeum. Modified from Jouin (1970b).

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ring and expands toward the pygidium first as a single row of cilia, broadening progressively to its adult configuration. The nuchal organs and unpigmented prostomial receptors also appear at the end of this stage, and the early development of the latter has been described to start from open pits extending deep into the brain that close right before metamorphosis (Jägersten 1952). The pygidial lobes get fully developed, and bacillary and chromophile glands cover the epidermis (denser coverage in *Lindrilus rubropharyngeus* and *Protodrilus ciliatus*). In *M. adhaerens*, fully functional segmental adhesive glands appear at this stage.

At least in *L. rubropharyngeus*, there are two pairs of dorsolateral larval protonephridia at this stage, each provided with an oval internally ciliated bladder. The bladder has thick walls, densely covered by golden granules, and connects to the body wall in front of each ciliary ring by a short duct, whereas a bent, longer duct goes from the bladder to the intestine. These protonephridia disappear during metamorphosis, when the nephridia present in the adult stages develop.

Metamorphosis is triggered by the contact of the mature larvae with the substrate. During metamorphosis, the body acquires the configuration of the adults, and new metameres appear at the posterior end. The palps start also developing during that stage, budding off lateroventrally from the prostomium. The larval eyes and ciliary rings disappear in most species during this stage.

Distribution and habitat

Species of Protodrilidae have been found all over the world, except for Antarctica, mostly in marine shallow water sediments. *Protodrilus spongioides* Pierantoni, 1903 is the only species described in freshwater so far, found in freshwater aquaria at the Napoli Marine Station (Pierantoni 1903). However, the species is only known from its original description, which lacks many important morphological characters and is insufficient for the reidentification of the species (Martínez et al. 2015). Other protodrilids prefer brackish waters and are common in coastal lagoons or estuarine areas, such as *Protodrilus leuckartii*, which is mostly recorded from coastal lagoons in Italy and the south of France (Hatschek 1881, Jouin 1970c). However, most protodrilids live in fully marine waters, where they prefer coarse well sorted sands at 0 to 10 m depth (Jouin 1970c, von Nordheim 1989a, Martínez et al. 2015) or coral sands (Jouin 1979). In tidal beaches, the upper intertidal zone is usually avoided, except for a few species such as *Meiodrilus adhaerens* (see von Nordheim 1984). Protodrilids are rarely reported below 50 m depth, the exceptions being a new species of *Claudrilus* from Iceland and *Protodrilus puniceus* from Japan (Sato-Okoshi et al. 2015).

Some species or genera prefer particular marine environments. *Astomus* lives exclusively in coral sands. Species of the genus *Lindrilus* are more common in very coarse sand or gravel in the slope of exposed beaches at the swash zone. Other protodrilids are abundant in the coarse and gravelly sediments accumulated at the surf zone of sandy beaches, including *Protodrilus albicans* in Banyuls-sur-mer, France, and in Isola Asinara, Sardinia, *Megadrilus hochbergi* at the Caribbean, and *Megadrilus schneideri* at the Mediterranean and the Canary Islands. These species cope with the turbulence in this highly hydrodynamic zone exhibiting swimming behavior facilitated by the well-developed body wall musculature and large size (Jouin 1970c, Martínez et al. 2013). Other protodrilids, such as the species of the genus *Meiodrilus* and the Brazilian species *Claudrilus corderoi*, cope with the hydrodynamics by penetrating deeper layers of the sediment column or adhering to individual grains with segmental adhesive glands (Di Domenico et al. 2013, Martínez et al. 2015). However, most of the species, except *Astomus*, *Protodrilus puniceus*, and *Megadrilus pelagicus*, can be found in a wide range of sedimentary environments without exhibiting a clear ecological preference in terms of sediment type or bathymetry.

Only two species of protodrilids were discovered outside of the interstitial realm: *Protodrilus puniceus* and *Megadrilus pelagicus*. *M. pelagicus* is endemic from La Corona lava tube, a 1600-m-long anchialine lava tube in Lanzarote, Canary Islands (Martínez et al. 2009, Wilkens et al. 2009). The species is never found crawling in the bottom but always in the water column, where it usually hoovers with the prostomium pointing at the bottom. It keeps buoyancy using its transverse and longitudinal ciliary bands and feeds on suspended organic matter with specialized long palps. In case of disturbance, it can also swim producing muscular waves of the entire trunk, favored by the lateral compression of the body and the presence of a dorsal keel. The lack of direct communication between the cave and the ocean facilitates this unique behavior, as it prevents the presence of large marine predators (e.g., fish) or turbulence (Martínez et al. 2017). The total darkness inside the cave limits the primary production by photosynthesis, and the only food available in the cave consists of suspended organic particles dragged inside by tidal currents.

Protodrilus puniceus was described from whale falls off Cape Noma Misaki, Kyushu Island (Japan) at 219 to 254 m depth. The species forms dense aggregations in the innumerable small pores of sperm whale bones. Some individuals were completely buried in the bones, whereas others were found with part of their bodies emerging from it (Sato-Okoshi et al. 2015). In aquaria, *P. puniceus* was

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observed to use their palps and midventral ciliary bands to gather small organic particles around the mouth. Braby et al. (2007) reported the presence of a similar protodrilid from whale falls in Monterrey Bay (California).

The distribution of the different protodrilid genera lack any clear biogeographical pattern, and most of the genera are found in every surveyed locality (Figs. 7.11.3.12F, 7.11.3.15D, 7.11.3.17F, 7.11.3.20E, 7.11.3.22E) (Jägersten 1952, von Nordheim 1989a, Martínez et al. 2013). The exception is *Astomus*, which is so far exclusively known from organic matter-rich sediments near coral reefs in the Indo-Pacific (Fig. 7.11.3.13D) (Jouin 1979). This lack of biogeographical patterns might reflect the dispersal abilities of the family or the ancient age of the family but could also highlight a poor knowledge on the actual diversity. A few species of protodrilids are only known from a single locality, whereas those described with a wide distribution ranges (Kirsteuer 1966, Jouin 1970a, Bailey-Brock et al. 2010) may also represent cryptic or pseudocryptic species. Certain species complexes seem to be restricted to Europe (e.g., *Claudrilus hypoleucus*, *Claudrilus helgolandicus*, *Protodrilus ciliatus*, and *Protodrilus affinis*) as well as represent clades with a Western Atlantic-Indo-Pacific distribution (e.g., *Protodrilus jagersteni*, *Protodrilus smithsoni*, and *Protodrilus submersus*). These distributions may either indicate the presence of certain biogeographical patterns in Protodrilidae or be a mere consequence of fragmentary and geographically biased sampling (Martínez et al. 2015).

Motility, feeding, and life cycles

Motility

Protodrilids glide among sand grains by means of the midventral motile ciliary band (Jägersten 1952, 1954, Jouin 1970b, c, Martin 1978a). The remaining ciliary bands in Protodrilidae are involved in the production of water currents running above the trunk, except for *Megadrilus pelagicus*, in which these ciliary bands are involved in swimming (Martínez et al. 2017). Transverse bands of motile cilia are present in *P. ciliatus*, which uses them to produce water currents along the body. The remaining cilia are mostly sensory in function and belong to different types of sensory cells (see above). The trunk body musculature serves to bend the trunk and change direction during gliding (Jägersten 1954). In large species, such as *Protodrilus albicans*, living in beach surf zone, this musculature is also involved in swimming during short time periods, generally as an escape reaction (Jouin 1970c, Martínez et al. 2017). These movements are primarily achieved by the four longitudinal muscle strands, allowing more differentiated movements than for instance in nematodes (Figs. 7.11.3.2B, 7.11.3.3A–C, 7.11.3.4A, B). In *Megadrilus*, the muscular contractions are often spasmodic and can lead to fragmentation of the body. Species of *Meiodrilus* and some *Claudrilus* possess segmental adhesive glands and stick to the sand grains by curling their bodies around them (Jägersten 1954, Jouin 1970c). These glands provide additional attachment, which may be advantageous for animals dwelling in turbulent interstitial environments, for example, the beach surf zone (Jägersten 1954). The adhesive pygidium not only provides posterior attachment to sand grains but also facilitates changes in direction and fast retraction of the body upon negative stimuli, acting in combination with the trunk musculature (Jägersten 1954, von Nordheim 1989a).

Feeding

Most protodrilids are subsurface deposit feeders and browse bacteria and diatoms growing on the sand grain surfaces as well as organic matter deposited in the interstices (Westheide 2008). Deposited organic matter is grazed by the combined action of the muscular pharyngeal apparatus and the ciliary bands round the mouth (Jägersten 1952, Jouin 1978a, 1978b). The palps in *Megadrilus*, *Protodrilus*, or *Lindrilus* have distinct frontal and ventral motile ciliary bands associated with mucous glands, which might facilitate the collection of particles, by producing water currents toward the mouth (Figs. 7.11.3.11C, 7.11.3.14K, 7.11.3.16H). Two strong ciliary areas are developed ventrally in front of the mouth in *Protodrilus brevis*, the only semisessile protodrilid species described, feeding on suspended organic matter (Jouin 1970c). Species of the genus *Astomus* lack mouth and pharynx, and their digestive gut is residual. They live in coral sediments enriched with organic matter. The epidermal cuticle of *A. taenioides* is very rich in microvilli and subcuticular vesicles, indicating a possible uptake of dissolved or particulate organic matter through the body wall (Jouin 1992). *Megadrilus pelagicus*, a stygobitic species endemic from La Corona lava tube in Lanzarote (Canary Islands), is the only reported swimming suspension feeding protodrilid (Martínez et al. 2017).

Life cycles

Temperature is one of the most important factors affecting abundances of Protodrilidae (von Nordheim 1984). In seasonal investigations in Helgoland (North Sea, Germany), an increase of the water temperature was correlated with an increase in the abundances of *Protodrilus oculifer* and *Megadrilus purpureus*, reaching their maximum abundance in August. This maximal abundance coincided

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with the main reproductive period of these species, which ranged from April to October in *P. oculifer* and from March to October in *M. purpureus*. In contrast, the abundances of *Claudrilus helgolandicus, Meiodrilus adhaerens*, and *Protodrilus ciliatus* were inversely related to temperature, with maximum abundances correlated with lower temperatures in December. These high abundances corresponded with the middle of the reproductive period (March–June in *M. adhaerens* and November–May in *P. ciliatus*), whereas in periods with the lowest abundances most of the recorded individuals were juveniles. Similarly, the density of *Lindrilus flavocapitatus* in Sevastopol Bay reached its maxima in November and December as well as in April (Kopiy 2013) and its minima in June; this is opposite to the observations for *Lindrilus rubropharyngeus* in Sweden, for which most mature individuals were found in late spring and summer (Jägersten 1952). The highest density of mature females was found during the second peak of abundance in April. The highest abundances of *L. flavocapitatus* were correlated with temperatures between 8°C and 18°C. *P. oculifer*, *P. ciliatus*, *M. purpureus*, *M. adhaerens*, and *C. helgolandicus* are species with a life span of approximately 1 year and probably spawn only once in their life cycle (von Nordheim 1983, 1984).

Systematics

The family Protodrilidae was erected by Hatschek (1888), who used the name to place *Protodrilus leuckartii*, a species that he previously described from sediments in a coastal lagoon in Sicily, Italy (Hatschek 1881). The names Protodrilidae and *Protodrilus*, however, were first introduced by Czerniavsky (1881), who erected them to place *Protodrilus mirabilis*, a filiform animal with a nematode-like cuticle, neither palps nor pharynx, and with a simple gut and two sublateral red vessels along the entire body. However, *P. mirabilis* has never been found again and is not considered as a valid species, as the absence of type material prevents the reidentification of the species and the short description contradicts the features of all other described Protodrilidae. Therefore, this name and Protodrilidae Czerniavsky, 1881 should be considered a *nomen dubium*. The authority of *Protodrilus* should hence be attributed to the first true *Protodrilus*, *P. leuckartii* Hatschek, 1881, and the authority of the family name Protodrilidae is given to Hatschek (1888) (Martínez et al. 2015).

Protodrilidae traditionally consisted of two genera, *Protodrilus* Hatschek, 1881 and *Astomus* Jouin, 1971. *Protodriloides* Jouin, 1966 was initially placed within Protodrilidae as well, but later it was transferred to Protodriloididae Purschke & Jouin, 1988 based on morphological analyses on the pharynx, the nervous system, and the palp structure. *Protodrilus* was defined by the presence of ciliated palps with internal canals connected behind the brain, two adhesive pygidial lobes, and lateral organs in the males involved in the production of spermatophores (Purschke and Jouin 1988). These features are present in *Astomus*, which additionally lacks mouth and possesses a residual gut (see above). The genus *Protannelis* was introduced by Lam (1922) to place the species *Protannelis meyeri* Lam, 1922 described from mud near a coral reef in Java (Read 2014). However, the original description was based on a fragmented single specimen preserved in ethanol and without a head. The description provides detailed information on the musculature and the nephridia but lacks references to any of the diagnostic features of Protodrilidae, including the presence of palps with canals, pygidial lobes, or lateral organs (Lam 1922).

A recent phylogenetic study of Protodrilidae employing 5 gene fragments, 55 morphological characters, and 66 species of protodrilids (30 of them still undescribed) and analyzed under parsimony and model-based methods revealed a new perspective on the phylogeny of Protodrilidae (Martínez et al. 2015): the family is shown to contain six cosmopolitan subclades, each supported by several morphological apomorphies (see diagnoses below), and with the genus *Astomus* consistently nested among the other five clades rather than as sister to these. The result of these analyses led to a rearrangement of the systematics of the family. The diagnosis of the genus *Protodrilus* was emended, *Astomus* remained unchanged, and the four remaining lineages were diagnosed and named as the new genera *Megadrilus*, *Meiodrilus*, *Claudrilus*, and *Lindrilus* to solve the paraphyly of *Protodrilus*. Although this was the first phylogenetic analysis of the internal relationships of Protodrilidae, some of the genera were congruent with morphological groups of species previously proposed. For example, Jouin (1970c) and von Nordheim (1989a) grouped several species now included in the emended *Protodrilus*, such as *P. affinis*, *P. leuckartii, P. ciliatus*, *P. albicans*, *Protodrilus hatscheki*, *P. litoralis*, *P. submersus*, and *P. jagersteni*; several species now included in the genus *Claudrilus*, such as *C. hypoleucus*, *C. tenuis*, *Claudrilus pierantonii*, and *C. helgolandicus*; and other species included in the genus *Meiodrilus*, such as *M. adhaerens*, *M. gracilis*, *Meiodrilus indicus*, and *Meiodrilus jouinae*.

Protodrilidae Hatschek, 1888

***Protodrilus* Hatschek, 1881** (type genus) (Figs. 7.11.3.10A–E, 7.11.3.11A–H, 7.11.3.12A–F)

Type species: *Protodrilus leuckartii* Hatschek, 1881

Diagnosis: Body opaque, prostomium with ciliated palps, with or without pigmented eyes, and with rounded,

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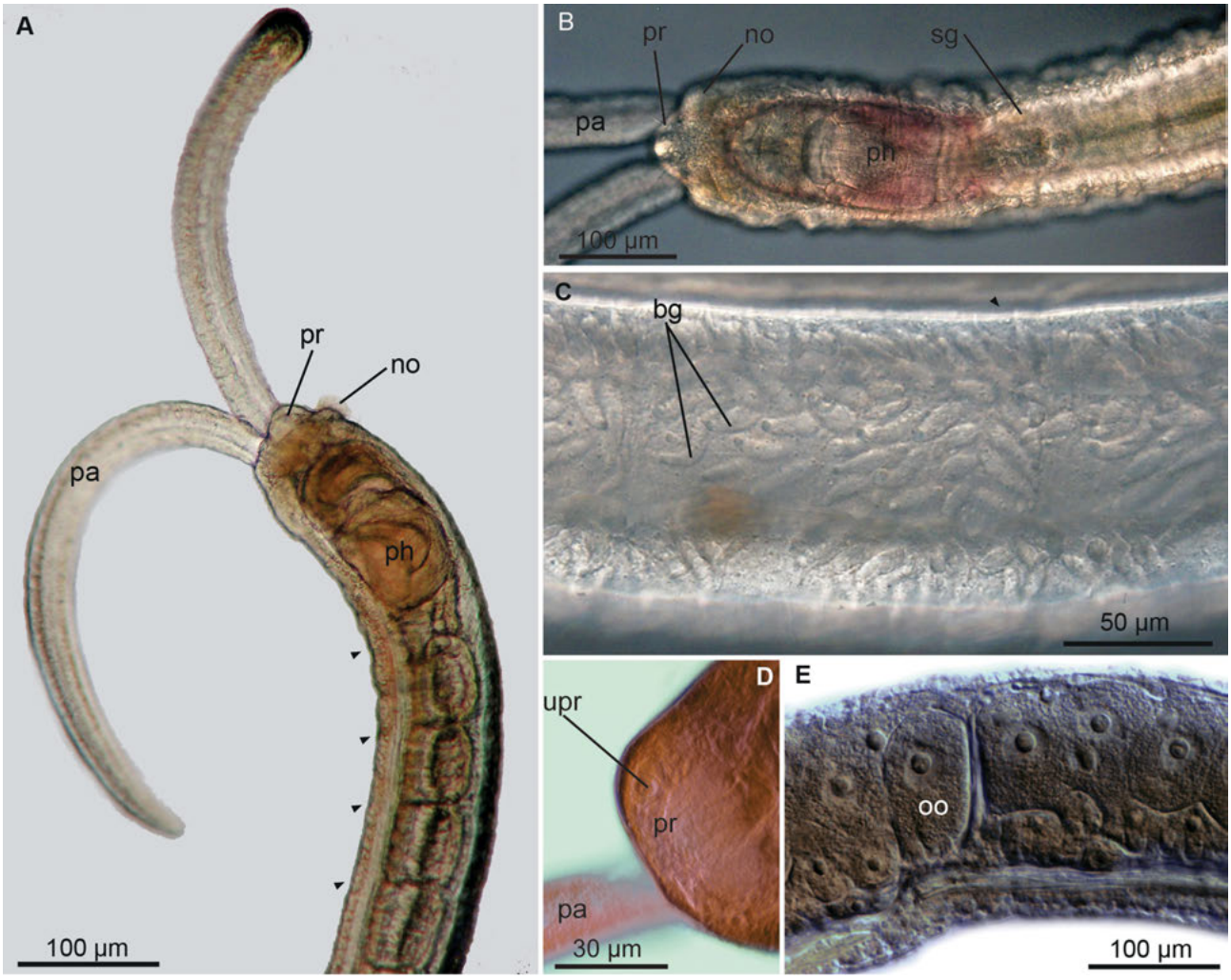


Fig. 7.11.3.10: Morphology of *Protodrilus*. LM micrographs. A, *P. smithsoni* (Bocas del Toro); B–D, *P. ciliatus* (Roscoff); E, G, *P. ciliatus* (Faroe Islands); F, *P.* cf. *submersus* (Lord Howe); H, *P. gelderi* (Massachusetts, USA); A, Anterior end; B, Dorsal view of prostomium; C, Bacillary glands on midbody segments; D, Bacillary glands; E, Midbody segments of a mature female; F, Palp ciliation; G, First lateral organ; H, Prostomium and unpigmented prostomial receptor. bg, bacillary glands; lo, lateral organ; log, glands on the lateral organ; no, nuchal organ; oo, oocytes; pa, palp; ph, pharynx; pr, prostomium; sg, salivary gland; upr, unpigmented prostomial receptor.

unpigmented receptors; nuchal organs dorsolateral and oval; salivary glands variable in extension, normally from segments 1 to 5–15; two pygidial lobes. Males with continuous or segmented lateral organs and three to four pairs of spermioducts; females without oviducts and about 10 small oocytes in each segment.

Distribution and habitat: *Protodrilus* consists of 15 nominal species and several undescribed taxa. *Protodrilus* species are known all over the world, except for Antarctica and Indian Ocean (Fig. 7.11.3.12E). Most of the nominal species occur in Europe (85 records) and Indo-Pacific (20 records). *Protodrilus* species are more common in coarse and *Amphioxus* sand or *Polygordius*-Bruch-Schill (69 records), with few records in medium sands (13 records). Although some species are common intertidally, most of the records are subtidal, down to 20 m (Jouin 1968, 1970a, 1970c).

Protodrilus leuckartii Hatschek, 1881 (Fig. 7.11.3.12E). 10 records. Type locality: Lago Piccolo di Faro, Messina (Italy). Additional records: Mediterranean (Gerlach 1953, Jouin 1970c, Boaden 1965, uncertain) and Northwestern Atlantic (Ruebush 1939, uncertain). Habitat: Medium sand with abundant detritus, common in coastal lagoons with brackish waters. Comments: The record from Ruebush lacks morphological description and more likely corresponds to a different species.

Protodrilus albicans Jouin, 1970 (Fig. 7.11.3.12C, E). 5 records. Type locality: shore of beach Le Troc, Banyuls-sur-Mer, Mediterranean Sea (France) (Jouin 1970c). Additional records: Mediterranean Sea (Villora-Moreno 1997,

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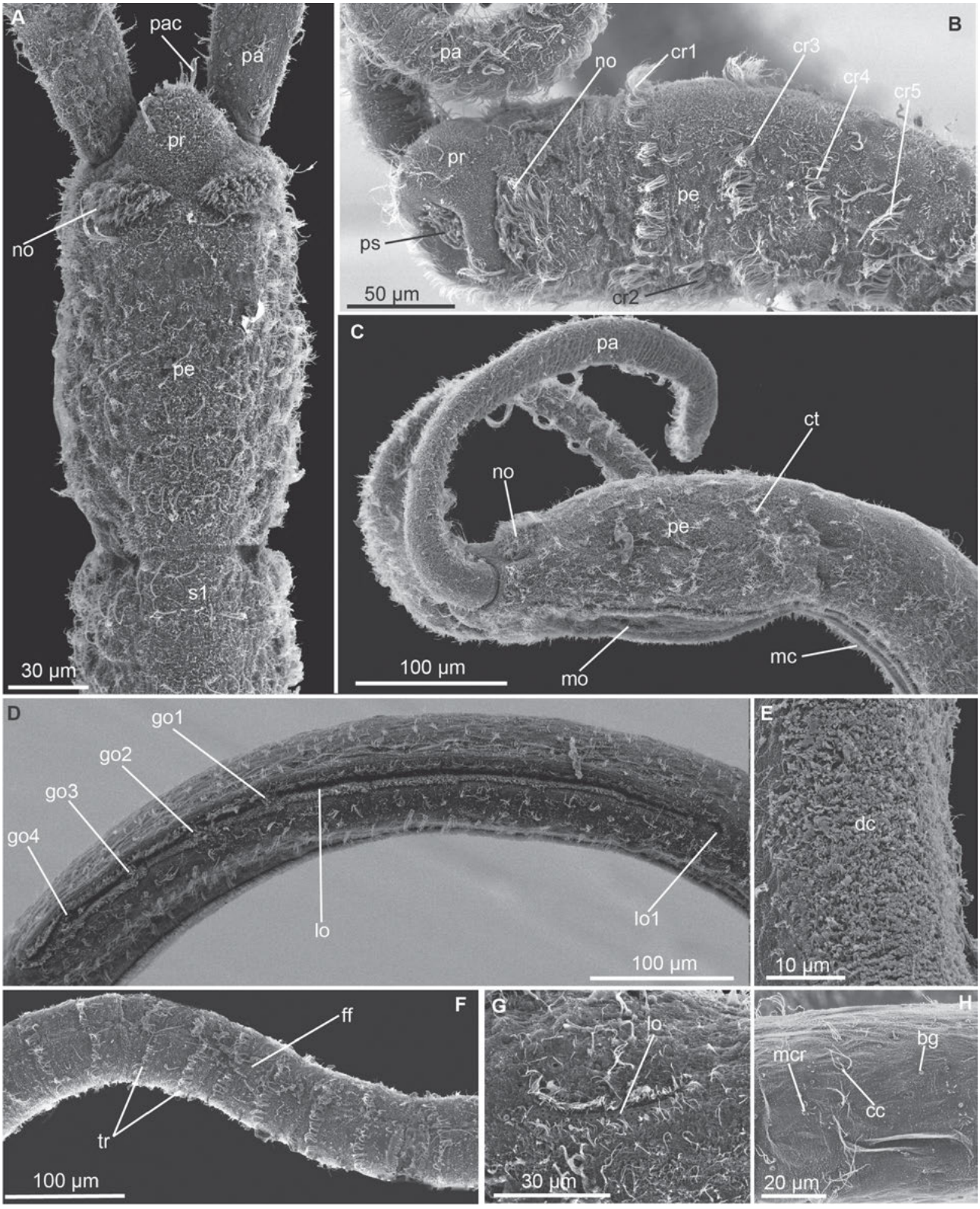


Fig. 7.11.3.11: Morphology of *Protodrilus*. SEM micrographs. A, C, E, *P.* cf. *jagersteni* (Lizard Island); B, F, *P. ciliatus* (Faroe Islands); D, H, *P. smithsoni* (Bocas del Toro); G, *Protodrilus* sp. (Naos); A, Dorsal view of prostomium; B, Lateral view of the prostomium with motile ciliary rings; C, Lateral view of the prostomium without motile ciliary rings; D, Lateral organs; E, Dorsal ciliary area on segments 4 to 5 of male; F, Midbody segment of a female with motile transverse ciliary bands and ciliary furrows; G, Detail of a segmented lateral organ; H, Sensory ciliary rings on a midbody segment. bg, bacillary glands (pore); cc, compound cilia; cr1-5, ciliary ring; ct, ciliary tuft; dc, dorsal ciliary area; ff, female ciliary furrow; go1-4, gonopore; lo, lateral organ; lo1, first lateral organ; mc, midventral ciliary bands; mcr, multiciliary receptor; mo, mouth; no, nuchal organ; pa, palp; pac, prostomial apical ciliation; pe, peristomium; pr, prostomium; ps, palp scar; s1, segment 1; tr, transversal ciliary band of motile cilia.

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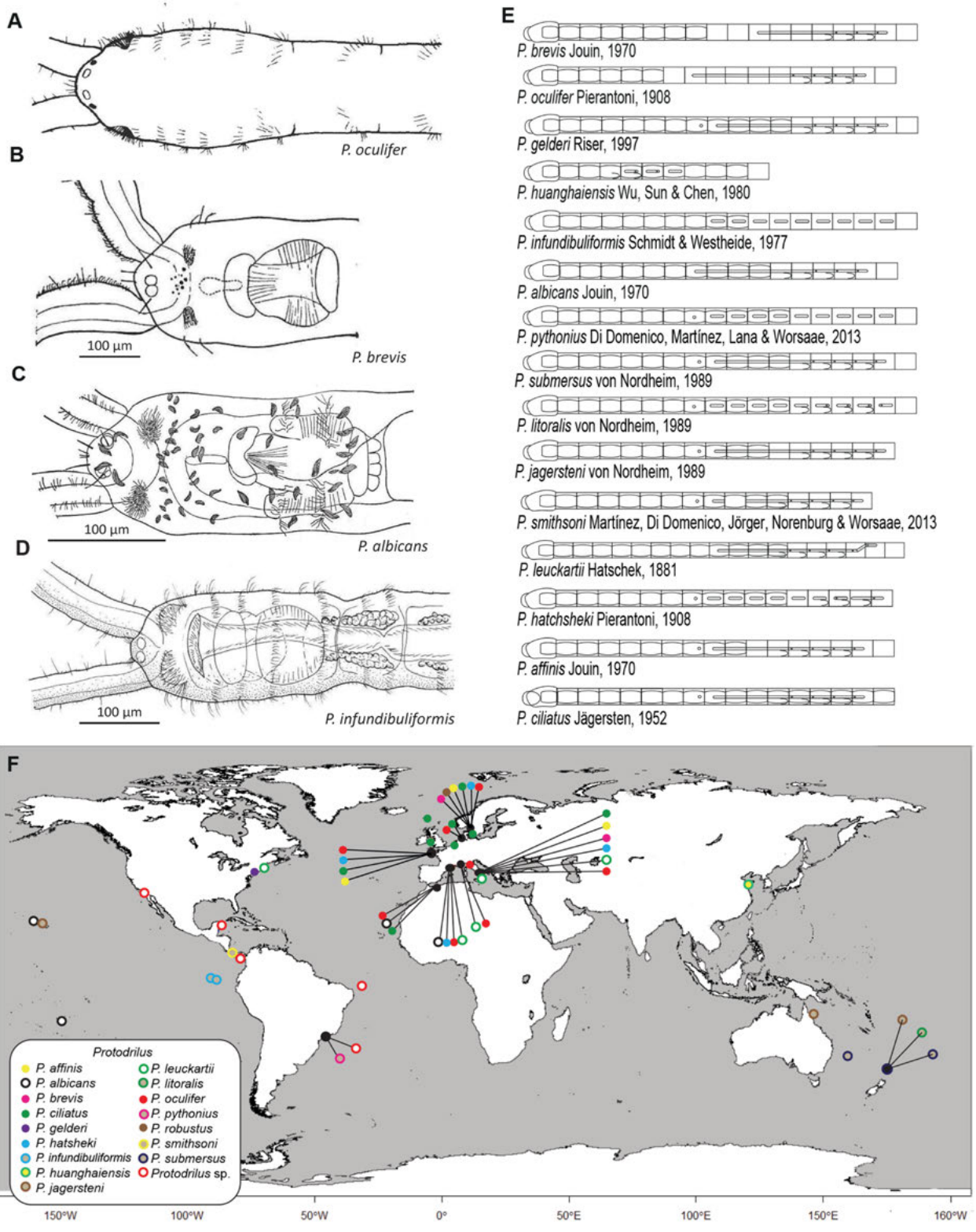


Fig. 7.11.3.12: *Protodrilus*. Species diversity and distribution. A–D, Drawing of anterior ends; A, *P. oculifer* (after Pierantoni 1908); B, *P. brevis* (after Jouin 1970c); C, *P. albicans* (after Jouin 1970c); D, *Protodrilus infundibuliformis* (after Schmidt and Westheide 1977); E, Arrangement of lateral organs and spermioducts in all described species of *Protodrilus*; F, Distribution of the species of the genus.

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Gusmão et al. 2016) and Indo-Pacific (Bailey-Brock et al. 2010). Habitat: Very coarse to coarse sand in the surf zone of sandy beaches. Comments: Records from Indo-Pacific area possibly correspond to a different species.

Protodrilus brevis Jouin, 1970 (Fig. 7.11.3.12B, E). Type locality: Gunnarskär, Gullmarfjord (Sweden). Additional records: Mediterranean (Jouin 1970c). Habitat: Coarse shelly sand, 6 to 13 m depth.

Protodrilus ciliatus Jägersten, 1952 (Figs. 7.11.3.3, 7.11.3.6A, 7.11.3.7C, 7.11.3.8A, 7.11.3.10E–G, 7.11.3.12E). 21 records. Type locality: Bonden, Gullmarfjord (Sweden). Additional records: Northeastern Atlantic (Jägersten 1952, Boaden 1963, 1976, Jouin 1968, 1970c, Wolff et al. 1980, von Nordheim 1984) and Mediterranean (Jouin 1970c, Villora-Moreno 1997). Habitat: Gravel to coarse sand, intertidal to -12 m depth.

Protodrilus gelderi Riser, 1997 (Figs. 7.11.3.10G, 7.11.3.12E). 2 records. Type locality: Egg Rock, Nahant, MA (USA). Additional records: Northwestern Atlantic (Riser 1997). Habitat: Shelly gravel and coarse sand, 15 to 20 m depth.

Protodrilus hatscheki Pierantoni, 1908 (Fig. 7.11.3.12E). 8 records. Type locality: Cinito, Gulf of Naples (Italy). Additional records: Northeastern Atlantic and Mediterranean (Pierantoni 1908, Jouin 1970c). Habitat: Coarse sand or shelly gravel, sublittoral 4 to 60 m depth.

Protodrilus huanghaiensis Wu et al., 1980 (Fig. 7.11.3.12E). 1 record. Type locality: Tsingtao, Yellow Sea (China) (Wu et al. 1980). Habitat: Coarse sand, sublittoral.

Protodrilus infundibuliformis Schmidt & Westheide, 1977 (Fig. 7.11.3. 7.11.3.12D, E). 2 records. Type locality: Academy Bay, La Española (Galapagos) (Schmidt and Westheide 1977). Habitat: Shelly gravel. Intertidal in sandy beaches. Comments: Females unknown.

Protodrilus jagersteni von Nordheim, 1989 (Figs. 7.11.3.11A, C, E, 7.11.3.12E). 6 records. Type locality: Goat Island Channel, Hauraki Gulf (New Zealand). Additional records: Indo-Pacific (von Nordheim 1989a, Martínez and Worsaae unpublished observations). Habitat: Coarse to medium sand, 5 to 15 m depth.

Protodrilus litoralis von Nordheim, 1989 (Fig. 7.11.3.12E). 3 records. Type locality: Silk Tree Beach, Hauraki Gulf (New Zealand) (von Nordheim 1989a). Habitat: Very coarse to coarse, intertidal in swash zone of sandy beaches or sheltered sediment patches in intertidal.

Protodrilus oculifer Pierantoni, 1908 (Figs. 7.11.3.1A, 7.11.3.2A, B, 7.11.3.7A, 7.11.3.12A, E). 28 records. Synonyms: *Protodrilus bahusiensis* Jägersten, 1952 and *P. oculifer borealis* Remane, 1932 (see Jouin 1970c). Type locality: Posillipo, Gulf of Naples (Italy). Additional records: Northeastern Atlantic (Remane 1932, Jägersten 1952, Jouin 1970c, von Nordheim 1984) and Mediterranean (Pierantoni 1908, Boaden 1965, Jouin 1970c, Magagnini 1980, Gusmão et al. 2016). Habitat: Coarse sand (swash and surf zones of sandy beaches) to *Amphioxus* sand 20 m depth.

Protodrilus puniceus Sato-Okoshi, Okoshi & Fujiwara, 2015. 1 record. Type locality: Northwest Pacific: off Cape Nomamisaki, Japan. Habitat: Whale-fall ecosystem (Sato-Okoshi et al. 2015).

Protodrilus pythonius Di Domenico, Martínez, Lana & Worsaae, 2013 (Fig. 7.11.3.12E). 1 record. Type locality: Praia da Feiticeira, São Paulo (Brazil) (Di Domenico et al. 2013). Habitat: Coarse sand, swash zone in a sandy beach.

Protodrilus smithsoni Martínez, Di Domenico, Jörger, Norenburg & Worsaae, 2013 (Figs. 7.11.3.10A, 7.11.3.11D, H, 7.11.3.12E). 2 records. Type locality: Bird Rock, Bocas del Toro (Panama). Distribution: Caribbean (Martínez et al. 2013, Martínez and Worsaae unpublished observations). Habitat: Medium-coarse sand, 3 to 15 m depth.

Protodrilus submersus von Nordheim, 1989 (Figs. 7.11.3.10F, 7.11.3.12B). 2 records. Type locality: Goat Island Channel, Hauraki (New Zealand) (von Nordheim 1989a). Habitat: Coarse and medium-coarse, from swash zone of sandy beaches to 5 m depth.

Protodrilus robustus Jägersten, 1952. 3 records. Type locality: Harbour of Bonden, Gullmarfjord (Sweden) (Jägersten 1952). Habitat: Very coarse and coarse sand, subtidal. Comments: Sexually mature specimens are unknown.

Undescribed species are known from the Indo-Pacific (California, USA; San Bartolomé and Tombolo, Panama), Caribbean Sea (Quintana Roo, Mexico), and Southwestern Atlantic (Fernando de Noronha and Itaçucê, Brazil) (Martínez and Worsaae, unpublished observations).

***Astomus* Jouin, 1979** (Figs. 7.11.3.1B, 7.11.3.8B–D, 7.11.3.13A–D)
Type species: *Astomus taenioides* Jouin, 1979
Monotypic, three additional undescribed species (Martínez et al. 2015)
Diagnosis: Body whitish, with festooned segments; prostomium with ciliated palps, unpigmented receptors present, but no pigmented eyes; nuchal organs dorsal and rounded; mouth and pharyngeal organ absent; ciliated gut residual all along the body, comprising few ciliated cells with large vacuoles containing spherocrystals; salivary glands reduced and opening to the body surface; two pygidial lobes; males with lateral organs on segments 13 to 22 extending over two consecutive segments, two short

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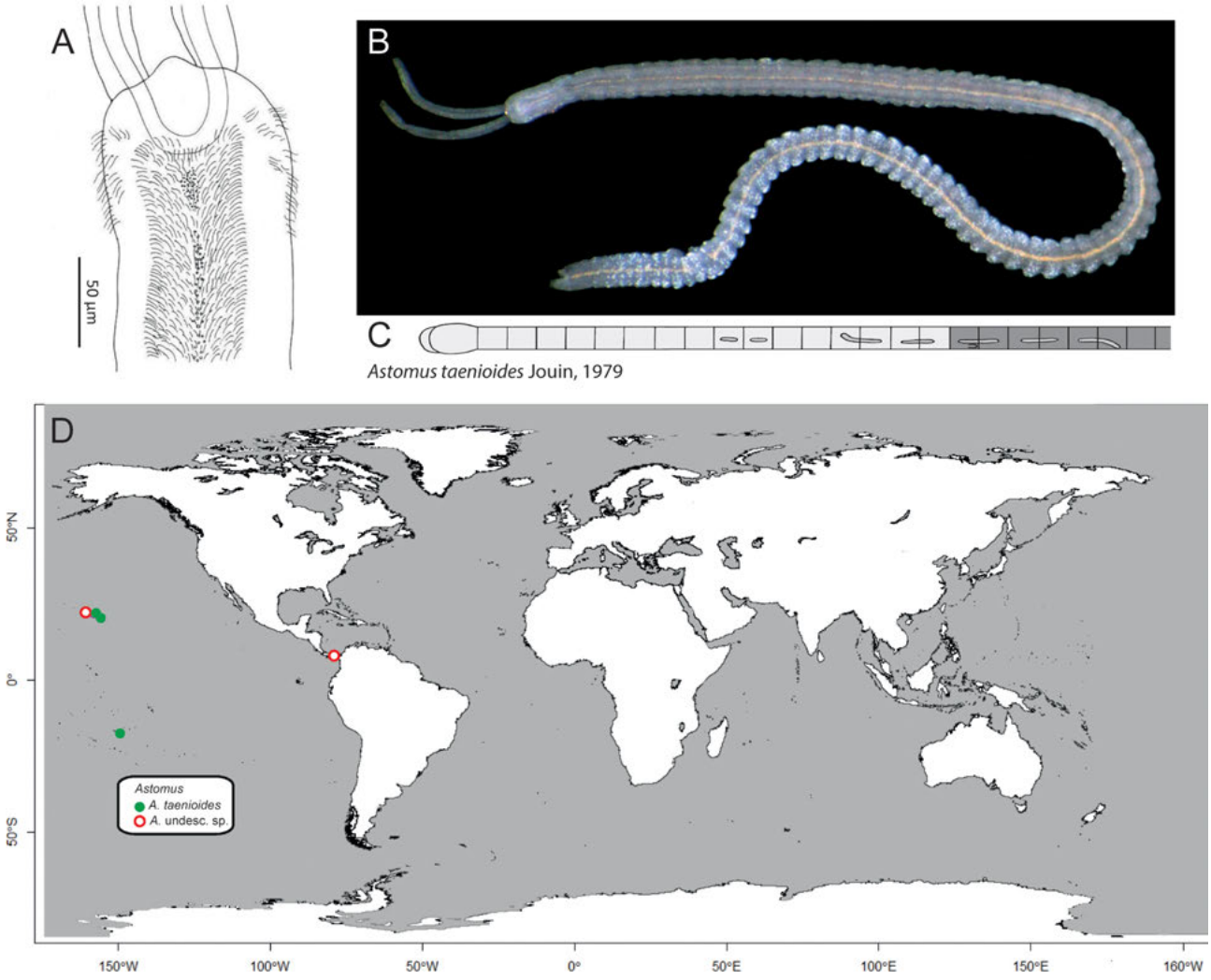


Fig. 7.11.3.13: *Astomus*. Species diversity and distribution. A, Drawing of the anterior end of *A. taenioides* (after Jouin 1979); B, Habitus of *Astomus* sp., LM micrograph of live specimen (from Martínez et al. 2015); C, Arrangement of lateral organs and spermioducts in *A. taenioides*; D, Distribution of the species of the genus.

ciliated grooves on segments 9 and 10, and one pair of spermioducts on segment 17.

Distribution and habitat: *Astomus* is known by one described and three undescribed species (Fig. 7.11.3.13C). The five records for the genus are from the Indo-Pacific, always from coral sands of coral reefs.

Astomus taenioides Jouin, 1979. Indo-Pacific. 3 records. Type locality: Tiahura, Mo'orea (French Polynesia). Distribution: Indo-Pacific (Jouin 1979, 1992, Bailey-Brock et al. 2010). Habitat: Coarse to fine sands near coral reefs, 1.5 m depth.

Undescribed species are known from the Indo-Pacific (Lizard Island, Australia; Hawaii, USA; and Las Perlas, Panama) (Bailey-Brock et al. 2010, Martínez et al. 2015, Martínez and Worsaae unpublished observations)

***Lindrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015** (Figs. 7.11.3.14A–K, 7.11.3.15A–D)

Type species: *Lindrilus rubropharyngeus* (Jägersten, 1940) (as *Protodrilus rubropharyngeus*)

3 species.

Diagnosis: Body large and pigmented, pharynx red; prostomium with long ciliated palps, pigmented eyes and rounded, large, and medial unpigmented receptors; nuchal organs dorsolateral and rounded; salivary glands extending further than segment 15; two pygidial lobes; males with segmented and equal lateral organs and one pair of spermioducts; females with oviducts and abundant small oocytes in each segment; dorsal organs in two species.

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Distribution and habitat: *Lindrilus* consists of three nominal and at least three undescribed species (Fig. 7.11.3.15D). There are 21 records for the genus, mostly in Europe. Most of the records come from gravel or very coarse sand sediments, often in the uppermost littoral zone or in brackish waters.

Lindrilus rubropharyngeus (Jägersten, 1940) (Figs. 7.11.3.5, 7.11.3.14H–J, 7.11.3.15A–C). 12 records. Type locality: Bonden, Gullmarfjord (Sweden). Additional records: Northeastern Atlantic (Jägersten 1940, 1952, Boaden 1963, von Nordheim and Schrader 1994, Willems et al. 2009) and Indo-Pacific (Wu et al. 1980). Habitat: Very coarse or coarse sand, 0 to 2 m depth. Remarks: Records from Tsingtao, China, probably represent a different undescribed species.

Lindrilus flavocapitatus (Uljanin, 1877) (Fig. 7.11.3.15C). 4 records. Type locality: Sevastopol Bay (Black Sea). Distribution: Mediterranean (Pierantoni 1908), Black Sea (Mastepanova 2004, Kopiy 2013), and Northeastern Atlantic (Goodrich 1931, Boaden 1963). Habitat: Gravel or very coarse sand in the uppermost littoral area. Common in brackish waters.

Lindrilus haurakiensis (von Nordheim, 1989) (Fig. 7.11.3.15C). 3 records. Type locality: Goat Island Beach, Hauraki Gulf (New Zealand) (von Nordheim 1989a).

Remarks: Undescribed species are known from Northeastern Atlantic (Canary Islands), Caribbean (Cuba), and Indo-Pacific (Israel).

Megadrilus Martínez, Di Domenico, Rouse & Worsaae, 2015 (Figs. 7.11.3.16A–J, 7.11.3.17A–F)

Type species: *Megadrilus purpureus* (Schneider, 1868) (as *Protodrilus purpureus*)

4 species.

Diagnosis: Body large and pigmented, pharynx reddish; prostomium with long ciliated palps, no eyes, small and rounded unpigmented receptors, sometimes absent; nuchal organs long and transverse; three pygidial lobes; males with lateral organs from segment 6, first rounded and smaller; females with oviducts and abundant and small oocytes in each segment.

Distribution and habitat: *Megadrilus* consists of four nominal and at least three undescribed species, with most records in the Northeast Atlantic (Fig. 7.11.3.17E). *Megadrilus* species prefer gravel and well-sorted coarse sediments (17 records), between 2 and 5 m. Many species are found subtidally in the exposed surf zones of rocky or coral reefs. Exceptionally, *M. pelagicus* dwells in an anchialine lava tube in Lanzarote, exhibiting a unique pelagic suspension feeding behavior (Martínez et al. 2016, 2017).

Megadrilus purpureus (Schneider, 1868) (Figs. 7.11.3.16C, E, 7.11.3.17B–E). 21 records. Type locality: Helgoland, North Sea (Germany). Additional records: Northeastern Atlantic (Jouin 1968, 1970c, von Nordheim 1984), Mediterranean (Pierantoni 1908, Boaden 1965, Jouin 1970c, Magagnini 1980), and Black Sea (Uljanin 1877). About 16 rather large oocytes, 65 µm in diameter, in each segment. Habitat: Very coarse to coarse sand, 5 to 20 m depth.

Megadrilus hochbergi (Martínez, Di Domenico, Jörger, Norenburg & Worsaae, 2013) (Figs. 7.11.3.16D, 7.11.3.17A, E). 2 records. Type locality: Wild Cane Rock, Bocas del Toro (Panama). Additional records: Caribbean (Martínez et al. 2013). Habitat: Very coarse sand in the surf zone of coral reefs.

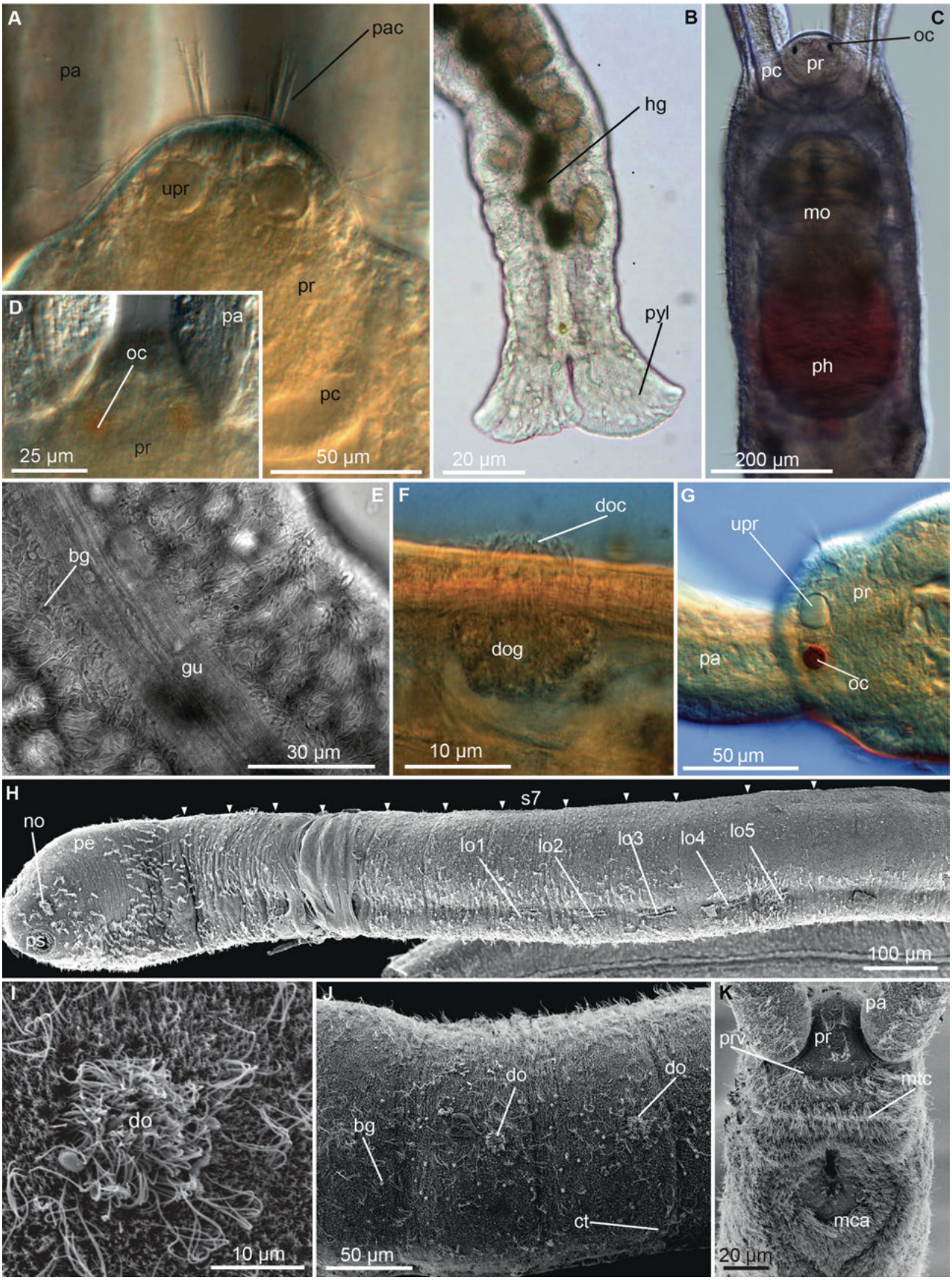
Megadrilus pelagicus (Martínez, Kvindebjerg, Iliffe & Worsaae, 2017) (Figs. 7.11.3.1C, 7.11.3.19E). 1 record. Type locality: Túnel de la Atlántida, La Corona lava tube, Lanzarote (Canary Islands). Habitat: Suspension feeder in the water column of anchialine caves (Martínez et al. 2016, 2017).

Megadrilus schneideri (Langerhans, 1880) (Figs. 7.11.3.16A, B, F–J, 7.11.3.17E). 4 records. Type locality: Funchal beach. Madeira (Portugal). Distribution: Northeastern Atlantic (Langerhans 1881), and Mediterranean (Curini-Galletti et al. 2012, Gusmão et al. 2016). Habitat: Gravel to coarse sand, subtidal.

Remarks: Undescribed species are known from Indo-Pacific (Lord Howe, Panama), Southwestern Atlantic (Brazil), and the Caribbean (México)

▸ **Fig. 7.11.3.14:** Morphology of *Lindrilus*. LM (A–G) and SEM (H–K) micrographs. A, C, D, G, K. *Lindrilus* n. sp. (Canary Islands); B, E, F, H, I, J, *L. rubropharyngeus* (Sweden); A, Dorsal view of the prostomium and unpigmented receptors; B, Pygidium of a mature female; C, Prostomium of a live specimen; D, Ventral view of the prostomium and pigmented eyes; E, Arrangement of the bacillary glands; F, Detail of a dorsal organs on a female showing the dorsal organ glands and ciliation; G, Lateral view of the prostomium showing relative position of eyes and unpigmented prostomial receptors; H, Lateral view of the anterior end showing the arrangement of the lateral organs; I, Dorsal organs on a female; J, Dorsal organs on two consecutive midbody segments; K, Ventral view of the head showing the different ciliary bands around the mouth. bg, bacillary glands; do, dorsal organ; doc, dorsal organ ciliation; dog, dorsal organ gland; gu, gut; hg, hindgut; lo1-5, lateral organs 1 to 5; mca, mouth ciliary area; mo, mouth; mtc, mouth transverse ciliation; no, nuchal organ; oc, pigmented eye; pa, palp; pac, prostomial apical ciliation; pc, palp canal; pe, peristomium; ph, pharynx; ps, palp scar; pr, prostomium; prv, prostomium ventral ciliation; pyl, pygidial lobe; upr, unpigmented prostomial receptor.

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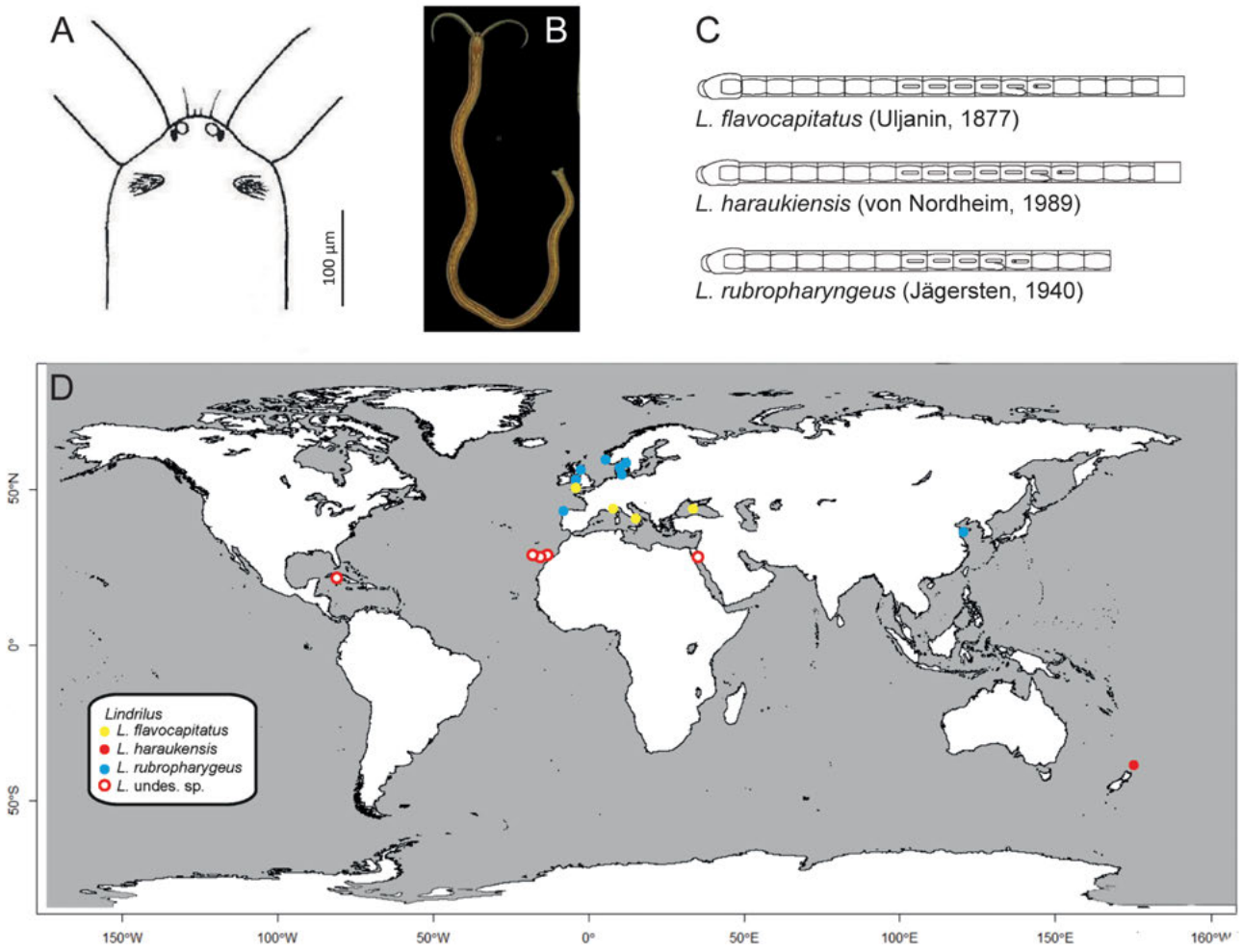
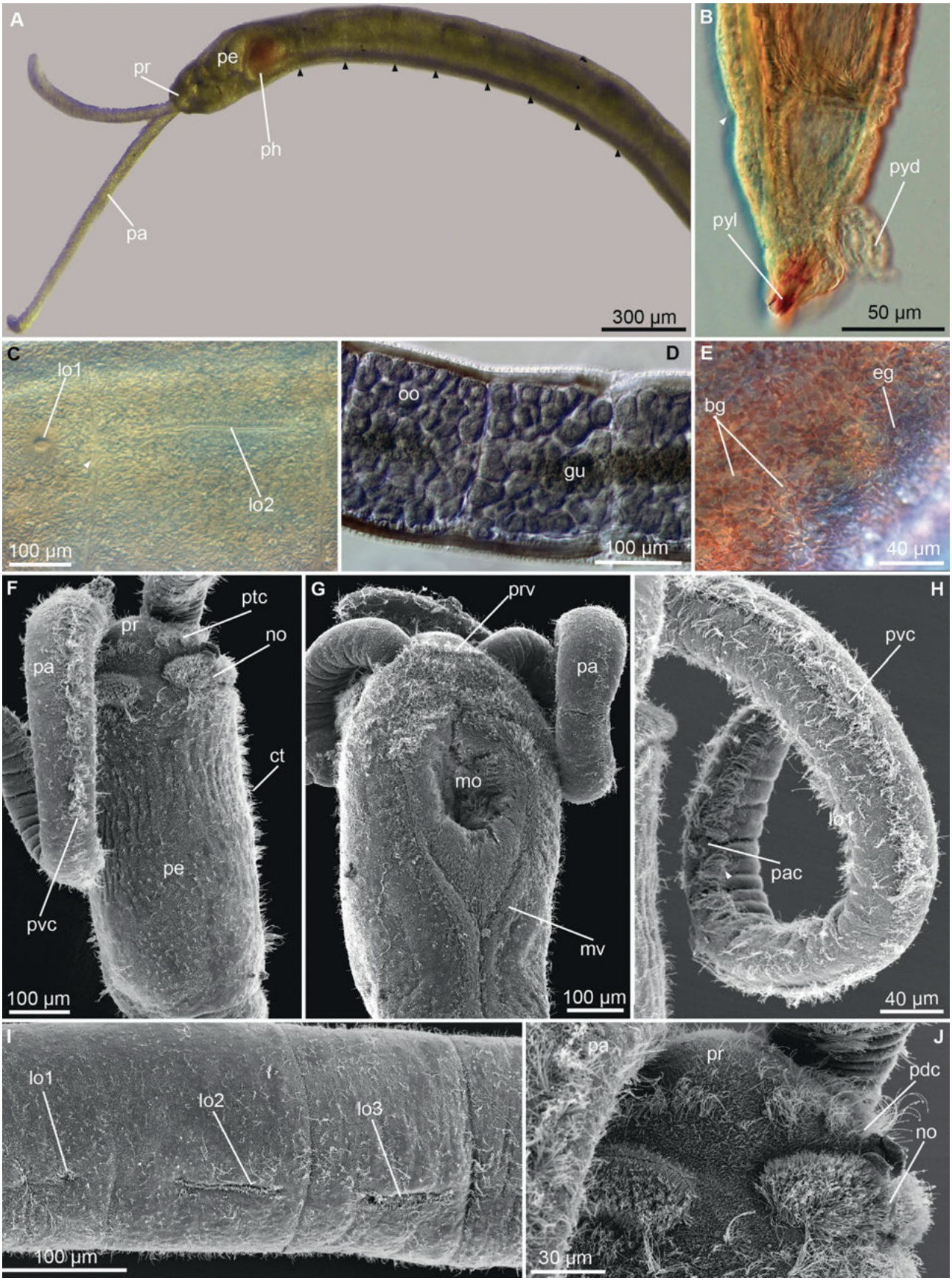


Fig. 7.11.3.15: *Lindrilus*. Species diversity and distribution. A, Drawings of the anterior end of *L. rubropharyngeus* (after Jägersten 1940); B, Habitus of *L. flavocapitatus* (after Pierantoni 1908); C, Arrangement of lateral organs and spermioducts of all described species; D, Distribution of the species of the genus.

***Meiodrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015** (Figs. 7.11.3.18A–G, 7.11.3.19A–G, 7.11.3.20A–E)
Type species: *Meiodrilus adhaerens* (Jägersten, 1952)
4 species.
Diagnosis: Body short and translucent, pharynx unpigmented; prostomium with short and poorly ciliated palps, no eyes, oval lateral unpigmented receptor, sometimes absent; nuchal organs rounded and dorsal; salivary glands on segments 1 to 5; paired segmented adhesive glands ventrally on trunk segments; two pygidial lobes; males with continuous or segmented lateral organs; females with cocoon glands and a few comparatively large oocytes in each segment.
Distribution and habitat: *Meiodrilus* is known from four described and several undescribed species. The genus is worldwide distributed with most of the records from the Atlantic Ocean (52 records, 80%), especially in Europe

▸ **Fig. 7.11.3.16:** Morphology of *Megadrilus*. LM (A–E) and SEM (F–J) micrographs. A, B, F–J. *M. schneideri* (Canary Islands); C, E, *M. purpureus* (Galicia); D, *M. hochbergi* (Bocas del Toro); A, Lateral view of the anterior end; B, Lateral view of pygidium; C, Lateral organs on segments 6 and 7; D, Dorsal view of a female with developing oocytes; E, Glandular patterns on the epidermis, stained with muchaematin; F, Dorsal view of the anterior end; G, Ventral view of anterior end; H, Ventral view of palp; I, Lateral organs on segments 6 to 8; J, Prostomial transverse dorsal bands and nuchal organs. bg, bacillary glands; ct, ciliary tuft; eg, epidermal glands; gu, gut; lo1-3, lateral organ; no, nuchal organ; mo, mouth; oo, oocytes; pa, palp; pac, palp abfrontal ciliation; pdc, prostomium dorsal transverse ciliation; pe, peristomium; ph, pharynx; pr, prostomium; prv, prostomium ventral transverse ciliation; pvc, palp ventral ciliation; pyd, pygidial dorsal lobe; pyl, pygidial lateral lobe.

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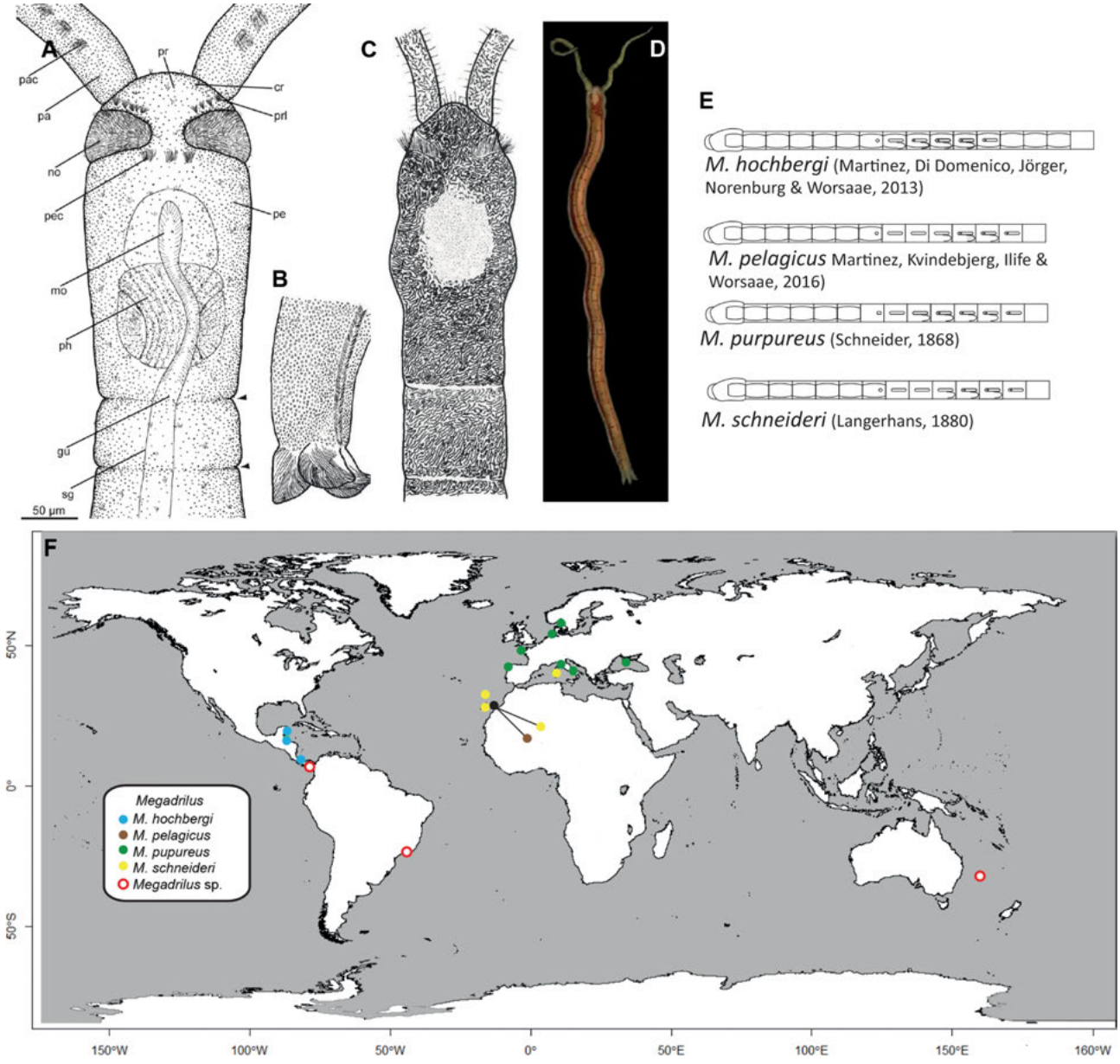


Fig. 7.11.3.17: *Megadrilus*. Species diversity and distribution. A, Drawings of the anterior end of *M. hochbergi* (after Martínez et al. 2013); B, Drawing of the posterior end of *M. purpureus* (after Jägersten 1952); C, Drawing of the anterior end of *M. purpureus* (after Jägersten 1952); D, Habitus of *M. purpureus* (after Pierantoni 1908); E, Arrangement of lateral organs and spermioducts of all described species; F, Distribution of the species of the genus.

(26 records) (Fig. 7.11.3.20E). *Meiodrilus* is more common in medium to medium-fine intertidal sediments (33 records, 72%), with only 8 records below 10 m depth. Species of the genus are common in the swash zones of exposed beaches.

Meiodrilus adhaerens (Jägersten, 1952) (Figs. 7.11.3.6C, D, 7.11.3.7B, 7.11.3.18A, D, F, 7.11.3.19B, C, E, G, 7.11.3.20B–D). 28 records. Type locality: Bondhålet, Gullmarfjord (Sweden). Additional records: Northeastern Atlantic (Jägersten 1952, Jouin 1970c, Boaden 1976, Willems et al. 2009) and Mediterranean (Jouin 1970c). Habitat: Medium-coarse to fine sand, 0 to 20 m, more abundant intertidally. Comments: *M. adhaerens* occurs in sympatry with *M. gracilis*, and both species may have been confused in the past (von Nordheim 1989a).

Meiodrilus gracilis (von Nordheim, 1989) (Fig. 7.11.3.20D). 9 records. Type locality: Helgoland (Germany). Additional records: Northeastern Atlantic (Jouin 1970c, Boaden 1976, von Nordheim 1989a) and Mediterranean (Jouin 1970c, Curini-Galletti et al. 2012, Gusmão et al. 2016). Habitat: Medium to fine sand, 0 to 37 m.

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Meiodrilus indicus (Aiyar & Alikunhi, 1944) (Fig. 7.11.3.20A, D). 6 records. Type locality: Madras Beach, Bay of Bengal (India). Additional records: Indo-Pacific (Aiyar and Alikunhi 1944, Jouin 1970a). Habitat: Medium sand, intertidally in exposed beaches.

Meiodrilus jouinae (von Nordheim, 1989) (Fig. 7.11.3.20D). 2 records. Type locality: Goat Island Beach, Hauraki Gulf (New Zealand) (von Nordheim 1989a). Habitat: Medium sand, intertidally in sandy beaches.

Remarks: Undescribed species are known from Northeastern Atlantic (Canary Islands), Northwestern Atlantic (Bermuda), Caribbean (Belize), and Indo-Pacific (Thailand, South Korea, Australia, Hawaii, and Panama).

***Claudrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015** (Figs. 7.11.3.21A–L, 7.11.3.22A–E)

Type species: *Claudrilus hypoleucus* (Armenante, 1903)

10 species.

Diagnosis: Body whitish, pharynx unpigmented or grayish; prostomium with palps, these sometimes with motile ciliation, no eyes, oval and lateral unpigmented ciliary receptor absent in a few species; nuchal organs dorsal and rounded, or indistinct; salivary glands at least from segment 1 to 8 and may extend to segment 20; epidermis sometimes with abundant glasslike vacuolar glands; two pygidial lobes; females with a few large oocytes (50 µm in diameter) per segment.

Distribution and habitat: *Claudrilus* consists of eight described species. The genus has been recorded worldwide (except for Africa and Antarctica) (Fig. 7.11.3.22E), although most of the records come from the Atlantic Ocean (52 records), especially in Europe (25 records). The species within *Claudrilus* present different habitat preferences: some species prefer coarse sand sediments (19 records), whereas others are more common in medium and medium-fine sediments (27 records). Most *Claudrilus* are recorded between 0 and 10 m (52 records).

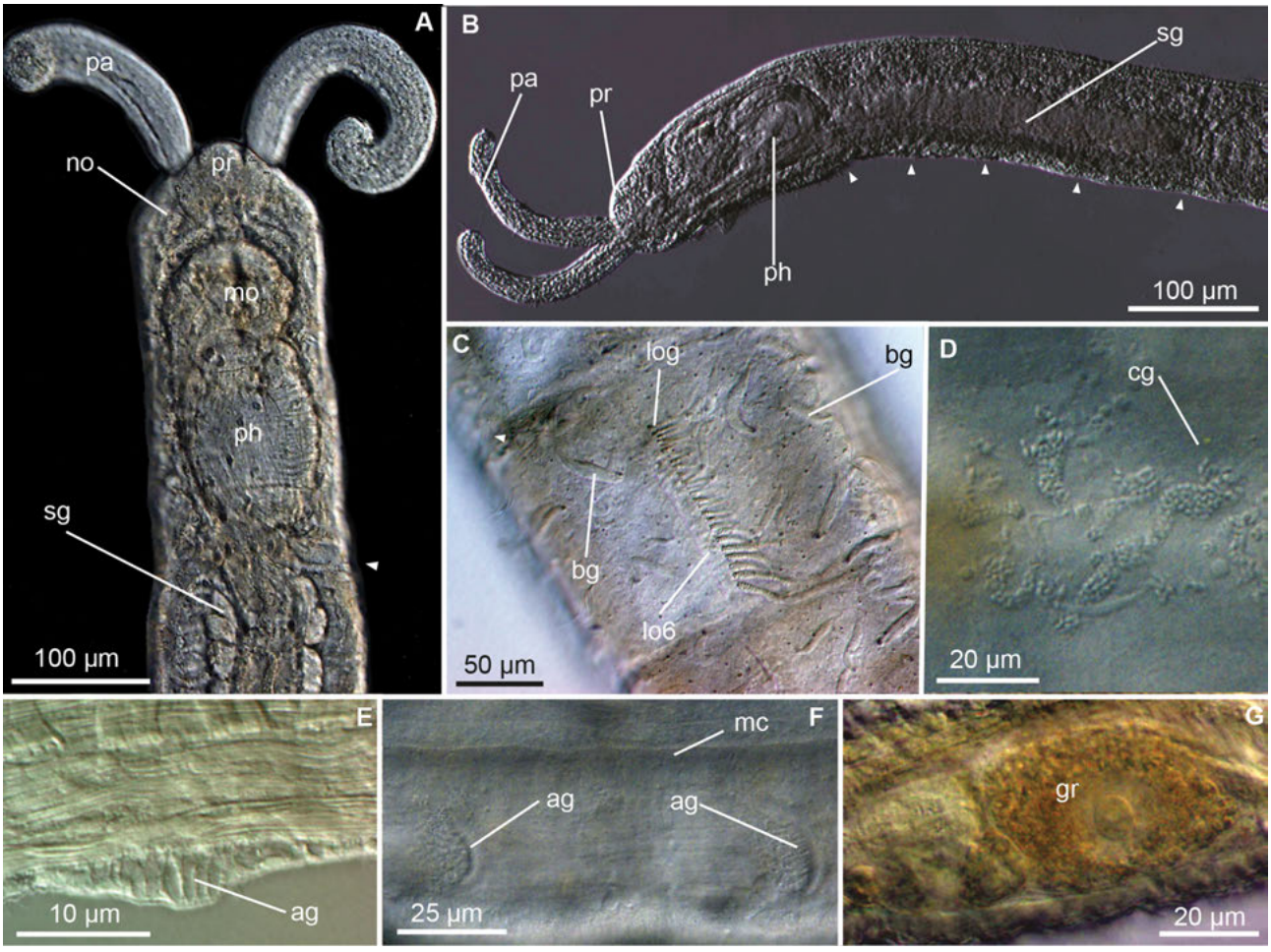


Fig. 7.11.3.18: Morphology of *Meiodrilus*. LM micrographs. A, D, F, *M. adhaerens* (Roscoff); B, E, *Meiodrilus* n. sp. (Bermuda); C, *M. adhaerens* (Denmark); G, *Meiodrilus* n. sp. (Canary Islands); A, Dorsal view of anterior end; B, Lateral view anterior end; C, Lateral organ and glandular patterns; D, Cocoon glands (cg); E, Segmental adhesive gland (ag); F, Segmental adhesive gland; G, Coelomic gregarine parasite (gr). ag, adhesive glands; bg, bacillary glands; cg, cocoon gland; gr, gregarine; lo6, lateral organ on segment 6; log, lateral organ glands; mc, midventral ciliary band; mo, mouth; no, nuchal organ; pa, palp; pe, peristomium; ph, pharynx; pr, prostomium; sg, salivary glands.

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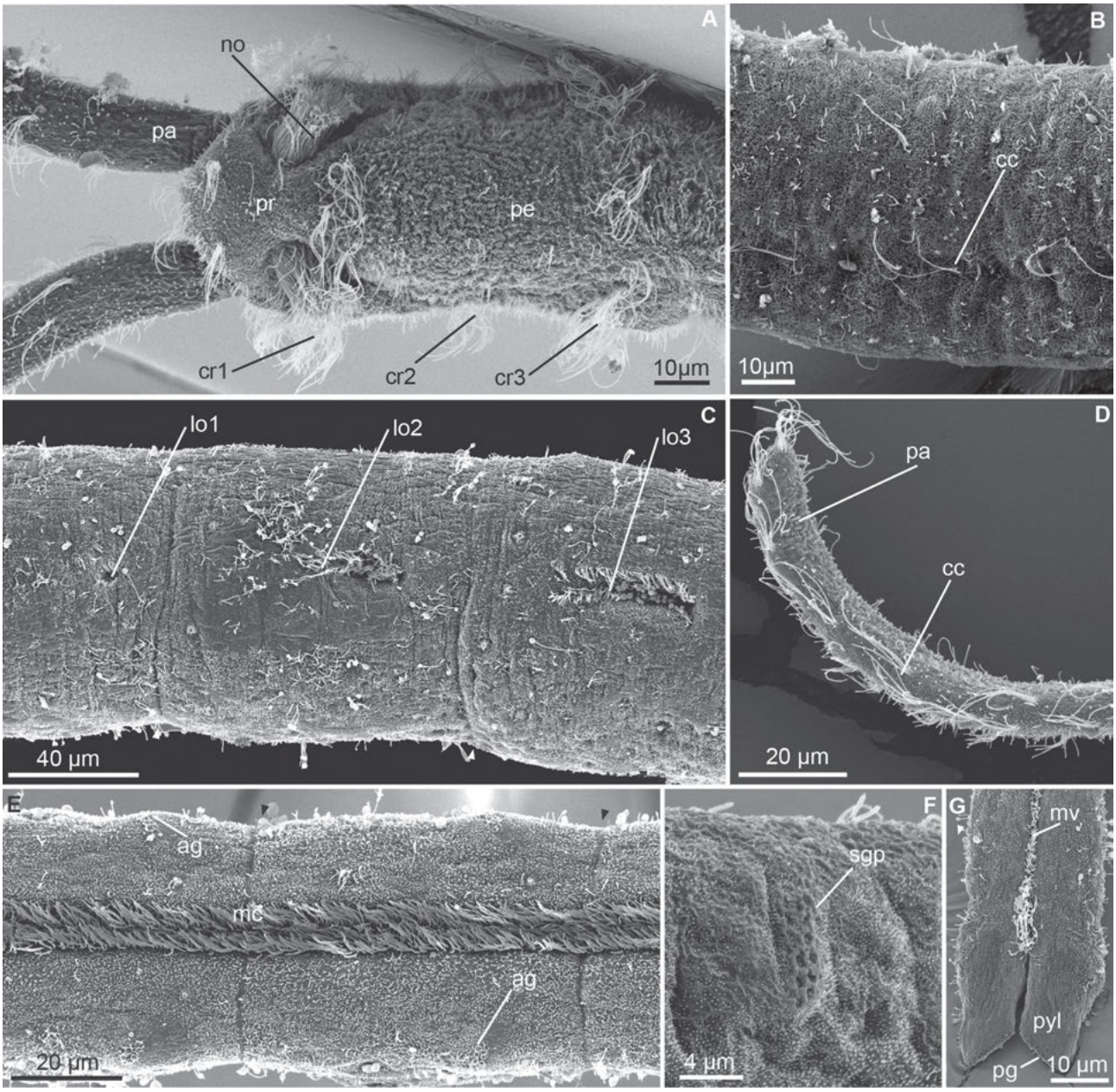


Fig. 7.11.3.19: Morphology of *Meiodrilus*. SEM micrographs. A, D, F, *Meiodrilus* sp. (Phuket); B, C, E, G, *M. adhaerens* (Roscoff); A, Dorsal view of anterior end; B, Ciliation on trunk; C, Lateral organs; D, Lateral view of palp; E, Midventral ciliary band and segmental adhesive glands; F, Segmental adhesive gland; G, Ventral view of the pygidium. ag, segmental adhesive gland; cc, compound cilia; cr, ciliary ring; lo, lateral organ; mc, midventral ciliary band; no, nuchal organ; pa, palp; pe, peristomium; pr, prostomium; sgp, segmental adhesive gland pore.

Claudrilus hypoleucus (Armenante, 1903) (Figs. 7.11.3.2B, 7.11.3.3B, C, 7.11.3.4A–C, 7.11.3.21B–D, 7.11.3.22B, D). Synonymy: *Protodrilus sphaerulatus* Pierantoni, 1908 (see Jouin 1970c). 23 records. Type locality: Gulf of Naples (Italy). Additional records: Northeastern Atlantic (Jouin 1970c) and Mediterranean (Jouin 1970c, Villora-Moreno 1997, Curini-Galletti et al. 2012). Habitat: Coarse to medium sand from intertidal to 20 m depth. Remarks: Often with coelomic parasites (gregarines), which may be mistaken as large oocytes (Jouin 1968).

Claudrilus corderoi (du Bois-Reymond Marcus, 1948) (Figs. 7.11.3.21J, 7.11.3.22C, D). 5 records. Type locality: São Sebastião, São Paulo (Brazil). Distribution: Southwestern Atlantic (Di Domenico et al. 2009, 2013); *P.* cf. *corderoi* in the Caribbean (Kirsteuer 1967). Habitat: Medium coarse sand in the swash zone of reflective beaches.

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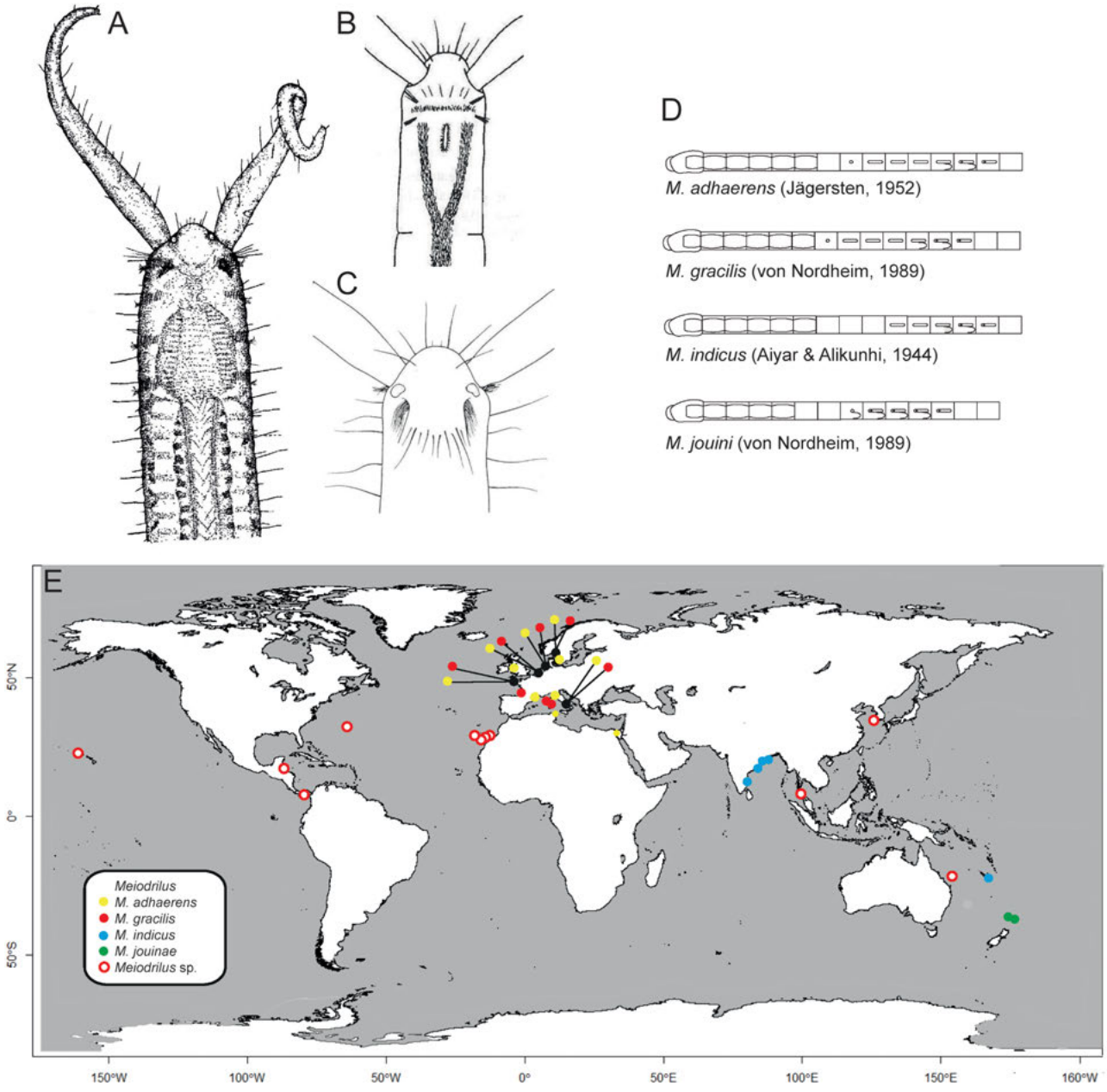


Fig. 7.11.3.20: *Meiodrilus.* Species diversity and distribution. A, Drawing of the anterior end of *M. indicus* (after Aiyar and Alikunhi 1944) in dorsal view; B, Drawing of the anterior end of *M. adhaerens*, ventral view; C, Drawing of the anterior end of *M. adhaerens*, dorsal view; D, Arrangement of lateral organs and spermioducts of all described species; E, Distribution of the species of the genus. B, C, After Jägersten (1952).

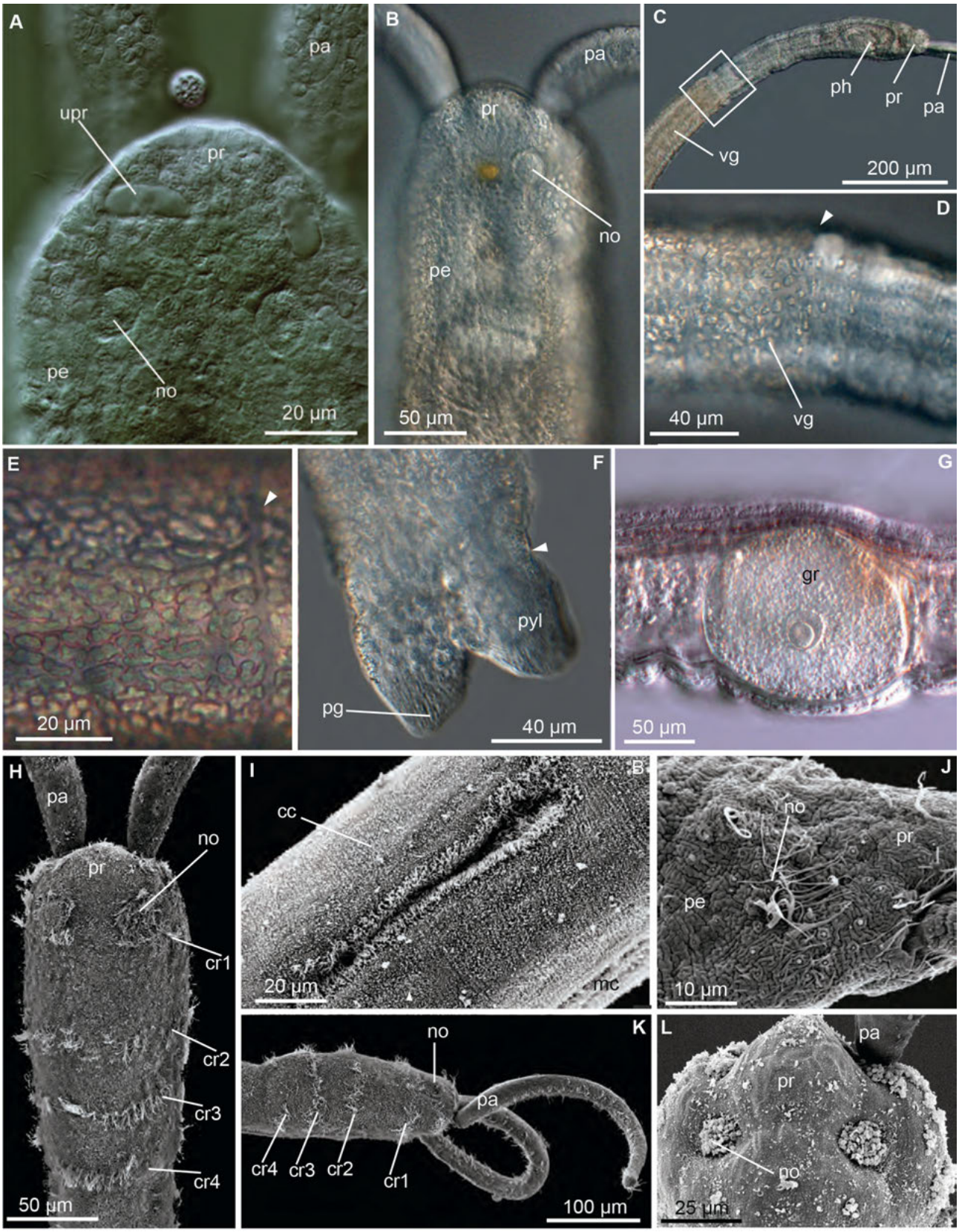
Claudrilus draco (Martínez, Di Domenico, Jörger, Norenburg & Worsaae, 2013) (Figs. 7.11.3.21L, 7.11.3.22A, D). 1 record. Type locality: Wild Cane Key, Bocas del Toro (Panama) (Martínez et al. 2013). Habitat: Medium-fine sand, subtidally.

Claudrilus flabelliger (Wieser, 1957) (Fig. 7.11.3.22D). 2 records. Type locality: Puget Sound, Washington (USA) (Wieser 1957). Habitat: Coarse sand, intertidally in sheltered beaches.

Claudrilus helgolandicus (von Nordheim, 1983) (Fig. 7.11.3.22D). 9 records. Type locality: Helgoland (Germany). Additional records: Northeastern Atlantic (von Nordheim 1983, 1984, 1989a, Delgado et al. 2003, Núñez et al. 2005, Willems et al. 2009, Riera et al. 2018). Habitat: Coarse to medium sand, 0 to 20 m.

Claudrilus minutus (Kirsteuer, 1966) (Fig. 7.11.3.22D). 1 record. Type locality: Ataqa, Gulf of Suez (Egypt)

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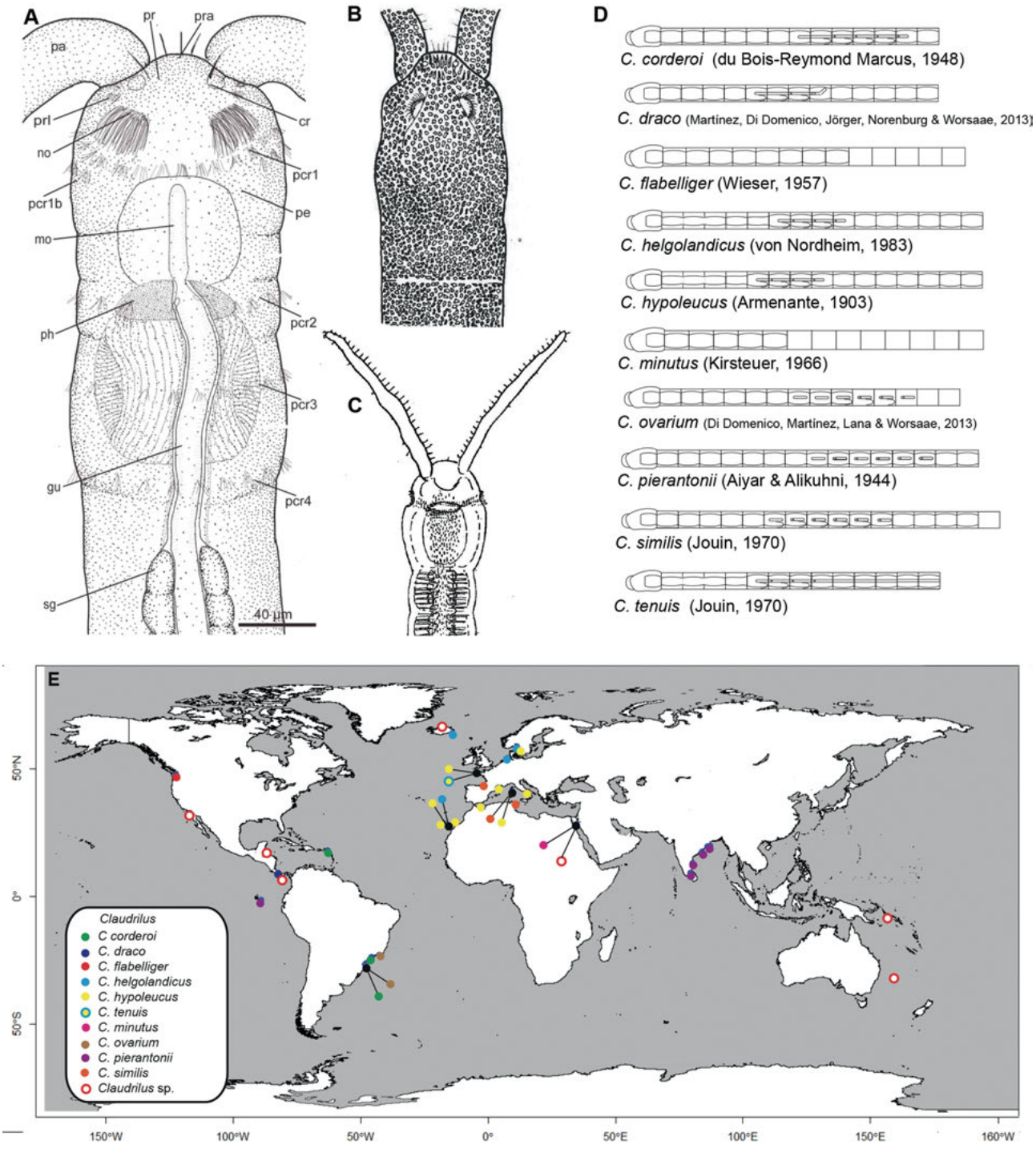


Fig. 7.11.3.22: *Claudrilus*. Species diversity and distribution. A, Drawing of the anterior end of *C. draco* (after Martínez et al. 2013) in dorsal view; B, Drawing of the anterior end of *C. hypoleucus* (after Pierantoni 1908) in ventral view; C, Drawing of the anterior end of *C. corderoi* (after Du Bois-Reymond Marcus, 1948) in dorsal view; D, Arrangement of lateral organs and spermioducts of all described species; E, Distribution of the species of the genus.

◂ **Fig. 7.11.3.21:** Morphology of *Claudrilus*. LM (A–G) and SEM (H–L) micrographs. A, *C. hypoleucus* (Sardinia); B–D, *C. hypoleucus* (Roscoff); E–G, *C. tenuis* (Roscoff); H, K, *C.* cf. *hypoleucus* (Canary Islands); I, *C. ovarium*; J, *C. corderoi* (southeast Brazil); L, *C. draco* (Bocas del Toro); A, Dorsal view of prostomium; B, Anterior end; C, Anterior end showing the change in the epidermal glandular patterns; D, Detail of the glands on the anterior end corresponding to the square in C; E, Detail of the epidermal glands; F, Pygidium; G, Coelomic parasite (gregarine); H, Dorsal view of anterior end; I, Lateral organ; J, Reduced nuchal organ; K, Lateral view of the anterior end; L. Dorsal rounded nuchal organs typical of the genus. cr, ciliary ring; no, nuchal organ; oo, oocyte; pa, palp; pe, peristomium; pg, pygidial gland; ph, pharynx; pr, prostomium; pyl, pygidial lateral lobe; upr, unpigmented prostomial receptor; vg, vacuolar glands.

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(Kirsteuer 1966). Habitat: Medium-fine sand, intertidally in sandy beaches.

Claudrilus tenuis (Jouin, 1970c) (Figs. 7.11.3.21E–G, 7.11.3.22D). 7 records. Type locality: Perharidy, Roscoff (France). Additional records: Northeastern Atlantic (Jouin 1968, 1970c). Habitat: Medium-fine and fine sand in intertidal flats.

Claudrilus ovarium (Di Domenico, Martínez, Lana & Worsaae, 2013) (Figs. 7.11.3.21I, 7.11.3.22D). 3 records. Type locality: Estaleiro Beach, Santa Catarina (Brazil). Additional records: Southwestern Atlantic (Di Domenico et al. 2013, Gusmão et al. 2016). Habitat: Medium sand in the swash zone of reflective beaches.

Claudrilus pierantonii (Aiyar & Alikunhi, 1944) (Fig. 7.11.3.22D). 8 records. Type locality: Crangore, Madras (India). Additional records: Indo-Pacific (Aiyar and Alikunhi 1944, Alikunhi 1948, Schmidt and Westheide 1977). Habitat: Coarse to medium sand, swash zone of sandy beaches.

Claudrilus similis (Jouin, 1970c) (Fig. 7.11.3.22D). Type locality: Gammarth (Tunisie), Additional records: Atlantic: Eyrac, Arcachon (France), Mediterranean (Jouin 1970c, Westheide 1972, Curini-Galletti et al. 2012). Habitat: Medium-fine to fine sand, 0 to 5 m in sandy beaches or sea grass meadows.

Remarks: Undescribed species are known from the Caribbean (Belize), Indo-Pacific (Egypt, Solomon Islands, Lord Howe, Panama, USA), and Northeastern Atlantic (Iceland).

Key to the genera of Protodrilidae

1. Gut absent, festooned body (Figs. 7.11.3.1B, 7.11.3.13B) — *Astomus*
   Gut present, cylindrical body (Fig. 7.11.3.1A) — 2
2. Pygidium trilobed (Fig. 7.11.3.16B) — *Megadrilus*
   Pygidium bilobed or missing (only anterior end available) (Fig. 7.11.3.14B) — 3
3. Rounded, large, and medial unpigmented receptors, visible in LM (Fig. 7.11.3.10D) — 4
   No rounded, large, and medial unpigmented receptors (Figs. 7.11.3.18A, 7.11.3.21A) — 6
4. No pigmented eyes (Fig. 7.11.3.10D) — *Protodrilus* (part)
   Pigmented eyes present (Fig. 7.11.3.14G) — 5
5. Opaque and yellowish body; salivary glands on segments 1–10 or further (Fig. 7.11.3.22D) — *Lindrilus*
   Translucent or whitish body; salivary glands on segments 1–6 or shorter — *Protodrilus* (part)
6. Segmental adhesive glands (Fig. 7.11.3.18E, F) — 7
   No segmental adhesive glands (Fig. 7.11.3.10A) — 8
7. Salivary glands on segments 1–5/6, nuchal organs visible in LM (Fig. 7.11.3.18A); females with cocoon glands (Fig. 7.11.3.18D) — *Meiodrilus*
   Salivary glands on segments 1–15, nuchal organs not visible in LM (Fig. 7.11.3.22C) — *Claudrilus*
8. Body yellowish, large, red pharynx, no ciliary bands (Fig. 7.11.3.16A) — *Megadrilus*
   Body whitish or translucent, no red pharynx (Figs. 7.11.3.21C, 7.11.3.22C) — *Claudrilus*

References

Aiyar, G. & Alikunhi, K.H. (1944): On some archiannelids of Madras coast. *Proceedings of the National Institute of Sciences of India* 10: 113–139.

Alikunhi, K.H. (1948): On some archiannelids of the Krusadai Island. *Proceedings of the National Institute of Sciences of India* 14: 373–383.

Andrade, S.C., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Arendt, D., Hausen, H. & Purschke, G. (2009): The 'division of labour' model of eye evolution. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364: 2809–2817.

Armenante, Z. (1903): *Protodrilus hypoleucus* n. sp. *Monitore Zoologico Italiano* 14: 221–222.

Bailey-Brock, J.H., Jouin-Toulmond, C. & Brock, R.E. (2010): Protodrilidae (Annelida: Polychaeta) from the Hawaiian Islands and comparison with specimens from French Polynesia. *Pacific Science* 64: 463–472.

Boaden, P.J.S. (1963): The interstitial fauna of some North Wales beaches. *Journal of Marine Biology Association of the United Kingdom* 43: 79–96.

Boaden, P.J.S. (1965): Interstitial Fauna from Porto Paone. *Pubblicatione Stazione Zoologica di Napoli* 34: 235–239.

Boaden, P.J.S. (1976): Soft meiofauna from the delta region of the Rhine, Meuse and Scheldt. *Netherlands Journal of Sea Research* 10: 461–471.

Braby, C.E., Rouse, G.W., Johnson, S.B., Jones, W.J. & Vrijenhoek, R.C. (2007): Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep Sea Research Part I:* Oceanographic Research Papers 54: 1773–1791.

Bubko, O.V. (1981): The nervous system of *Protodrilus* (Archiannelida). *Zoologicheskii Zhurnal* 60: 1749–1755.

Curini-Galletti, M., Artois, T., Delogu, V., De Smet, W.H., Fontaneto, D., Jondelius, U., Leasi, F., Martínez, A., Meyer-Wachsmuth, I., Nilsson, K.S., Tongiorgi, P., Worsaae, K. & Todaro, M.A. (2012): Patterns of diversity in soft-bodied meiofauna: Dispersal ability and body size matter. *PLoS One* 7: e33801.

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Czerniavsky, V. (1881): Materialia ad zoographiam Ponticam comparatam. *Bulletin de la Société Impériale des naturalistes de Moscou* 56: 338–420 [in Russian]

Delgado, J.D., Núñez, J., Riera, R. & Monterroso, Ó. (2003): Abundance and diversity patterns of annelids from intertidal sandy beaches in Iceland. *Hydrobiologia* 496: 311–319.

Di Domenico, M., Lana, P.d.C. & Garrafoni, A.R.S. (2009): Distribution patterns of interstitial polychaetes in sandy beaches of southern Brazil. *Marine Ecology* 30: 47–62.

Di Domenico, M., Martínez, A., Lana, P.d.C. & Worsaae, K. (2013): *Protodrilus* (Protodrilidae, Annelida) from the southern and southeastern Brazilian coasts. *Helgoland Marine Research* 67: 733–748.

Di Domenico, M., Martínez, A., Lana, P.d.C. & Worsaae, K. (2014): Molecular and morphological phylogeny of Saccocirridae (Annelida) reveals two cosmopolitan clades with specific habitat preferences. *Molecular Phylogenetics and Evolution* 75: 202–218.

Du Bois-Reymond Marcus, E. (1948). Further Archiannelids from Brazil. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo.* 2(48): 1–17.

Eakin, R.M., Martin, G.G. & Reed, C.T. (1977): Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphologie* 88: 1–18.

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. 1. Archiannelids and other small polychaetes. *Zoomorphologie* 95: 235–249.

Fransen, M.E. (1988): Coelomic and vascular systems. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of the Polychaeta*. *Microfauna Marina* 4: 199–213.

Franzén, Å. (1977): Ultrastructure of spermatids and spermatozoa in Archiannelida. *Zoon* 5: 97–105.

Gerlach, S.A. (1953): Zur Kenntnis der Archianneliden des Mittelmeeres. *Kieler Meeresforschungen* 9: 248-251.

Giere, O. (2009): *Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments*. Springer, Berlin.

Goodrich, E.S. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science* 44: 413–428.

Goodrich, E.S. (1931): Notes on *Protodrilus*. *Quarterly Journal of Microscopical Science* 2-74s: 303–320.

Gusmão, F., Di Domenico, M., Amaral, A.C.Z., Martínez, A., Gonzalez, B.C., Worsaae, K., do Sul, J.A.I., & da Cunha Lana, P.d.C. (2016): *In situ* ingestion of microfibres by meiofauna from sandy beaches. *Environmental Pollution* 216: 584–590.

Hatschek, B. (1881): *Protodrilus leuckartii*. Eine neue Gattung Archianneliden. *Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 3: 79–93.

Hatschek, B. (1888): *Lehrbuch der Zoologie, eine morphologische Übersicht des Thierreiches zur Einführung in das Studium dieser Wissenschaft*. Gustav Fischer, Jena.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Jägersten, G. (1940): Zur Kenntnis der äusseren Morphologie, Entwicklung und Ökologie von *Protodrilus rubropharyngeus* n. sp. *Arkiv för Zoologi* 32: 1–19.

Jägersten, G. (1952): Studies on the morphology, larval development and biology of *Protodrilus*. *Zoologiska bidrag från Uppsala* 29: 425–512.

Jägersten, G. (1954): On the locomotion and attachment of *Protodrilus*, with remarks on the function of locomotory cilia. *Zoologiska bidrag från Uppsala* 31: 315–320.

Jouin, C. (1968): In: Cabioch, L., L'Hardy, J.P. & Rullier, F. (eds.), *Annélides. Inventaire de la Faune*. Editions de la Station Biologique de Roscoff, Roscoff: 1–94.

Jouin, C. (1970a): Archiannélides interstitielles de Nouvelle-Calédonie. In Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie, 1960–1963. *Editions de la Fondation Singer-Polignac* 4: 147–167.

Jouin, C. (1970b): *Recherches sur les archiannélides interstitielles: Systématique, anatomie et développement des Protodrilidae et des Nerillidae*. Thèse Doctorat d'État, 212 pp.

Jouin, C. (1970c): Recherches sur les Protodrilidae (Archiannelides). I. Etude morphologique et systématique du genre *Protodrilus*. *Cahiers de Biologie Marine* 11: 367–434.

Jouin, C. (1978a): Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida) I. Muscle and myo-epithelial junctions. *Tissue and Cell* 10: 269–287.

Jouin, C. (1978b): Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida). II. The stomodeal epithelium and its cuticle. *Tissue and Cell* 10: 289–301.

Jouin, C. (1979): Description of a free-living polychaete without gut: *Astomus taenioides* n. gen., n. sp. (Protodrilidae, Archiannelida). *Canadian Journal of Zoology* 57: 2448–2456.

Jouin, C. (1992): The ultrastructure of a gutless annelid, *Parenterodrilus* gen. nov. *taenioides* (= *Astomus taenioides*) (Polychaeta, Protodrilidae). *Canadian Journal of Zoology* 70: 1833–1848.

Jouin-Toulmond, C. & Purschke, G. (2004): Ultrastructure of the spermatozoa of *Parenterodrilus taenioides* (Protodrilida: "Polychaeta") and its phylogenetic significance. *Zoomorphology* 123: 139–146.

Kirsteuer, E. (1966): Zur Kenntnis der Archianneliden des Roten Meeres. *Zoologischer Anzeiger* 177: 288–296.

Kirsteuer, E. (1967): Bredin-Archbold-Smithsonian Biological Survey of Dominica. 3. Marine archiannelids from Dominica. *Proceedings of the United States National Museum* 123: 1–6.

Kopiy, V. (2013): Some aspects of the biology and the present state of the population of *Protodrilus flavocapitatus* (Polychaeta: Protodrilidae) in the coastal zone of Crimea (the Black Sea). *Journal of the Black Sea/Mediterranean Environment* 19: 162–168.

Lam, H.J. (1922): Über den Bau und die Verwandschaft der *Protoannelis meyeri*, nov. gen., nov. spec., eine neue Archiannelide. *Tijdschrift der Nederlandsche Dierkundige Vereeniging, Leiden* 18: 44–84.

Langerhans, P. (1880): Die Wurmfauna von Madeira. II. *Zeitschrift für wissenschaftliche Zoologie* 33: 267–316.

Langerhans, P. (1881): Über einige Kanarische Anneliden. *Nova Acta der Kaiserlichen Leopold-Carolin Deutschen Akademie der Naturforscher, Halle* 42: 95–124.

Magagnini, G. (1980): Archianellidi della Meloria (Livorno). *Atti della Società Toscana de Scienze Naturali di Pisa*, Mem 87: 299–308.

Martin, G.G. (1978a): Ciliary gliding in marine invertebrates. *Zoomorphologie* 91: 249–261.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Martin, G.G. (1978b): The duo-gland adhesive system of the archiannelids *Protodrilus* and *Saccocirrus* and the turbellarian *Monocelis*. *Zoomorphologie* 91: 63–75.

Martin, G.G. (1978c): A new function of rhabdites: Mucus production for ciliary gliding. *Zoomorphologie* 91: 235–248.

Martínez, A., Palmero, A.M., Brito, M.d.C., Núñez, J. & Worsaae, K. (2009): Anchialine fauna of the Corona lava tube (Lanzarote, Canary Islands): diversity, endemism and distribution. *Marine Biodiversity* 39: 169–187.

Martínez, A., Di Domenico, M., Jörger, K., Norenburg, J. & Worsaae, K. (2013): Description of three new species of *Protodrilus* (Annelida, Protodrilidae) from Central America. *Marine Biology Research* 9: 676–691.

Martínez, A., Di Domenico, M., Rouse, G. & Worsaae, K. (2015): Phylogeny of Protodrilidae (Annelida) inferred by total evidence analyses. *Cladistics* 31: 250–276.

Martínez, A., Gonzalez, B.C., Worsaae, K., Wilkens, H., Núñez, J., Oromí, P. & Iliffe, T.M. (2016): *Guide to the anchialine ecosystems of Jameos del Agua and Túnel de la Atlántida*. Medio Ambiente, Cabildo de Lanzarote, Arrecife, Lanzarote.

Martínez, A., Kvindebjerg, K., Iliffe, T.M. & Worsaae, K. (2017): Evolution of cave suspension feeding in Protodrilidae (Annelida). *Zoologica Scripta* 46: 214–226.

Mastepanova, E.A. (2004): The interstitial Polychaeta of Russian Seas. *Invertebrate Zoology* 1: 59–64.

Merker, G. & Vaupel-von Harnack, M. (1967): Zur Feinstruktur des "Gehirns" und der Sinnesorgane von *Protodrilus rubropharyngeus* Jaegersten (Archiannelida). *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 81: 221–239.

Müller, M.C. (1999): *Das Nervensystem der Polychaeten: Immunhistochemische Untersuchungen an ausgewählten*. Ph.D. thesis, University of Osnabrück.

Núñez, J., Brito, M.d.C. & Docoito, J.R. (2005): Anélidos poliquetos de Canarias: Catálogo de especies, distribución y hábitats. *Vieraea* 33: 297–321.

Orrhage, L. (1974): Über die Anatomie, Histologie und Verwandtschaft der Apistobranchidae (Polychaeta Sedentaria) nebst Bemerkungen über die Systematische Stellung der Archianneliden *Zeitschrift für Morphologie der Tiere* 79: 1–45.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.

Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. (2016): The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society B* 283: 20161378.

Pierantoni, U. (1903): Sopra un nuovo *Protodrilus* d'acqua dolce. *Monitore Zoologico Italiano* 14: 324–327.

Pierantoni, U. (1906a): Organi genitali e glandole salivari nei Protodrili. *Bollettino della Società di Naturalisti in Napoli* 20: 154–157.

Pierantoni, U. (1906b): Sulla sessualita dei Protodrili. *Bollettino della Società di Naturalisti in Napoli* 18: 437–439.

Pierantoni, U. (1906c): Sullo sviluppo del *Protodrilus* e del *Saccocirrus*. *Mittheilungen aus der zoologischen Station zu Neapel* 17: 515–523.

Pierantoni, U. (1908): *Protodrilus*. *Fauna Flora des Golfes von Neapel* 31: 1–226.

Purschke, G. (1988): Comparative electron microscopic investigation of the nuchal organs in *Protodriloides*, *Protodrilus* and *Saccocirrus* (Annelida, Polychaeta). *Canadian Journal of Zoology* 68: 325–338.

Purschke, G. (1990a): Fine structure of the so-called statocysts in *Protodrilus adhaerens* (Protodrilidae, Polychaeta). *Zoologischer Anzeiger* 224: 286–296.

Purschke, G. (1990b): Ultrastructure of the "statocysts" in *Protodrilus* species (Polychaeta): Reconstruction of the cellular organization with morphometric data from receptor cells. *Zoomorphology* 110: 91–104.

Purschke, G. (1993): Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology* 113: 1–20.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 535/536: 53–78.

Purschke, G. (2006): Problematic annelid groups. In: Rouse, G.W. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida* Vol. 4, Science Publishers, Enfield, Jersey, Plymouth: 639–667.

Purschke, G. (2016): Annelida: Basal groups and Pleistoannelida. In: Schmidt-Rhaesa, A., Harzsch, S. & Purschke, G. (eds.), *Structure and Evolution of Invertebrate Nervous Systems*. Oxford University Press, Oxford: 254–312.

Purschke, G. & Jouin, C. (1988): Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationships within Protodrilida (Annelida: Polychaeta). *Journal of Zoology* 215: 405–432.

Purschke, G. & Jouin-Toulmond, C. (1993): Ultrastructure of presumed ocelli in *Parenterodrilus taenioides* (Polychaeta, Protodrilidae) and their phylogenetic significance. *Acta Zoologica (Stockholm)* 74: 247–256.

Purschke, G. & Jouin-Toulmond, C. (1994): Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta). *Mémoires du Muséum National D'Histoire Naturelle. Actes de la 4ème Conference internationale des Polychètes* 162: 119–128.

Read, G. (2014): *Protoannelis* Lam, 1922. In: Read, G. & Fauchald, K. (eds.), World Polychaeta Database. Accessed at: http://www.marinespecies.org/polychaeta/

Remane, A. (1932): Archiannelida. In: Grimpe, G. & Wagner, E. (eds.), *Tierwelt der Nord- und Ostsee* VIa 1, Geest und Portig, Leipzig: 1–36.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the Spiralia. *Acta Zoologica (Stockholm)* 57: 53–68.

Riera, R., Monterroso, Ó., Núñez, J. & Martínez, A. (2018): Distribution of meiofaunal abundances in a marine cave complex with secondary openings and freshwater filtrations. *Marine Biodiversity* 48: 203–217.

Riser, N.W. (1997): *Protodrilus gelderi*, a new species of infralittoral, interstitial polychaete from Massachusetts Bay. *Proceedings Biological Society of Washington* 110: 552–557.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Ruebush, T.K. (1939): The occurrence of the two rare genera, *Protohydra* and *Protodrilus*, on the East coast of North America. *Science* 90: 617–618.

Salensky, W. (1907): Morphogenetische Studien an Würmern. II. Über die Anatomie der Archianneliden. *Mémoires de l'Academie Impériale des Sciences de St Pétersbourg* 8 cl. Phys. Math. 19: 1–349.

Sato-Okoshi, W., Okoshi, K. & Fujiwara, Y. (2015): A new species of *Protodrilus* (Annelida, Protodrilidae) covering bone surfaces bright red, in whale-fall ecosystems in the Northwest Pacific. *The Biological Bulletin* 229: 209–219.

Schmidt, P. & Westheide, W. (1977): Interstitielle Fauna von Galapagos. XVII. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). *Mikrofauna des Meeresbodens* 62: 1–36.

Schneider, A. (1868): Ueber Bau und Entwicklung von *Polygordius*. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* 1868: 51–60.

Struck, T.H., Schultz, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7:57.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Swedmark, B. (1964): The interstitial fauna of marine sand. *Biological Reviews* 39: 1–42.

Uljanin, B. (1877): Recherches sur les *Polygordius* de la baie de Sebastopol. *Bulletin de la Société Impériale des naturalistes de Moscou* 52: 53–96. [in Russian]

Uljanin, B. (1878): Sur le genre *Sagitella* N. Wagner. *Archives de Zoologie Expérimentale et Générale* 7: 1–32.

Villora-Moreno, S. (1997): Environmental heterogeneity and the biodiversity of interstitial polychaeta. *Biological Marine Science* 60: 494–501.

von Nordheim, H. (1983): Systematics and Ecology of *Protodrilus helgolandicus* sp. n., an interstitial polychaete (Protodrilidae) from subtidal sands off Helgoland, German Bight. *Zoologica Scripta* 12: 171–177.

von Nordheim, H. (1984): Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchugen* 38: 1–20.

von Nordheim, H. (1989a): Six new species of *Protodrilus* (Annelida, Polychaeta) from Europe and New Zealand, with a concise presentation of the genus. *Zoologica Scripta* 18: 245–268.

von Nordheim, H. (1989b): Vergleichende Ultrastrukturuntersuchungen der Eu- und Paraspermien yon 13 *Protodrilus*-Arten (Polychaeta, Annelida) und ihre taxonomische und phylogenetische Bedeutung. *Helgoländer Meeresuntersuchugen* 43: 113–156.

von Nordheim, H. (1991a): Ultrastructure and functional morphology of the female reproductive organs in *Protodrilus* (Polychaeta, Annelida). *Helgoländer wissenschaftliche Meeresuntersuchungen* 45: 465–485.

von Nordheim, H. (1991b): Ultrastructure and functional morphology of the male genital organs and spermatophore formation in *Protodrilus* (Polychaeta, Annelida). *Zoomorphology* 111: 81–94.

von Nordheim, H. & Schrader, A. (1994): Ultrastructure and functional morphology of the protonephridia and segmental fenestrated lacunae in *Protodrilus rubropharyngeus* (Polychaeta, Protodrilidae). *Helgoländer Meeresuntersuchugen* 48: 467–485.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Westheide, W. (1972): La faune des polychétes et des archiannèlides dans les plages sableuses a ressac de la côte mediterraneennée de la Tunisie. *Bulletin Institute Océanographique Pêche, Salammbô* 2: 449–468.

Westheide, W. (1984): The concept of reproduction in polychaetes with small body size — Adaptations in interstitial species. *Fortschritte der Zoologie* 29: 265–287.

Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21: 843–854.

Westheide, W. (2008): *Polychaetes: Interstitial Families*, Vol. 44. The Linnean Society of London, Shrewsbury.

Wieser, W. (1957): Archiannelids from the intertidal of Puget Sound. *Transactions of the American Microscopical Society* 76: 275–285.

Wilkens, H., Iliffe, T.M., Oromí, P., Martínez, A., Tysall, T.N. & Koenemann, S. (2009): The Corona lava tube, Lanzarote: Geology, habitat diversity and biogeography. *Marine Biodiversity* 39: 155–167.

Willems, W.R., Curini-Galletti, M., Ferrero, T.J., Fontaneto, D., Heiner, I., Huys, R., Ivanenko, V.N., Kristensen, R., Kanneby, T., Macnaughton, M.O., Martínez Arbizu, P., Todaro, M.A., Sterrer, W. & Jondelius, U. (2009): Meiofauna of the Koster-area, results from a workshop at the Sven Lovén Centre for Marine Sciences (Tjärnö, Sweden). *Meiofauna Marina* 17: 1–34.

Wolff, W.J., Sandee, A.J.J. & Stegenga, H. (1980): The archiannelida of the estuarine area of the rivers Rhine, Meuse and Scheldt, with some remarks on their ecology. *Netherlands Journal of Sea Research* 14: 94–101.

Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). *Hydrobiologia* 535/536: 319–340.

Wu, B.-L., Sun, R.-P. & Chen, M. (1980): On archiannelids of the Yellow Sea. I. *Protodrilidae*. *Acta Oceanologica Sinica* 2: 132–148.

Zrzavý, J., Riha, P., Piálek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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Alejandro Martínez, Katrine Worsaae, and Günter Purschke

7.11.4 Protodriloididae Purschke & Jouin, 1988

Introduction

Protodriloididae is a small family of simple-looking, thread-like interstitial annelids up to 13 mm long. They superficially resemble Protodrilidae and Saccocirridae due to the presence of a pair of frontal palps and a bilobed adhesive pygidium (Fig. 7.11.4.1) (Westheide 2008). However, the palps in Protodriloididae represent frontal prolongations of the prostomium, positioned terminally with their bases close together and not delimited from the prostomium by a basal furrow as to be observed in Protodrilidae (Fig. 7.11.4.2A, B) (Jouin 1966, Martínez et al. 2015). Furthermore, Protodriloididae are generally more contractible and, due to their highly developed adhesive glands, are more sticky than Saccocirridae and Protodrilidae. Their bodies bear conspicuous gland cells with greenish content, interpreted as symbionts by Giard (1904), who accordingly named the first species *Protodrilus symbioticus* (*Protodriloides symbioticus*) (Figs. 7.11.4.1A, B, 7.11.4.3A, B). Chaetae are absent in *P. symbioticus*, but two pairs of oligochaete-like, sigmoid chaetae are present on each segment of *Protodriloides chaetifer* (Figs. 7.11.4.2A, 7.11.4.3B, E, 7.11.4.4D, G).

First described as *Protodrilus* species (Giard 1904, Remane 1926), the genus *Protodriloides* was created by Jouin (1966) following a detailed morphological analysis, which revealed fundamental differences from *Protodrilus* Hatschek, 1881. The family Protodriloidae was erected by Purschke and Jouin (1988) (corrected to Protodriloididae by Rouse and Fauchald 1997) as a result of a morphological phylogenetic analysis of *Astomus* Jouin, 1979, *Protodrilus* Hatschek, 1881, *Saccocirrus* Bobretzky, 1872, and *Protodriloides* Jouin, 1966, which found the former Protodrilidae paraphyletic. Because *Protodriloides symbioticus* (Giard, 1904) and *Protodriloides chaetifer* (Remane, 1926) were initially described as protodrilids, early researchers also considered the current *Protodriloides* spp. as part of the now dismissed "Archiannelida". Hence, their apparently simple morphology was likewise interpreted as retention of plesiomorphic annelidan features (Pierantoni 1908) or by some authors as a secondary adaptation to interstitial life (Remane 1932, Hermans 1969). Due to the lack of synapomorphies, later morphological studies disregarded the taxon Archiannelida, and superficial similarities among their former members have been interpreted as retention of plesiomorphies and convergent paedomorphic adaptations to the interstitial life (Orrhage 1974, Westheide 1985, Purschke and Jouin 1988). The monophyly of the subgroup Protodrilida comprising Protodriloididae, Protodrilidae, and Saccocirridae has been consistently supported by morphological and molecular phylogenetic analyses (e.g., Purschke and Jouin 1988, Andrade et al. 2015) and is sometimes also found to be a sister group to Polygordidae Schneider, 1868 (Zrzavy et al. 2009, Struck et al. 2015, naming this clade Protodriliformia). However, the phylogenetic position of Protodrilida has changed across different analyses. First, a relationship to spiomorph polychaetes was discussed mainly based on common structures in their nervous system, palp morphology, and nuchal organs (Orrhage 1974, Purschke 1988). Consequently, early morphological cladistic analyses recovered the clade within the Canalipalpata (Rouse and Fauchald 1997), whereas more recent phylogenetic hypotheses based on phylogenomic data place Protodrilida as a deep branch within Errantia (Andrade et al. 2015, Struck et al. 2015). Regardless of the exact position of the clade, all analyses consistently placed Protodrilida among large-sized annelids. This suggests that the slender body and simple morphology of *Protodriloides* is the result of a secondary miniaturization originated either through a gradual evolutionary change

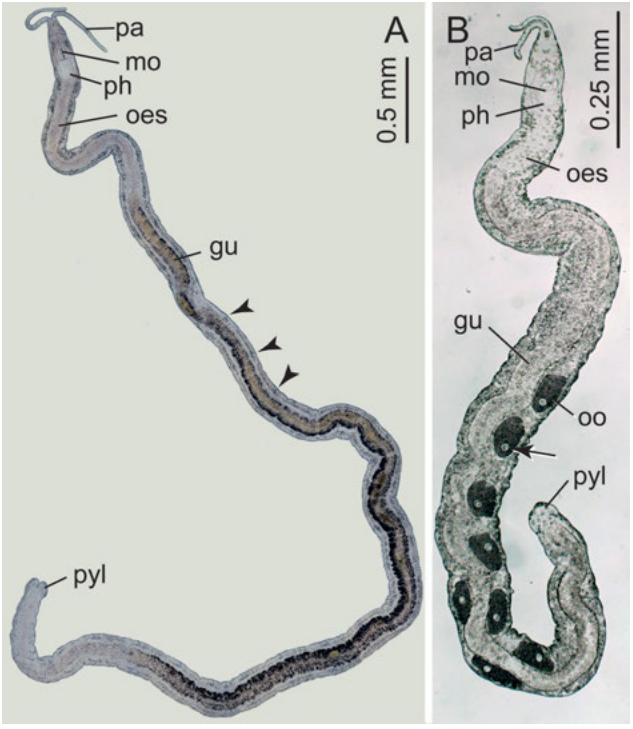


Fig. 7.11.4.1: General organization and habitus of Protodriloididae. Light microscopy images of living individuals. A, *Protodriloides chaetifer*; B, *Protodriloides symbioticus*. Micrographs of slightly squeezed living organisms; arrowheads point to segment borders and arrow points to oocyte nucleus. gu, gut; mo, mouth opening; oes, esophagus; oo, oocyte; pa, palp; ph, pharynx; pyl, pygidial lobe.

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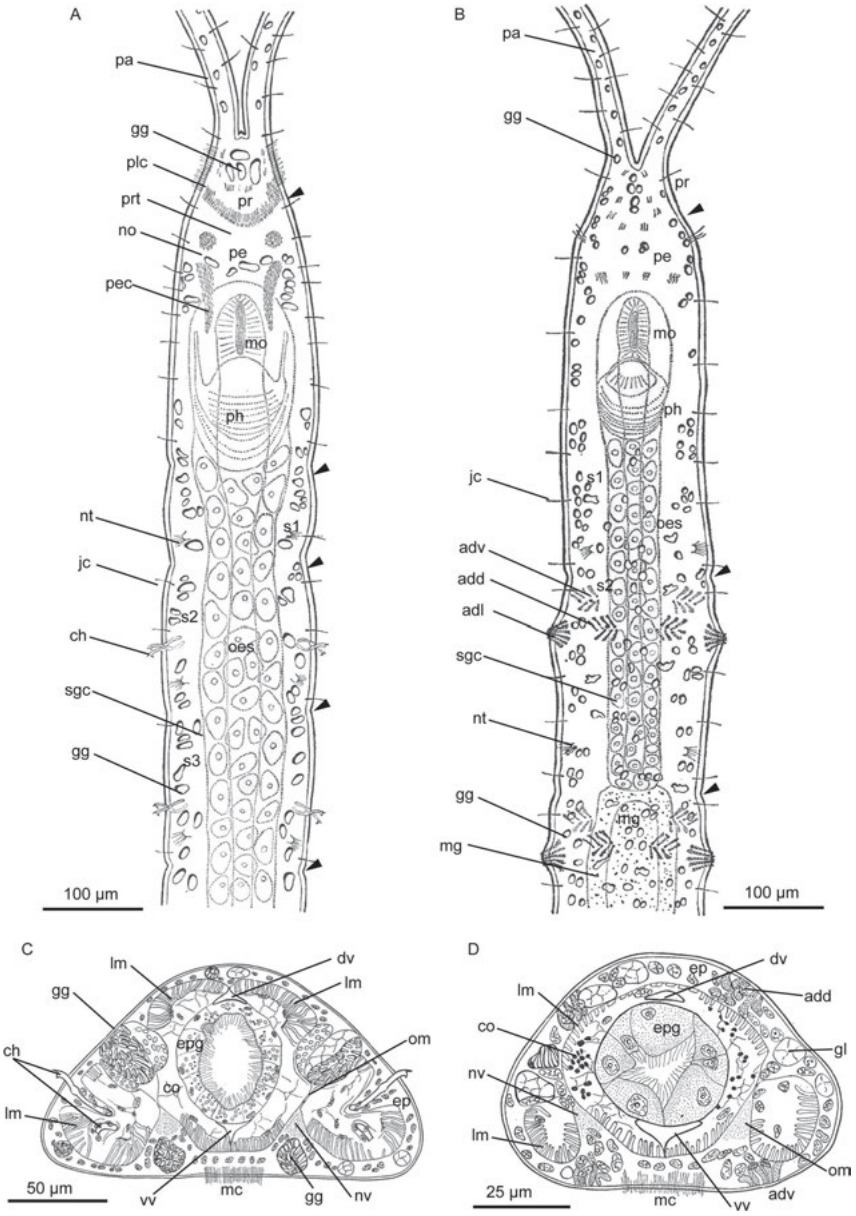


Fig. 7.11.4.2: General organization of Protodriloididae. A, C, *Protodriloides chaetifer*; B, D, *Protodriloides symbioticus*; A, B, Schematic drawings of the anterior region of the body; C, D, Schematic drawings of transverse sections of the interstitial region of the trunk. add, dorsal adhesive gland; adl, lateral adhesive gland; adv, ventral adhesive gland; ch, chaeta; co, coelenchymal cells; dv, dorsal vessel; gg, green glandular cell; gl, gland cell; jc, joint cilia; lm, longitudinal muscle; mc, midventral ciliation; mg, midgut; mo, mouth; no, nuchal organs; nt, notopodial papilla; nv, nerve cord; om, oblique muscle; pa, palp; pe, peristomium; pec, peristomial ciliation; ph, pharynx; plc, prostomial lateral ciliation; pr, prostomium; prt, prostomial transversal ciliation; s1, segment 1; sgc, salivary gland cell; vv, ventral vessel. After Jouin (1966).

(Struck et al. 2015) or through a faster progenetic process (Westheide 1984, 1987, Worsaae and Kristensen 2005).

Morphology

External morphology

Protodriloididae have a distinct head formed by the prostomium and peristomium (Figs. 7.11.4.1, 7.11.4.2, 7.11.4.3A, B, 7.11.4.4A). The prostomium is small and indistinct and extends anteriorly forming a pair of solid palps (Figs. 7.11.4.3A, B, 7.11.4.4A–C). These palps resemble anterior extensions of the prostomium and lack a basal furrow (Figs. 7.11.4.1, 7.11.4.2, 7.11.4.3A, B, 7.11.4.4C) (Purschke 1993) in contrast to the palps in the related families Protodrilidae and Saccocirridae (Di Domenico et al. 2014, Martínez et al. 2015). Palps in Protodriloididae also lack the internal coelomic canals or basal ampulla (Fig. 7.11.4.3A, B),

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typical of those families, and bear a longitudinal ventral band of motile cilia extending from the near the base to the tip (Fig. 7.11.4.4B). Joint cilia, presumably sensory, are scattered over the surface of the palps (Figs. 7.11.4.2A, B, 7.11.4.4C). The prostomium lacks pigmented eyes or unpigmented receptors, as those described in other members of Protodrilida. However, two pairs of unique unpigmented ciliary receptors are present in *Protodriloides* spp. (Purschke and Müller 1996). A dorsal band and a ventral ciliary band extend transversely across the prostomium, near the border of the peristomium (Fig. 7.11.4.4C).

The peristomium is longer than the prostomium and possesses the mouth, the nuchal organs, and a pair of peristomial lateral ciliary bands (Fig. 7.11.4.4A). The mouth is ventral and consists of a longitudinal slit-like opening (Fig. 7.11.4.4C) (Purschke and Jouin 1988). The dorsal nuchal organs are discoid and densely ciliated in *P. chaetifer*, extending slight obliquely to the longitudinal body axis anterior to the peristomial lateral ciliary bands (Fig. 7.11.4.4A) (Purschke 1988). In contrast, nuchal organs are reduced to a pair of almost invisible dorsal papillae in *P. symbioticus* (see below) (Purschke 1988, 1997).

The trunk is slightly compressed dorsoventrally and consists of 45 to 50 segments in *P. chaetifer* versus 15 to 20 in *P. symbioticus* (see Jouin 1966). Segments are delimited by incomplete septa and approximately equal in length, except for the shorter first segment (Figs. 7.11.4.1, 7.11.4.2A, B) (Jouin 1966, Fransen 1980). The midventral side of the trunk carries a longitudinal ciliary band, which extends from the mouth to the last four to five segments and covers approximately two-thirds of the ventral side of each trunk segment (Fig. 7.11.4.4C) (Jouin 1966). The midventral band consists of a few longitudinal rows of multiciliated cells flanked by mucous glands, which propel the animals forward on the substrate.

Three types of segmentally arranged structures are found on each trunk segment in Protodriloididae, except for segment 1 and the last four to five segments anterior to the pygidium (Jouin 1966). (1) Sensory ciliated organs are present in both *P. symbioticus* and *P. chaetifer* (Figs. 7.11.4.2A, B, 7.11.4.4D). They consist of groups of several cilia projecting from small papillae, approximately 15 µm long. They are situated laterodorsally and pairwise on each trunk segment, between the chaetae and the lateral adhesive organ (Figs. 7.11.4.2A, B, 7.11.4.4D) (Jouin 1966). (2) Adhesive organs, exclusive for *P. symbioticus* (Swedmark 1954, Jouin 1966, Westheide 2008), typically consisting of 10 to 25 adhesive gland cells present laterally on each trunk segment (Figs. 7.11.4.2B, 7.11.4.3A, C, 7.11.4.D). Three pairs of adhesive organs are found on the anterior third of each trunk segment: the ventral pair is the most anterior followed by the dorsal pair and the lateral pair (Fig. 7.11.4.2B) (Jouin 1966). Ventral, dorsal, and lateral pairs of adhesive organs are aligned along successive trunk segments, forming characteristic longitudinal bands (Swedmark 1954, Jouin 1966). Finally, (3) two sigmoid chaetae occur on each lateral side in the posterior half of each trunk segment, only on *P. chaetifer* (Figs. 7.11.4.2A, 7.11.4.3B, E, 7.11.4.4D, G). Each chaeta protrudes 35 to 40 µm from the body wall and consists of bifid tip with a curved and robust, rostrum-like structure (Remane 1926, Jouin 1966). Each chaeta inserts individually into a chaetal sac, but the two chaetal sacs on each lateral side are surrounded by a single muscular layer and supplied by a pair of retractor muscles, which move both chaetae together (Jouin 1966). Although both chaetal and chaetal sac morphologies are superficially similar to those found in tubificid clitellates or in *Questa* orbiniids, details on the chaetogenesis have not yet being investigated (Rouse and Pleijel 2001). Chaetae are constantly replaced during the lifetime of each individual, so single chaetae or small developing chaetae are a common feature (Jouin 1966).

The pygidium possesses a pair of lobes, which are well developed and rounded in *P. chaetifer* and somewhat smaller and less swollen in *P. symbioticus* (Figs. 7.11.4.3F, 7.11.4.4E). Approximately 60 to 80 adhesive glands open subterminally on the ventral side of each lobe arranged as an oblique band (Figs. 7.11.4.3F, 7.11.4.4F) (Swedmark 1954, Jouin 1966).

Body wall: epidermis and trunk musculature

The epidermis of *Protodriloides* is transparent and rich in unicellular glands. Externally, it is covered by a smooth, 1- to 1.5-µm-thick cuticle underlined by an extracellular matrix (ECM) (Fig. 7.11.4.2C, D, 7.11.4.5) (Jouin 1966). The epidermal glands are the most conspicuous epidermal structures. They are sparsely distributed over the entire body but more abundant laterodorsally and lateroventrally, where they are arranged in paired longitudinal bands from the peristomium to the pygidium (Figs. 7.11.4.2A–D, 7.11.4.3A–F) (Jouin 1966). Laterodorsal bands are well developed in both *P. chaetifer* and *P. symbioticus*. However, lateroventral bands of glands are only visible and narrower on *P. symbioticus*, running along each side of the midventral ciliary band.

Several types of unicellular epidermal glands have been described for *Protodriloides* based on light microscopy observations. (1) Green vacuolar glands are large, very abundant, and characterized by the presence of greenish inclusions (Giard 1904, Remane 1926, Jouin 1966), probably representing a synapomorphy of the family (Fig. 7.11.4.3A, B) (Jouin 1966). (2) Bacillary glands, resembling those in Protodrilidae, are scarcer and banana-shaped,

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Fig. 7.11.4.3: External morphology of Protodriloididae. Note the greenish epidermal gland cells. Light microscopy images. A, C, D, F, *P. symbioticus* (Roscoff, France); B, E, *P. chaetifer* (Disko Island, Greenland); A, Anterior end, dorsal view; B, Anterior end, lateral view; C, Midbody showing oocytes, dorsal view; D, Details of the lateral segmental adhesive glands; E, Midbody showing the chaeta, lateral view; F, Pygidium, dorsal view. adl, adhesive gland lateral; an, anus; ch, chaeta; gg, green glands; gu, gut; hg, hindgut; mg, midgut; mo, mouth; oe, esophagus; oo, oocyte; pa, palp; pag, pygidial adhesive glands; pe, peristomium; ph, pharynx; pr, prostomium; pyl, pygidial lobe.

varying in size and filled with dense fibrous content, which can be discharged through a cuticular pore (Jouin 1966, Martínez et al. 2015). Other types of glands have been described only superficially and their homology and function remain unclear (Jouin 1966).

Trunk musculature extends below the epidermis, separated by the basal membrane. It has never been investigated in detail but only described as consisting of conspicuous longitudinal muscles and a few oblique muscles (Figs. 7.11.4.2C, D, 7.11.4.5) (Pierantoni 1908, Jouin 1966), with

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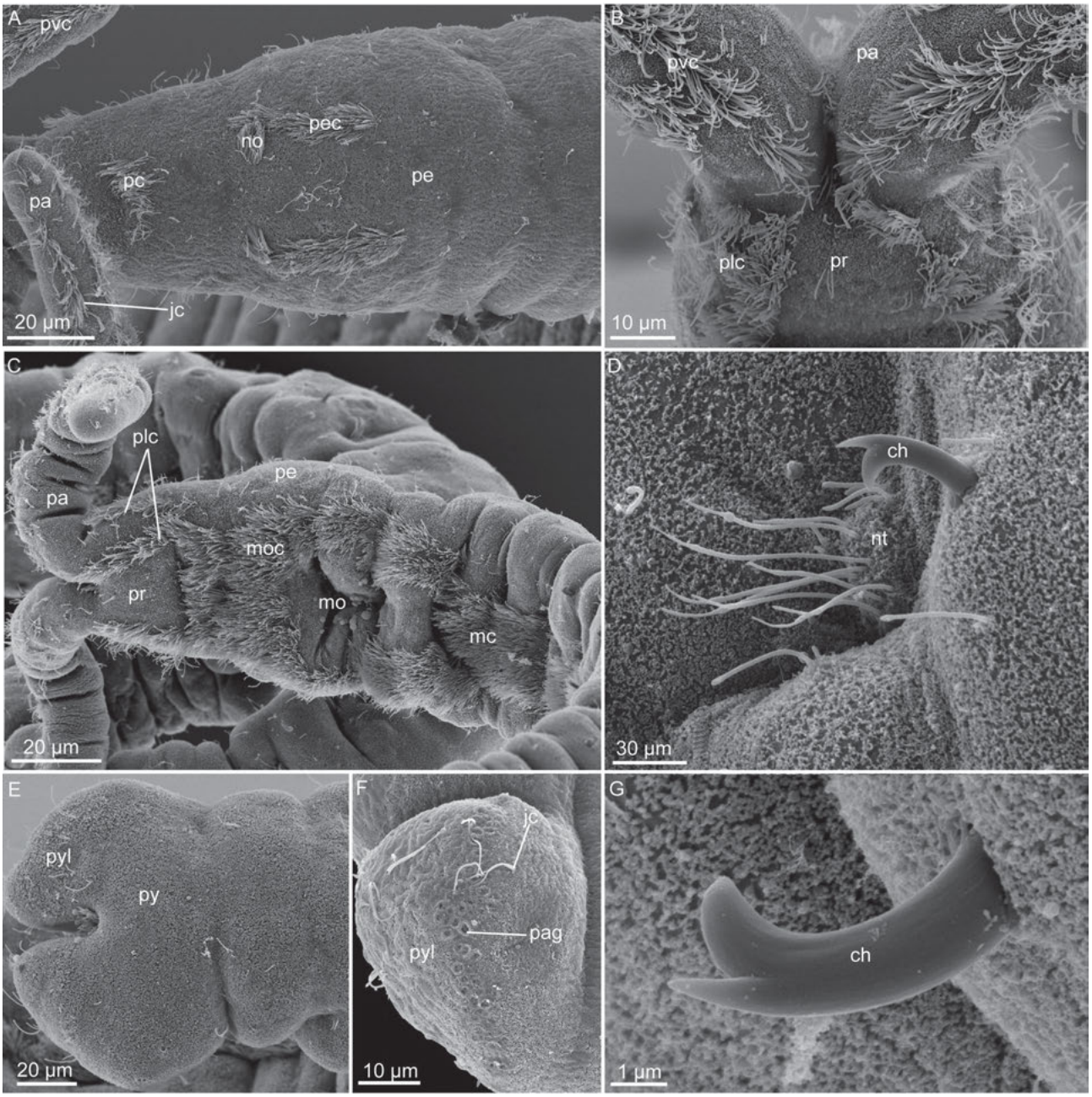


Fig. 7.11.4.4: External morphology of Protodriloididae. Scanning electron microscopy (SEM) images of *P. chaetifer* (Disko Island, Greenland). A, Anterior end, dorsal view; B, Details of the palp insertion, ventral view; C, Anterior end, ventral view; D, Chaetae and notopodial papilla; E, Pygidium, dorsal view; F, Details of pygidial adhesive glands; G, Details of the chaeta. ch, chaeta; jc, joint cilia; mc, midventral ciliary band; mo, mouth; moc, mouth ciliation; no, nuchal organ; nt, notopodial papilla; pa, palp; pag, pygidial adhesive gland; pc, prostomial ciliation; pe, peristomium; pec, peristomial ciliation; plc, prostomial lateral ciliation; pr, prostomium; pvc, palp ventral ciliation; py, pygidium; pyl, pygidial lobe.

no mention of circular or outer bracing muscles muscular elements. Palps are provided by a longitudinal ribbon of muscle fibers surrounded by an extracellular matrix (Purschke 1993). The musculature of the trunk is dominated by massive longitudinal fibers organized as three pairs of dorsal, round ventrolateral, and ventromedian fiber bundles (Figs. 7.11.4.2C, D, 7.11.4.5) (Pierantoni 1908, Jouin 1966). The dorsolateral and ventrolateral bundles anteriorly pass the pharynx, taper, enter the palps, and end close to their tips. In the anterior end, these bundles furthermore give off several smaller fibers constituting the complicated musculature of the mouth and prostomium. The circular musculature is represented by minute and inconspicuous isolated fibers situated between longitudinal musculature and epidermis. Although formerly regarded as being reduced (Jouin 1966), oblique muscles

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are present in each segment and represented by separate bundles running from the ventral nerve cords diagonally to the lateral furrow (Fig. 7.11.4.5). Thus, they separate the ventrolateral longitudinal bands from the rest of the body.

Digestive system and ventral pharynx

Protodriloididae possess a linear tubular alimentary canal, which consists of a mouth cavity and a ventral pharyngeal organ followed by a short esophagus, a midgut, a hindgut, and a terminal anus (Figs. 7.11.4.1, 7.11.4.2A, B, 7.11.4.3A, B, F). The unciliated mouth opening leads to the densely ciliated mouth cavity and the short esophagus (Fig. 7.11.4.6), which lines the muscular pharynx dorsally and extends along two to eight segments (Figs. 7.11.4.1, 7.11.4.2A, B). Distinct salivary glands are absent, but the esophageal epithelium contains numerous glandular cells (Figs. 7.11.4.1, 7.11.4.2A, B), which discharge directly into the esophageal lumen at the esophageal folds through glandular processes (Fig. 7.11.4.6) (Jouin 1966). The esophagus continues into the midgut, characterized by the presence of brownish lipid granules in the epithelial cells (Fig. 7.11.4.3C, E), and the hindgut, which is wider and extends through the last 4 to 10 trunk segments. The hindgut finishes as a ciliated anal ampulla and opens into a dorsoterminal anus situated between the pygidial lobes (Fig. 7.11.4.3F).

The ventral pharyngeal organ is a prominent structure in the posterior part of the peristomium and occupies the space between the mouth cavity, the esophagus, and the first trunk segment (Figs. 7.11.4.2A, B, 7.11.4.3A, B). It resembles the ventral pharyngeal organ described in Protodrilidae and *Pharyngocirrus* Di Domenico, Martínez, Lana & Worsaae, 2014 (Saccocirridae) (see Purschke and Jouin 1988) and consists of two antagonistic muscle systems: the bulbous muscle and the investing or sagittal muscle (Fig. 7.11.4.6) (Jouin 1978a, b, Purschke and Jouin 1988, Martínez et al. 2015). The bulbous muscle is the most conspicuous part of the pharyngeal organ in *P. chaetifer* (Fig. 7.11.4.3B) (Jouin 1966). It is 15 µm wide and comprises 35 to 40 muscle fibers arranged in upright position and separated by several interstitial cells. The bulbous muscle is much smaller in *P. symbioticus*, consisting of only 20 small transverse muscle fibers and a single interstitial cell (Fig. 7.11.4.3A) (Purschke and Jouin 1988). A tongue-like organ, as described in Saccocirridae and Protodrilidae, is absent in Protodriloididae, and browsing is probably done by the specialized dorsal cuticle covering the epithelium of the bulbous muscle and differentiated into teeth-like elements (Purschke and Jouin 1988). The investing or sagittal muscle surrounds the bulbous muscle, made up of a varying number of fibers (Fig. 7.11.4.6). In *P. symbioticus*, the sagittal muscle completely envelopes the reduced bulbous muscle (Purschke and Jouin 1988).

Body cavity, blood vascular system, and nephridia

The body cavity is completely obliterated and filled by the cell bodies of the muscle cells, coelenchymal cells with abundant lipid granules, nephridia, and, upon maturity, eventually gametes (Figs. 7.11.4.1, 7.11.4.2C, D, 7.11.4.5) (Jouin 1966, Fransen 1980). The circulatory system is closed and consists of a large space situated in the prostomium, anteriorly to the mouth, from which two anterior vessels branch off toward the insertion of the palps, and a dorsal and ventral vessel extend posteriorly (Figs. 7.11.4.2C, D, 7.11.4.5, 7.11.4.7B) (Purschke and Jouin 1988). The dorsal vessel contracts peristaltically from posterior to anterior (Jouin 1966). At the region of the terminal cells of the nephridia, the ventral vessel gives off a pair of segmental vessels and then continues to the dorsal vessel. Each blood vessel is delineated by an ECM, which is continuous with the ECM between the body epithelium and the musculature (Purschke 1993).

Nephridia are small and represent protonephridia (Jouin 1966, Purschke et al. unpublished observation). Each nephridium extends along two consecutive trunk segments. The segmental blood vessels are closely associated with the terminal cell and form a wider space in this region. The terminal cell is situated above the main trunk of the ventral nerve cord, gives rise to a comparatively long and thin canal, passes between the oblique muscles, turns posteriorly, and, upon reaching the midsegment region, turns laterally with the nephridiopore opening anterior to the chaetae or the lateroventral adhesive organs in *P. chaetifer* and *P. symbioticus*, respectively (Jouin 1966).

Nervous system and sensory organs

The nervous system in Protodriloididae has been studied by Pierantoni (1908) and more recently by Purschke (1993) and Müller (1999) using different methods. It is entirely basoepithelial and consists of a conspicuous brain, divided into a dorsal part and a ventral part and situated in the posterior part of the prostomium, and the ventral nerve cord extending toward the pygidium (Fig. 7.11.4.7A–F). The main nerves of the brain include two or three pairs of ventral palp nerves running anteriorly (vpn1, 3, 4) (Fig. 7.11.4.7B, C) as well as the following nerves running posteriorly: four pairs of small dorsal nerves (dn1–4) (Fig. 7.11.4.7B), one pair of nuchal nerves (nn) (Fig. 7.11.4.7B), and two stomatogastric nerves (sn) (Fig. 7.11.4.7B–D) (nomenclature of brain nerves after Purschke 1993). However, the dorsal nerves could not be found again with confocal laser scanning microscopy (CLSM) following staining with antibodies against acetylated α-tubulin (Müller 1999); in part, they may also represent posterior

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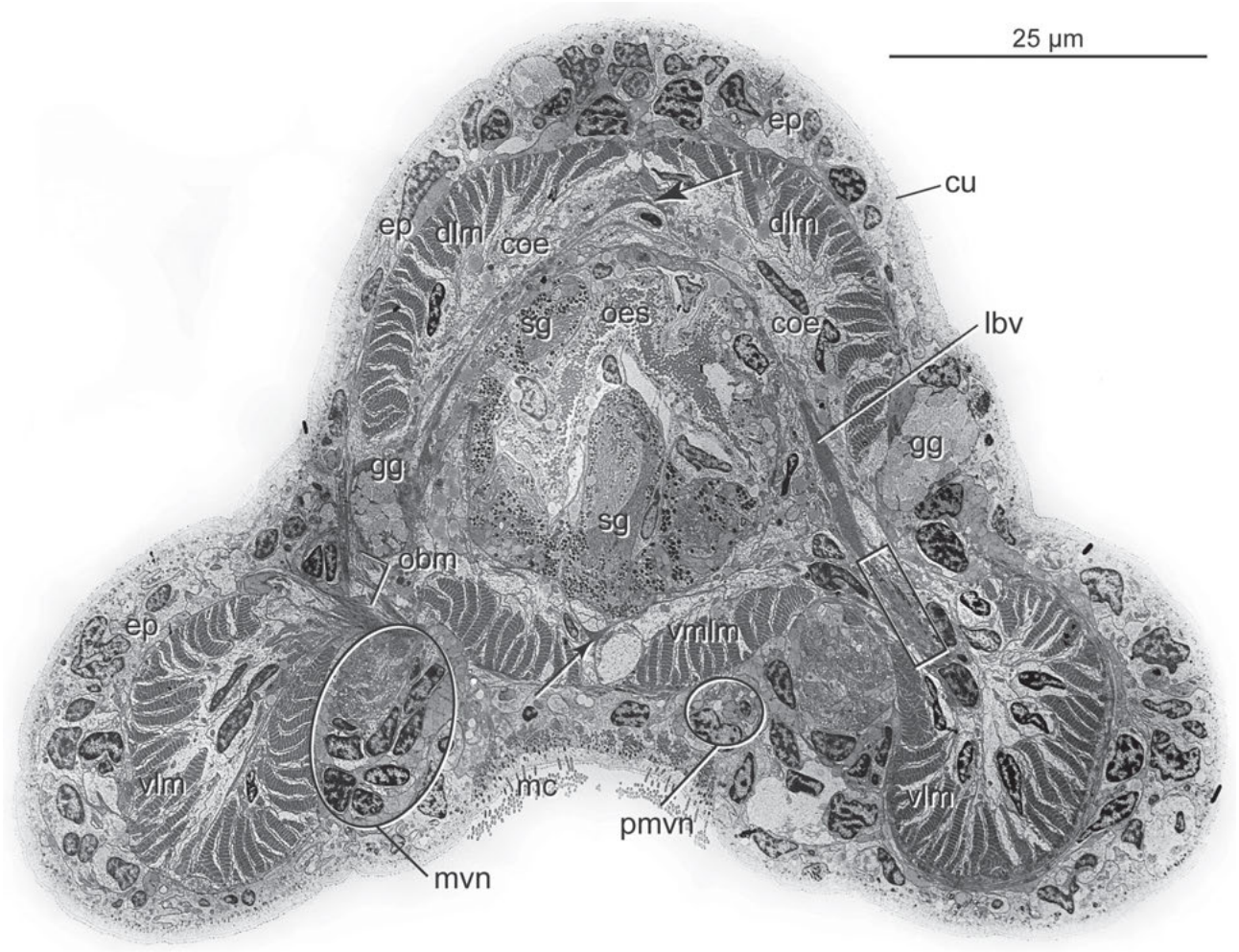


Fig. 7.11.4.5: *P. chaetifer.* Internal morphology and organization of trunk musculature. Cross-section of the trunk at the level of the glandular esophagus. Arrows point to ventral and dorsal blood vessels. coe, coelomic parenchyme; cu, cuticle; dlm, dorsal longitudinal musculature; ep, epidermis; gg, green glands; lbv, lateral blood vessel; mc, midventral ciliary band; mvn, main ventral nerve; obm, oblique muscle; pmvn, paramedian ventral nerve; sg, salivary gland; vlm, ventral longitudinal muscle; vmlm, ventromedian longitudinal muscle. Transmission electron microscopy (TEM) micrograph by Isabel Dykstra, Osnabrück.

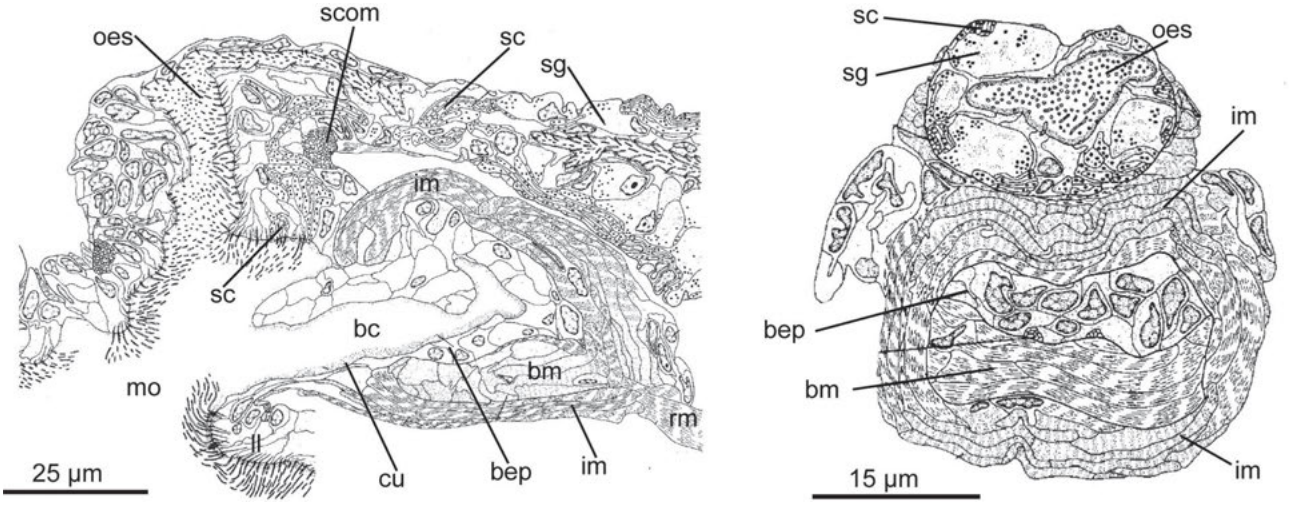


Fig. 7.11.4.6: Ventral pharynx. Schematic drawings of the ventral pharynx of *P. chaetifer.* A, Longitudinal section; B, Transverse section. bc, buccal cavity; bep, bulbus muscle epithelium; bm, bulbus muscle; cu, cuticle; im, investing muscle; mo, mouth; oes, esophagus; rm, retractor muscle; sc, salivary gland duct; scom, subesophageal commissure; sg, salivary gland. After Purschke and Jouin (1988).

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prolongations of the brain leading to groups of neuronal somata. The ventral nerve cord communicates with the brain via the circumesophageal connectives, which are split up into a prominent ventral root (Fig. 7.11.4.7B–D) and a minute dorsal root (Fig. 7.11.4.7C) (Müller 1999). The ventral nerve cord is constituted by two main nerve cords, which are widely separated from each other and accompanied by two minor paramedian nerve cords (Fig. 7.11.4.7C–F). Ganglia do not exist in the ventral cord, although the serotonergic and FMRFamidergic somata show a repetitive pattern (Fig. 7.11.4.7D, E) (Müller 1999). There are three main commissures in each segment accompanied by several indistinct smaller ones in *P. symbioticus* (Fig. 7.11.4.7F), whereas in *P. chaetifer* the former are not clearly set off and the two cords are connected by numerous small, more or less regularly arranged commissural nerves (Fig. 7.11.4.7D, E) (Müller 1999). Numerous segmentally arranged nerves innervate the periphery of each segment (Fig. 7.11.4.7F).

Sensory structures comprise numerous ciliated sensory cells of different types (Fig. 7.11.4.8A) (Purschke 1993). There are three main sense organs: the palps, the nuchal organs, and two pairs of unpigmented ciliary photoreceptor-like sense organs.

The palps are innervated by two nerves in *P. chaetifer* (vpn 1, 4; nomenclature following Purschke 1993) and three in *P. symbioticus* (vpn1, 3, 4) (Fig. 7.11.4.7B, C) composed of afferent and efferent fibers. In both species, the medial nerve (vpn4) (Fig. 7.11.4.7A, B) is the largest one and comprises more than 100 fibers originating from two roots coming from the dorsal and ventral parts of the brain. The other palp nerves are smaller and only consist of 5 to 25 fibers, branching off from the dorsal root of the circumesophageal connectives and situated more ventrally than the main palp nerve (vpn4).

Nuchal organs are small and more or less reduced; as typical of nuchal organs, they consist of supportive ciliated and bipolar sensory cells supplied by a retractor muscle (Purschke 1988, 1997). In *P. chaetifer*, they are visible as rounded spots anteromedially to a small band of peristomial cilia (Fig. 7.11.4.4A); in *P. symbioticus*, they are represented by two small ciliated papillae (Fig. 7.11.4.8A). The supportive ciliated cells are arranged as a single layer with basal interdigitating processes resting upon an ECM. Their microvilli form a dense cover above the olfactory chamber (Fig. 7.11.4.8B). The bipolar sensory cells occur as one cluster of about eight cells, arranged below the apical level of the ciliated supportive cells and forming one single olfactory chamber (Fig. 7.11.4.8B, C). The bipolar cells are uniciliated, the cilia of which are short and have a 9x2 + 0 axoneme (Fig. 7.11.4.8C, inset). In *P. symbioticus,* nuchal organs are reduced to rudimentary ciliated papillae, each papilla with only three ciliated cells, as well as one group of six sensory cells forming the olfactory chamber. As in Protodrilidae and most other polychaetes, the somata of the sensory cells form the nuchal ganglia and their axons form the nuchal nerves in both species.

The unpigmented ciliary photoreceptor-like organs are situated behind the neuropil of the brain and may easily be detected with staining against α-tubulin where they appear as donut-like structures (cso_2) (Fig. 7.11.4.7A–C) (Purschke and Müller 1996). Each organ comprises a multiciliated receptor cell and a glial-like supportive cell, which form an intercellular cavity into which the cilia project. In each organ, the long cilia are coiled and form a regular bundle of modified cilia. The 9x2 + 0 axoneme is transformed into a 3x1 axoneme immediately above the basal bodies (Fig. 7.11.4.8B–G). There are about 220 cilia in *P. chaetifer* and 120 cilia in *P. symbioticus*. This structure is unique for *Protodriloides* and has been discussed to represent an autapomorphy of the genus and family (Purschke 1993, Purschke and Müller 1996, Westheide 2008). In addition, there are so-called basal ciliated cells at the anterior edge of the neuropil and within the palps (cso_1) (Fig. 7.11.4.7B, C), which should not be mixed with the former. These possess a bundle of a few cilia twisted around the cell body of the receptor cell.

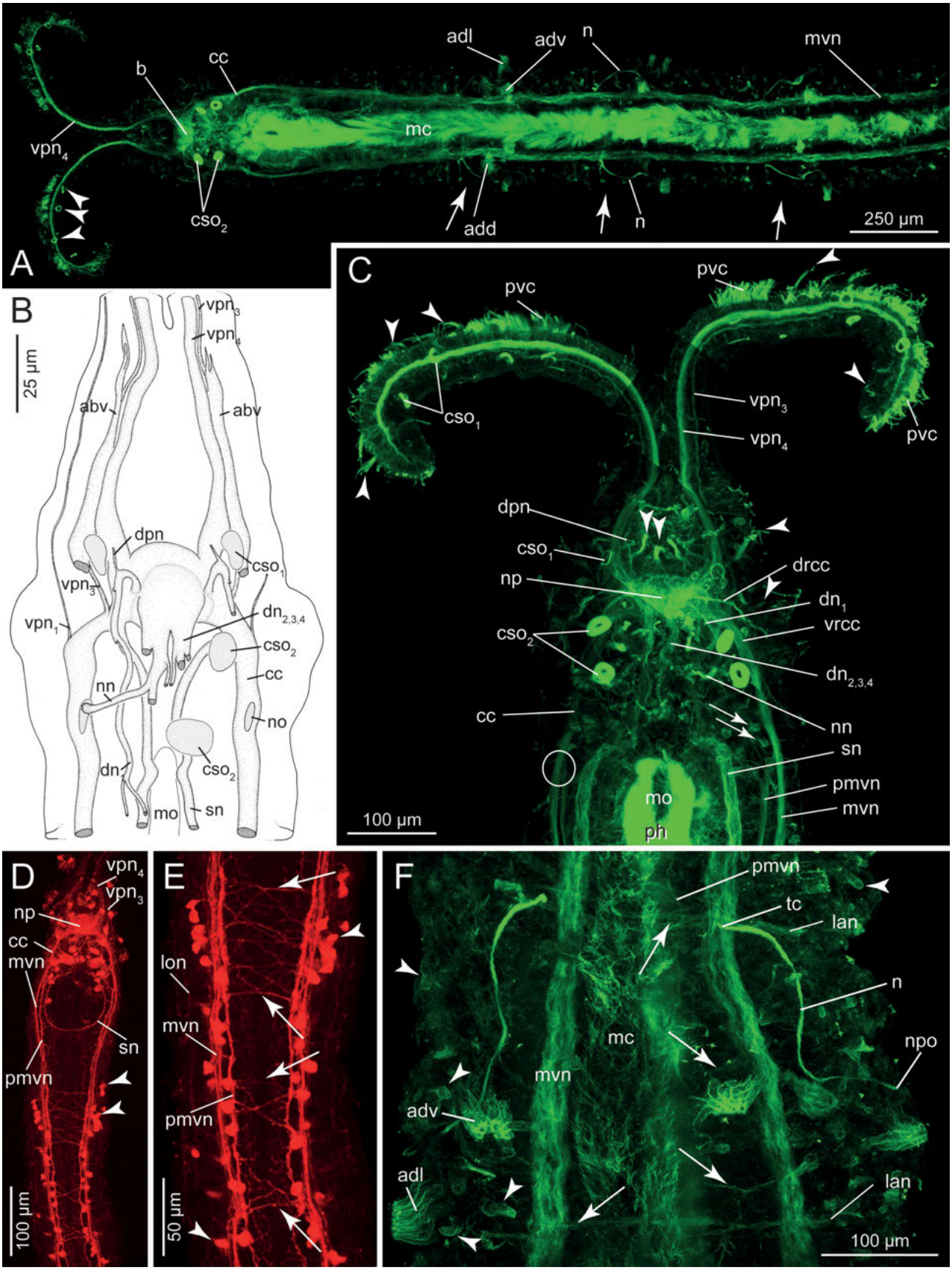
Reproduction, development, and life cycles

In Protodriloididae, reproduction and development have been studied by Swedmark (1954) and Jouin (1962, 1970, 1978–1979) and reviewed by Purschke (2006) and Westheide (2008). Sexes are separate, and in *P. chaetifer*, the fertile region extends from segment 20 to the pygidium, except for the last four to five segments; *P. symbioticus* comprises, in total, about 15 fertile segments starting around segment 7 (Figs. 7.11.4.1B, 7.11.4.3C). There are no genital organs, and the structure and arrangement of the fertile segments and gonads are comparable in both species. The eggs are fertilized inside cocoons after they are laid by the females, possibly by some kind of pseudocopulation. The development is direct, and it takes place inside the cocoon.

Males

Mature males lack external genital organs. Fertile segments are whitish due to the presence of sexual products and abundant epidermal glands containing small refractive granules (Jouin 1966). Each fertile segment contains the gonads on both sides of the gut. Spermatogonia and immature spermatids are concentrated in the anterior part of each segment, whereas the mature spermatozoa are packed toward the posterior end. Mature spermatozoa are rounded

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and aflagellated (Jouin 1978–1979, Westheide 2008), each consisting of a dense nucleus surrounded by a little cytoplasm without a distinct acrosome rather than with several acrosomal vesicles (Fig. 7.11.4.9A) (Jouin 1978–1979).

Spermioducts occur in every fertile segment (Jouin 1966) and consist of a fully ciliated tube, which originates in the posterior half of a fertile segment, crosses the incomplete septa, and continues to open in the body wall of the posterior segment. Gonopores are situated laterally in front of chaetae in *P. chaetifer* and ventrally at each side of the midventral ciliary band in *P. symbioticus* (Jouin 1966, Jouin 1978–1979).

Females

Mature females carry one to two large whitish oocytes on each fertile segment (Figs. 7.11.4.1B, 7.11.4.3C) (Swedmark 1954, Jouin 1966). Oocytes are comparatively large and full of yolk (Figs. 7.11.4.1B, 7.11.4.3C). They occur in the body cavity at one side of the gut. In females of both species, cocoon glands are present on the epidermis of fertile segments. Cocoon glands consist of longitudinal bands of rounded cells arranged close to each other and filled with small secretive granules (Jouin 1978–1979). These glands resemble those found in the protodrilid genus *Meiodrilus* Martínez, Di Domenico, Rouse & Worsaae, 2015 (Jägersten 1952, Martínez et al. 2015). Oviducts are absent and oocytes are released through rupture of the body wall, aided by the contraction of the longitudinal muscles (Jouin 1978–1979). Oocytes (10–17 in *P. chaetifer* and 4–10 in *P. symbioticus*) are laid inside transparent or brownish ovoid cocoons (400–700 µm long) with tapering extensions and jelly walls that stick to the sand grains (Fig. 7.11.4.10F).

Reproductive strategies and development

The reproductive period spans the entire year, although fertile individuals are more common in the summer period. Males discharge sperm cells directly on the cocoons, where fertilization is assumed to take place, although the exact mechanism remains unknown. After having entered the oocyte, the first and second meiotic divisions take place and the polar bodies are formed (Fig. 7.11.4.9B–D). Immediately thereafter, the first cleavage divisions start (Fig. 7.11.4.9E). Development is direct and takes place inside the cocoons (Fig. 7.11.4.10F). It lasts 10 to 20 days in *P. symbioticus* and up to 32 days or more in *P. chaetifer* (Swedmark 1954, Jouin 1962, Westheide 2008).

Our knowledge on the development of *Protodriloides* relies on laboratory observations done by Swedmark (1954) and Jouin (1962, 1970, 1978–1979) on *P. symbioticus* and *P. chaetifer*, respectively.

In *P. symbioticus*, the first cilia appear in the 2-day-old embryo (Fig. 7.11.4.10A), arranged in dorsal and ventral fields. Afterward, the prototroch appears. The endoderm and the ectoderm differentiate when the embryos reach 130 to 140 µm in length (Fig. 7.11.4.10B). This embryo already possesses two preoral ciliary rings, dorsally incomplete, and a midventral ciliary band. Subsequently, the body elongates posteriorly, and the pygidial lobes, provided with few adhesive glands, are differentiated. The mouth and the anus open when the embryos reach 200 to 250 µm in length, although the gut remains filled with yolk (Fig. 7.11.4.10C). The first pair of segmented adhesive organs and the epidermal glands appear at this stage. The juveniles leave the cocoon when they reach 300 to 350 µm in length (Fig. 7.11.4.10D). At this stage, the juveniles

◂ **Fig. 7.11.4.7**: Nervous system. A–C, F, *P. symbioticus*, anti-acetylated α-tubulin IR; D, E, *P. chaetifer*, anti-serotonin IR; A, Anterior end showing general organization of nervous system; brain (b) with main palp nerves (vpn_4), circumesophageal connectives, and main nerves of ventral cord (mvn). Ciliary sensory organs (cso_2; arrowheads), nephridia (n), and segmental dorsal, lateral, and ventral adhesive glands also labeled (add, adl, and adv, respectively); other nervous structures are masked by signal from midventral ciliary band (mc); arrows point to segment borders; B, Reconstruction of the neuropil of the brain, its main nerves, and the most important sense organs after TEM observations; C, CLSM image of anterior end with brain, main nerves, ciliary sense organs, receptor cells (arrowheads), and ventral ciliary band of palps (pvc); note split of circumesophageal connectives (cc) into paramedian (pmvn) and main ventral nerve (mvn) at the level of the mouth opening in front of the first ganglion (encircled); D, Brain, circumesophageal connectives, and ventral nerve cord and serotonin-like IR somata (arrowheads); E, Ventral nerve cord comprises main ventral nerve (mvn) and small paramedian trunk (pmvn); arrowheads point to a few serotonin-LIR somata, somata evenly distributed along the ventral cord; note numerous commissures with a gap between segments (arrows); a minute longitudinal nerve (lon) gives a faint signal; F, Enlargement of trunk region with one pair of nephridia (n), ventral nerve cord, midventral ciliary band (mc), segmental adhesive glands (adl, adv), nerve cord with a few commissures (arrows), and lateral nerves (lan); in the nephridia, the terminal cell (tc) and the pore (npo) can be recognized; arrowheads point to gland cell openings, the fuzzy signal comes from the cilia of the digestive tract. abv, anterior blood vessel; add, dorsal adhesive gland; adl, lateral adhesive gland; adv, ventral adhesive gland; b, brain; cc, circumesophageal connective; $cso_{1,2}$, ciliary sensory $organ_{1,2}$; $dn_{1,2,3,4}$, dorsal $nerves_{1,2,3,4}$; dpn, dorsal palp nerve; drcc, dorsal root of circumesophageal connective; lan, lateral nerve; lon, longitudinal nerve; mc, midventral ciliary band; mo, mouth; mvn, main ventral nerve; n, nephridium; nn, nuchal nerve; no, nuchal organ; np, neuropil; npo, nephropore; ph, pharynx; pmvn, paramedian ventral nerve; pvc, ventral ciliary band of palp; sn, stomatogastric nerve; tc, terminal cell; $vpn_{1,2,3,4}$, ventral palp $nerve_{1,2,3,4}$; vrcc, ventral root of circumesophageal connective. B, From Purschke (1993). CLSM micrographs: Corinna Stühmeier, Osnabrück.

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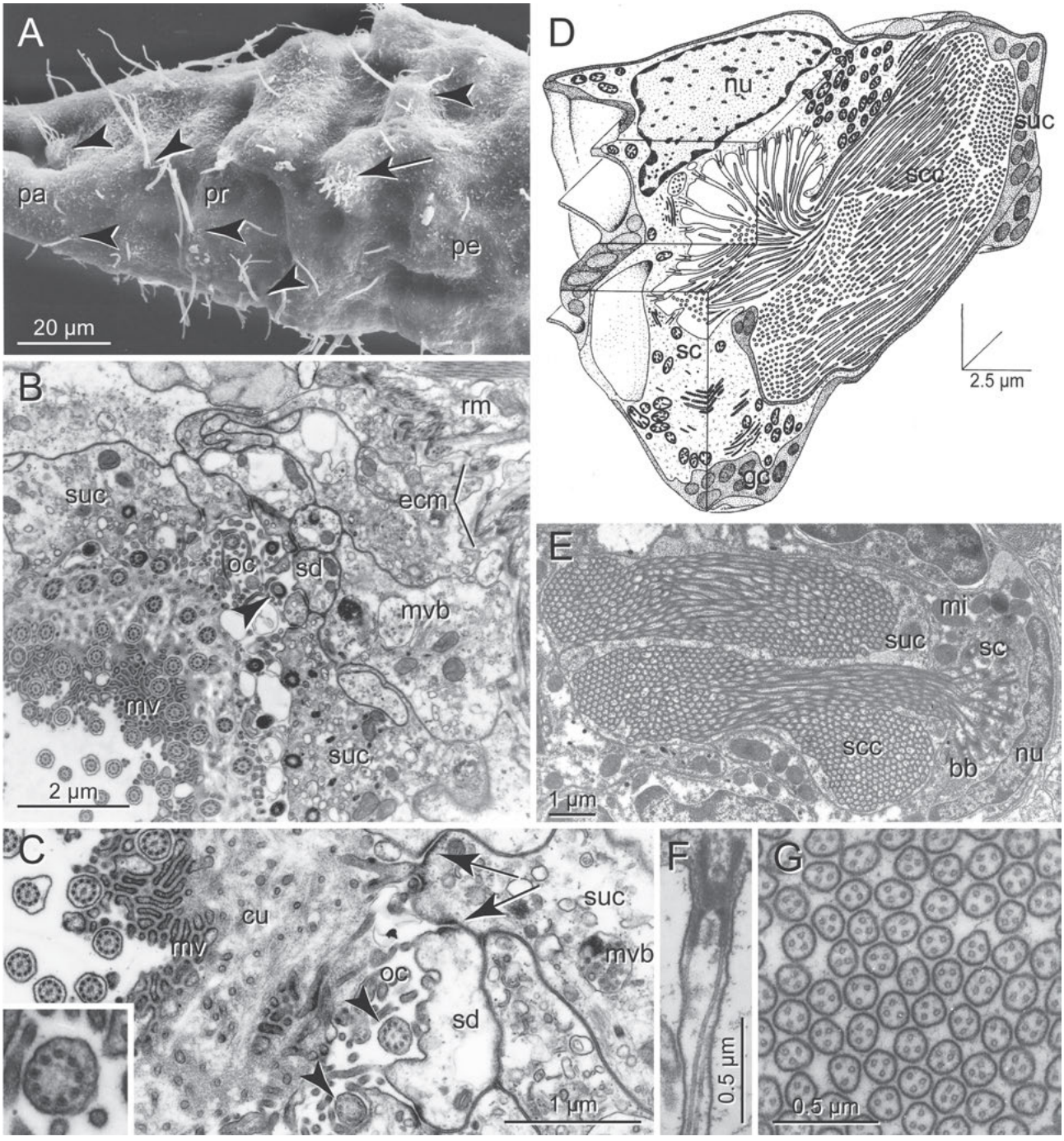


Fig. 7.11.4.8: Sense organs. A, *P. symbioticus*, anterior end, palp bases (pa), prostomium (pr), and peristomium (pe) in dorsolateral view with numerous cilia of different types of sensory cells (arrowheads) and nuchal organs (arrow); B, C, *P. chaetifer*, nuchal organ; B, Supportive cells (suc) resting on ECM (ecm) and retractor muscle (rm). Olfactory chamber (oc) with sensory cilia (arrowhead) and other processes. Tips of microvilli (mv) flattened forming dense apical cover; C, Sensory dendrites (sd), olfactory chamber (oc), cuticle (cu), and microvillar cover (mv), arrows point to junctional complexes, arrowhead point to sensory cilia, and inset shows sensory cilium with 9x2 + 0 axoneme; D–G, Unpigmented ciliary photoreceptor-like organ; D, F, G, *P. chaetifer*; D, Reconstruction of ciliary sense organ from TEM observation, organ comprises one multiciliated sensory cell (sc) and one glial supportive cell (suc) forming an extracellular cavity into which numerous sensory cilia project, these are rolled up several times; E, Exemplified section through an organ of *P. symbioticus*, cavity densely filled with sensory cilia (scc), basal bodies (bb) without ciliary rootles; F, Longitudinal section through basal part of sensory cilium showing a decrease of diameter and reduction of axoneme; G, Cross-section of sensory cilia cut distally showing 3x1 axoneme. bb, basal body; cu, cuticle; ecm, ECM; mi, mitochondrion; mv, microvillus; mvb, multivesicular body; nu, nucleus; oc, olfactory chamber; pa, palp; pe, peristomium; pr, prostomium; rm, retractor muscle; sc, sensory cell; scc, sensory cilium; sd, sensory dendrite; suc, supportive cell. A, SEM; B, C, E–G, TEM micrographs; D, After Purschke and Müller (1996).

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resemble the adults, apart from the lack of palps. Those start budding off from the prostomium when the juveniles reach a length of 400 µm (Fig. 7.11.4.10E). The development of the pharynx is complete in juveniles about 450 µm long. At this stage, the palps bud off laterally from the prostomium (Swedmark 1954).

The development of *P. chaetifer* resembles that described for *P. symbioticus,* but juveniles remain longer within the cocoon (Jouin 1962, 1970, 1978–1979). Four-day-old embryos already start moving inside the cocoons (Fig. 7.11.4.10F). After 13 days, when they reach 350 µm in length, the midventral ciliary band is well developed. They hatch within the cocoon at the 15-day-old stage when the palps and pygidial lobes are budding off and the mouth and the anus are formed, although the gut remains filled with yolk. The hatched 18-day-old juveniles (Fig. 7.11.4.10G) possess ciliated palps and greenish glands, mostly around the head and the pygidium. Segmentation becomes obvious in the 20-day-old juveniles (Fig. 7.11.4.10H), presenting a prostomium and six segments. The esophagus differentiates at this stage but remains filled with vitellus. The green glandular inclusions of the epidermis are very abundant. The juveniles leave the cocoon after 25 days (Fig. 7.11.4.10I), when the animals are about 800 µm long and possess well-developed palps and esophagus as well as chaetae and longitudinal muscles. The pharynx starts to develop in the first segment, which anteriorly will fuse with the prostomium, forming the "head" of the adult.

Motility, feeding, and habitat preferences

All Protodriloididae are interstitial marine animals and glide through the spaces between sand grains aided by the midventral ciliary band (Westheide 2008). The body is very contractile, and it can extend twice the relaxed body length (Pierantoni 1908). While gliding, changes in direction are done using the pygidial and the adhesive glands, which are also involved in anchoring the animals to the sand grains (Pierantoni 1908).

Protodriloididae are subsurface deposit feeders. They graze on microorganisms growing on the surfaces of the sand grains (Fauchald and Jumars 1979, Westheide 2008) by the combined action of the ciliation around the mouth and the muscular pharynx covered by a dentate cuticle (see above) (Purschke and Jouin-Toulmond 1993).

Protodriloididae prefer coarse to medium-coarse sandy sediments (Wolff et al. 1980, Westheide 2008). The two species normally do not co-occur in the same samples or their distribution ranges have only a slight overlap. The larger species, *P. chaetifer*, usually occurs in the beach slope of medium- and high-energy beaches, with only a slight extension into tidal flat areas, whereas *P. symbioticus* is a typical member of tidal flats where it settles on the uppermost sediment layers, often in high numbers (Schmidt 1969, Wolff et al. 1980, Westheide 2008, Purschke unpublished observation). However, some sublittoral records exist (Worsaae unpublished observation). The abundance of *P. symbioticus* has been reported to reach densities of more than 1,000 individuals per 100 cm^3 (Schmidt 1969, Wolff et al. 1980, Westheide 2008). *P. chaetifer* is less abundant and may reach a maximum of about 20 individuals per 100 cm^3. Other records mentioned up to 170 individuals per 100 cm^3 (Westheide 2008). However, it may be found in the entire beach slope up to the high tide level and down to the groundwater (Meineke and Westheide 1979) and may be a vertical migrator following the water level of the tides like several interstitial annelids such as *Hesionides arenaria* Friedrich, 1937 and the protodrilid *Meiodrilus adhaerens* (Jägersten, 1952). These

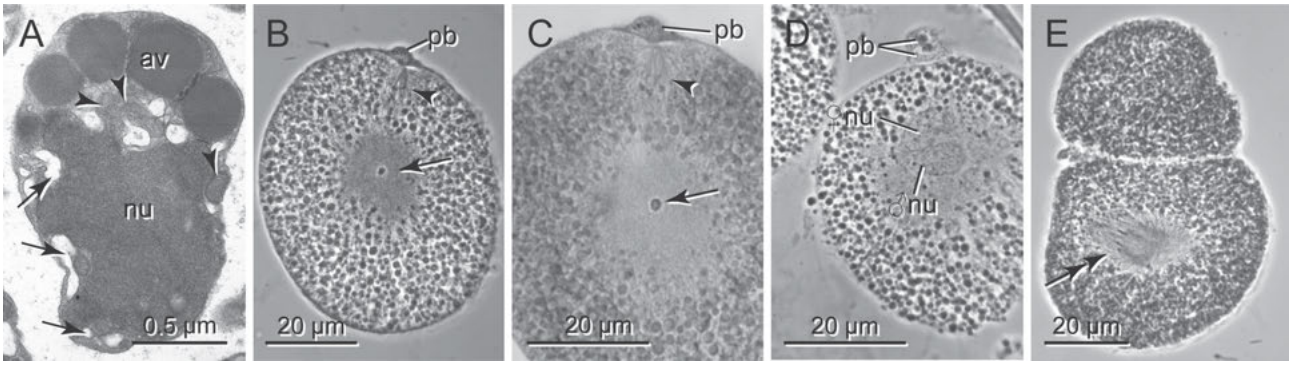


Fig. 7.11.4.9: Gametes and fertilization. *P. symbioticus*. A, Aflagellate spermatozoon, arrows: vacuoles, arrowheads: mitochondria, TEM; B, Formation of first polar body (pb) and male pronucleus (arrow), oocyte chromosomes (arrowhead); C, Formation of spindle apparatus of second meiotic division (arrowhead) and first polar body (pb), arrow points to male pronucleus; D, Second polar body formed; male and female pronuclei (nu) still separate; E, First cleavage and formation of spindle apparatus of second cleavage (double arrow). av acrosomal vesicle, nu nucleus, pb polar body. Micrographs courtesy of Claude Jouin-Toulmond, Roscoff.

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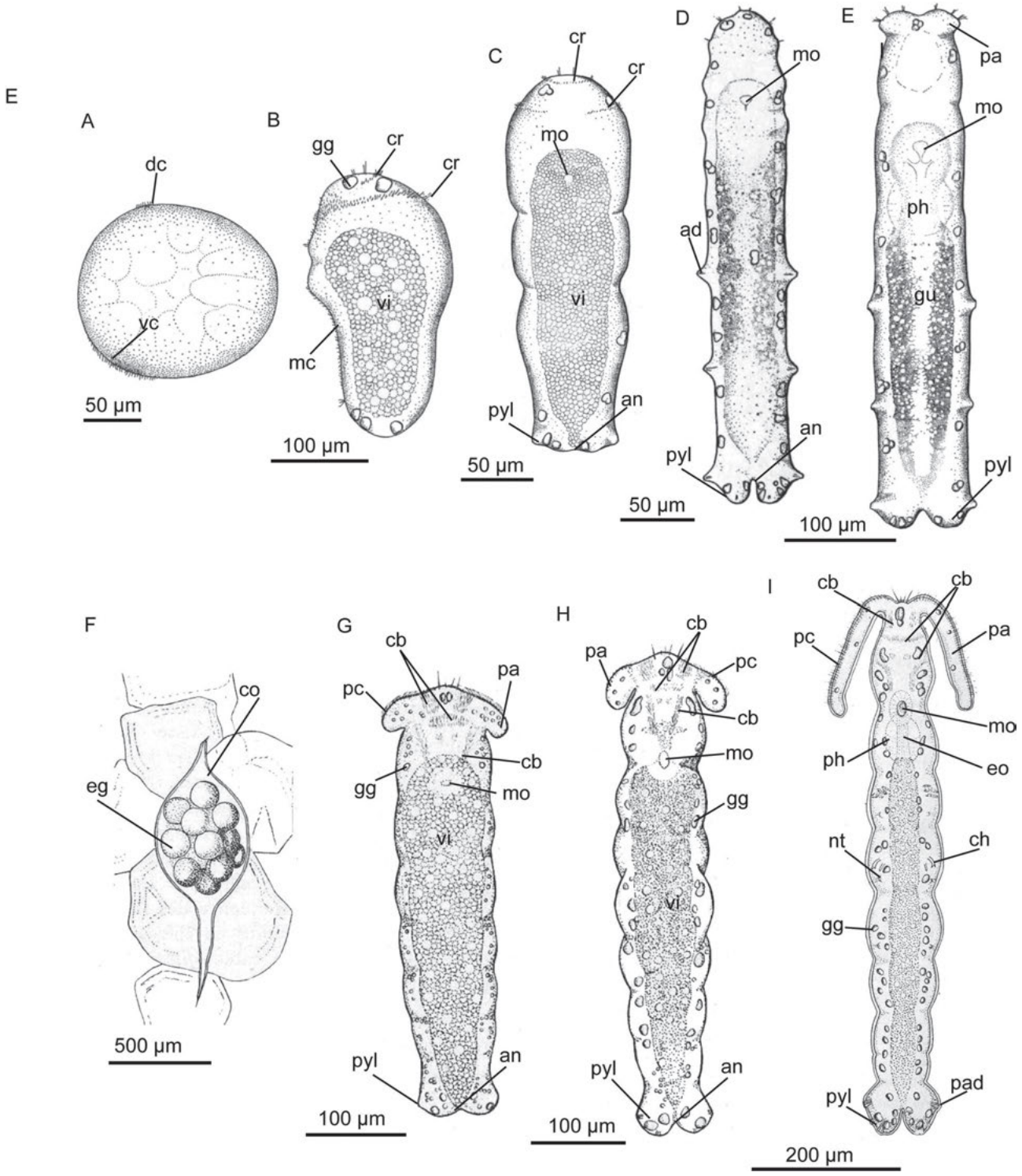


Fig. 7.11.4.10: Development. A–E, *P. symbioticus*; F–I, *P. chaetifer*; A, 110 µm embryo outside the cocoon, lateral view; B, 135 µm embryo view; C, 235 µm embryo, dorsal view; D, 340 µm embryo, dorsal view; E, 450 µm juvenile; F, Cocoon containing developing eggs adhered to the sand grains; G, 18-day-old embryo, dorsal view; H, 20-day-old embryo, dorsal view; I, 25-day-old juvenile stage just after leaving the cocoon, dorsal view. ad, adhesive gland; an, anus; cb, ciliary band; ch, chaeta; co, cocoon; cr, ciliary ring; dc, dorsal cilia; gg, green gland; gu, gut; eg, egg; eo, esophagus; mc, midventral ciliary band; mo, mouth; pa, palp; pc, ventral palp ciliary band; pad, pygidial adhesive gland; ph, pharynx; pyl, pygidial lobe; vc, ventral cilia; vi, vitellin. A–E, After Swedmark (1954); F–I, After Jouin (1962).

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species follow the changes in pore water content and may thus avoid harsher environmental conditions such as temperature and salinity changes during exposure of the beach to the air.

Laboratory experiments have shown that the distribution of *P. symbioticus* at different spatial scales depends on a combination of biotic and abiotic factors. At mesoscale (scale of meters), substrate selection depends on the presence of specific bacterial communities and biofilms on the grains (Gray 1966a), whereas distribution at microscale (scale of centimeters) is affected by oxygen concentration, light intensity, and temperature. The preference of *P. symbioticus* to highly oxygenated water attracts the animals to the surface of the sediment column (Gray 1966b). However, because the species prefers temperature at about 15°C, higher or lower temperatures favor the migration of the individuals toward deeper sediment layers (Gray 1965). The tolerance against low temperatures is comparatively low as in other inhabitants of tidal flats compared to those of the beach slope, which show higher tolerance levels (Purschke 1981). Similarly, individuals show photonegative klinokinesis and most of them prefer light intensities of 040-3013 lux, equivalent to the levels found 2 to 8 mm below the sediment surface (Gray 1966c).

Systematics

The first known protodriloidid, *P. symbioticus*, was described by Giard (1904) as a *Protodrilus* possessing unique greenish epidermal inclusions that he interpreted as symbiotic unicellular algae (Giard 1904). This initial description was later completed by Pierantoni (1908). He described the behavior of the species and provided several anatomical features, highlighting important differences between *P. symbioticus* and other described protodrilids as well as raising doubts on the symbiotic nature of the greenish epidermal inclusions (Pierantoni 1908). *P. chaetifer* was described about 20 years later by Remane (1926) from Helgoland (Germany). Both species have now been reported across wide geographic ranges (see distributions given below), but no molecular or detailed morphological studies have yet tested these identifications, some of which may in fact represent undescribed species. According to molecular random amplified polymorphic DNA data, *P. chaetifer* is a complex of at least four cryptic species, one of which comprises the European populations (Schmidt 1998).

Protodriloididae Purschke & Jouin, 1988
Protodriloides (Jouin, 1966)

Diagnosis: Body elongated and flattened with a midventral ciliary band. Prostomium with two anterior palps lacking internal canals. Unpigmented prostomial receptors (so-called statocysts) and pigmented eyes as present in *Protodrilus* absent. Two pairs of specific ciliary photoreceptor-like sense organs behind the brain, invisible with light microscopy. Pharyngeal organ with bulbous and sagittal muscles as well as interstitial cells but without tongue-like organ. Salivary glands indistinct on the esophageal epithelium, not visible under light microscopy. Epidermis with green glands. Pygidium with two rounded adhesive lobes. Fertile segments in the posterior half of the body. Males without lateral organs and with spermioducts in each fertile segment. Spermatozoa round and aflagellate. Large yolky eggs laid in cocoons produced by female cocoon glands. Fertilization and direct development inside the cocoon.

Type species: *Protodriloides symbioticus* (Giard, 1904)

Distribution and habitat: *Protodriloides* consists of two described species recorded around the world, although most of the records come from Europe.

Protodriloides symbioticus (Giard, 1904). Type locality: Ambleteuse, France (Giard 1904). Additional records: northeast Atlantic Ocean (Pierantoni 1908, Remane 1926, Swedmark 1954, Gray 1965, 1966a, b, c, d, Jouin 1966, 1968, Westheide 1966, Boaden 1976, von Nordheim 1984, Purschke and Jouin 1988, Purschke 1988, 1993, Besteiro et al. 2016), northwest Atlantic Ocean (Hamond 1972), and Mediterranean Sea (as *Protodriloides* sp.) (Westheide 1972).

Protodriloides chaetifer (Remane, 1926). Type locality: Helgoland, Germany. Additional records: northeast Atlantic Ocean (Remane 1926, Boaden 1962, 1963, 1976, Jouin 1962, 1966, 1968, Renaud-Debyser and Salvat 1963, Renaud-Debyser 1964, Westheide 1966, von Nordheim 1984, Purschke and Jouin 1988, Purschke 1988, 1993, Besteiro et al. 2016), Mediterranean Sea (Bellan 1964), northwestern Atlantic Ocean (Fransen 1980), Arctic Ocean (Kristensen and Nørrevang 1982, Mastepanova 2004), Pacific Ocean (Wieser 1957, Riser 1984). A record from New Zealand by Riser (1984) may also represent *P. chaetifer*.

References

Andrade, S.C., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution*: msv157.

Bellan, G. (1964): *Contribution à l'*étude systématique, bionomique et écologique des Annélides Polychètes de la Méditerrannée. Université d'Aix-Marseille: 1–371.

Besteiro, C., Eugenio, W., Henrique Carvalho, L., Veiga, P. & Rubal, M. (2016): Contributions to the autoecology and biogeography of some psammic species of Annelida Polychaeta from Galicia (north-west Iberian Peninsula). *Cahiers de Biologie Marine* 57: 253–259.

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Boaden, P.J.S. (1962): Colonization of graded sand by an interstitial fauna. *Cahiers de Biologie Marine* 3: 245–248.

Boaden, P.J.S. (1963): The interstitial fauna of some North Wales beaches. *Journal of Marine Biology Association of the United Kingdom* 43: 79–96.

Boaden, P.J.S. (1976): Soft meiofauna of sand from the delta region of the Rhine, Meuse and Scheldt. *Netherlands Journal of Sea Research* 10: 461–471.

Di Domenico, M., Martínez, A., Lana, P. & Worsaae, K. (2014): Molecular and morphological phylogeny of Saccocirridae (Annelida) reveals two cosmopolitan clades with specific habitat preferences. *Molecular Phylogenetics and Evolution* 75: 202–218.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marina Biology Annual Reviews* 17: 193–284.

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. 1. Archiannelids and other small polychaetes. *Zoomorphologie* 95: 235–249.

Giard, A. (1904): Sur une faunule caracteristique des sables a Diatomées d'Ambleteuse. *Comptes rendus des séances de la Société de Biologie* 56: 295–298.

Gray, J.S. (1965): The behaviour of *Protodrilus symbioticus* (Giard) in temperature gradients. *Journal of Animal Ecology* 34: 455–461.

Gray, J.S. (1966a): The attractive effect factor of intertidal sands to *Protodrilus symbioticus*. *Journal of Marine Biology Association of the United Kingdom* 46: 627–645.

Gray, J.S. (1966b): Factors controlling the localizations of populations of *Protodrilus symbioticus* Giard. Journal of Animal Ecology 35: 435–442.

Gray, J.S. (1966c): The response of *Protodrilus symbioticus* (Giard) (Archiannelida) to light. *Journal of Animal Ecology* 35: 55–64.

Gray, J.S. (1966d): Selection of sands by *Protodrilus symbioticus* Giard. *Veröffentlichungen des Institut für Meeresforschung, Bremerhaven* II: 105–116.

Hamond, R. (1972): The non-polychaetous annelids of Norfolk, England, with additional notes on Polychaetes. *Cahieres de Biologie Marine* 13: 341–350.

Hatschek, B. (1881): *Protodrilus leuckartii*. Eine neue Gattung Archianneliden. *Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 3: 79–93.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Jouin, C. (1962): Le développement larvaire de *Protodrilus chaetifer* Remane (Archiannelida). *Comptes rendus Academie des Sciences Paris* 255: 3065–3067.

Jouin, C. (1966): Morphologie et anatomie comparée de *Protodrilus chaetifer* Remane et *Protodrilus symbioticus* Giard, création du nouveau genre *Protodriloides* (Archiannélides). *Cahiers de Biologie Marine* 7: 139–155.

Jouin, C. (1968): Annélides. Inventaire de la Faune. In: Cabioch, L., L'Hardy, J.P. & Rullier, F. (eds.). *Editions de la Station Biologique de Roscoff*, Roscoff: 1–94.

Jouin, C. (1970): *Recherches sur les archiannélides interstitielles: Systématique, anatomie et développement des Protodrilidae et des Nerillidae*. Thèse Doctorat d'État, Université P. et M. Curie, Paris: 212 pp.

Jouin, C. (1978a): Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida) I. Muscle and myo-epithelial junctions. *Tissue & Cell* 10: 269–287.

Jouin, C. (1978b): Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Archiannelida) II. The stomodeal epithelium and its cuticle. *Tissue & Cell* 10: 289–301.

Jouin, C. (1978–1979): Spermatozoïde non flagellé et fécondation externe chez *Protodriloides symbioticus* (Giard) (Annélides Polychètes, Archiannélides). *Vie et Milieu* 28–29: 473–487.

Jägersten, G. (1952): Studies on the morphology, larval development and biology of *Protodrilus*. *Zoologische bijdragen Uppsala* 29: 425–512.

Kristensen, M.R. & Nørrevang, A. (1982): Description of *Psammodrilus aedificator* sp. n. (Polychaeta), with notes on the Arctic interstitial fauna of Disko Island, W. Greenland. *Zoologica Scripta* 11: 265–279.

Martínez, A., Di Domenico, M., Rouse, G. & Worsaae, K. (2015): Phylogeny of Protodrilidae (Annelida) inferred by total evidence analyses. *Cladistics* 31: 250–276.

Mastepanova, E.A. (2004): The interstitial Polychaeta of Russian Seas. *Invertebrate Zoology* 1: 59–64.

Meineke, T. & Westheide, W. (1979): Gezeitenabhängige Wanderungen der Interstitialfauna in einem Sandstrand der Insel Sylt (Nordsee). *Mikrofauna des Meeresbodens* 75: 1–36.

Müller, M.C. (1999): *Das Nervensystem der Polychaeten: Immunhistochemische Untersuchungen an ausgewählten Taxa*. Ph.D. thesis, University of Osnabrück: 1–402.

Orrhage, L. (1974): Über die Anatomie, Histologie und Verwandtschaft der Apistobranchidae (Polychaeta, Sedentaria) nebst Bemerkungen über die systematische Stellung der Archianneliden. *Zeitschrift für Morphologie und Ökologie der Tiere* 79: 1–45.

Pierantoni, U. (1908): *Protodrilus*. *Fauna Flora Golf, Neapel* 31: 1–226.

Purschke, G. (1981): Tolerance to freezing and supercooling of interstitial Turbellaria and Polychaeta from a sandy tidal beach of the Island of Sylt (North Sea). *Marine Biology* 63: 257–267.

Purschke, G. (1988): Comparative electron microscopic investigations of the nuchal organs in *Protodriloides*, *Protodrilus*, and *Saccocirrus* (Annelida, Polychaeta). *Canadian Journal of Zoology* 68: 325–338.

Purschke, G. (1993): Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology* 113: 1–20.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2006): Problematic annelid groups. In: Rouse, G.W. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida* Vol. 4 Science Publishers, Enfield, Jersey, Plymouth: 639–667.

Purschke, G. & Jouin, C. (1988). Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationships within Protodrilida (Annelida: Polychaeta). *Journal of Zoology* 215: 405–432.

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Purschke, G. & Jouin-Toulmond, C. (1993): Ultrastructure of presumed ocelli in *Parenterodrilus taenioides* (Polychaeta, Protodrilidae) and their phylogenetic significance. *Acta Zoologica (Stockholm)* 74: 247–256.
Purschke, G. & Müller, M.C. (1996): Structure of prostomial photoreceptor-like sense organs in *Protodriloides* species (Polychaeta, Protodrilida). *Cahiers de Biologie Marine* 37: 205–219.
Remane, A. (1926): Protodrilidae aus Ost- und Nordsee. *Zoologischer Anzeiger* 67: 119–125.
Remane, A. (1932): Archiannelida. In: Grimpe, G. & Wagler, G. (eds.), *Die Tierwelt der Nord- und Ostsee*. Akademische Verlagsgesellschaft, Leipzig: 1–36.
Renaud-Debyser, J. (1964): Note sur la fauna interstitielle du bassin d'Arcachon et description d'un gastrotriche nouveau. *Cahieres de Biologie Marine* 5: 111–123.
Renaud-Debyser, J. & Salvat, B. (1963): Elements de prospérité des biotopes des sediments meubles intertidaux et ecologie de leurs populations en microfaune et macrofaune. *Vie et Milieu* 14: 463–550.
Riser, N.W. (1984): General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239–250.
Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.
Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford.
Schmidt, H. (1998): *Molekulargenetische Untersuchungen (RAPD-PCR) an kosmopolitischen Meiofauna-Polychaeten*. Ph.D. thesis. University of Osnabrück.
Schmidt, P. (1969): Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordsee-Insel Sylt. II: Quantitative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobiologie* 54: 95–174.
Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.
Swedmark, B. (1954): Etude du développement larvaire et remarques sur la morphologie de *Protodrilus symbioticus* Giard (Archiannélides). *Arkiv för Zoologi* 6: 511–522.
von Nordheim, H. (1984): Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchugen* 38: 1–20.
Westheide, W. (1966): Zur Polychaetenfauna des Eulitorals der Nordseeinsel Sylt. *Helgoländer Meeresuntersuchugen* 13: 203–209.
Westheide, W. (1972): La faune des Polychetes et des Archiannelides dans les plages sableuses a ressac de la côte mediterranée de la Tunisie. *Bulletin Institute Océanographique Pêche, Salammbô* 2: 449–468.
Westheide, W. (1984): The concept of reproduction in polychaetes with small body size: Adaptations in interstitial species. *Fortschritte der Zoologie* 29: 265–287.
Westheide, W. (1985): The systematic position of the Dinophiliidae and the Archiannelid problem. In: Morris, C.S., George, D., Gibson, R. & Platt, H.M. (eds.). *The Origins and Relationships of Lower Invertebrates*. Oxford University Press, Oxford: 310–326.
Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21: 843–854.
Westheide, W. (2008): *Polychaetes: Interstitial Families. Synopses of the British Fauna (New Series)*, no. 44, 2nd ed. The Linnean Society of London, London: 1–169.
Wieser, W. (1957): Archiannelids from the intertidal of Puget Sound. *Transactions of the American Microscopical Society* 76: 275–285.
Wolff, W.J., Sandee, A.J.J. & Stegenga, H. (1980): The Archiannelida of the estuarine area of the rivers Rhine, Meuse and Scheldt, with some remarks on the ecology. *Netherlands Journal of Sea Research* 14: 94–101.
Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). *Hydrobiologia* 535: 319–340.
Zrzavy, J., Riha, P., Pialek, L., & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

7.12 Errantia: Eunicida

Nataliya Budaeva and Joana Zanol

7.12.1 Eunicida Dales, 1962

Introduction and phylogeny

The name Eunicida was introduced by Dales (1962) for a group of polychaete families previously known as superfamily Eunicea (Ehlers 1868, Hartman 1944), order Eunicemorpha (Uschakov 1955), or family Eunicidae (Fauvel 1923). Eunicidans comprise a well-defined group of recent and extinct polychaete families possessing a ventral muscular pharynx with mineralized or sclerotized jaws (Tzetlin and Purschke 2005). Their oldest records date from the latest Cambrian (ca. 488 Ma) (Williams et al. 1999, Hints and Eriksson 2007). These are remains of jaw apparatuses and isolated jaw pieces, so-called scolecodonts (worm jaws). The recent fauna of Eunicida, following Paxton (2000) and Rouse and Pleijel (2001), includes approximately 1000 species belonging to 100 genera grouped in seven families: Dorvilleidae Chamberlin, 1919; Eunicidae Berthold, 1827; Hartmaniellidae Imajima, 1977; Histriobdellidae Vaillant, 1890; Lumbrineridae Schmarda, 1861; Oenonidae Kinberg, 1865; and Onuphidae Kinberg, 1865. The extinct fauna includes 18 families known just by the jaw apparatuses (Tab. 7.12.1.1).

The complex jaw apparatus of eunicidans comprises dorsal maxillae and ventral mandibles — cuticular elements consisting of scleroprotein, in some families

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associated with calcium carbonate (Colbath 1987). Mandibles are represented by paired more-or-less fused elongated structures of proximal shafts widening distally into cutting plates (Fig. 7.12.1.1). They are relatively similar in all eunicidans and are believed to grow throughout life (Paxton 1986, Colbath 1987). Orensanz (1990) recognized three types of mandibles: the oenonid-dovilleid type (Fig. 7.12.1.1A) is unmineralized and black in color with unfused or slightly connected left and right parts lacking calcified distal plates, the lumbrinerid type (Fig. 7.12.1.1B) is almost completely fused with growing rings on the distal plates, and the eunicid-onuphid type (Fig. 7.12.1.1C) is partly fused anteriorly with calcified cutting plates. Several types of maxillary apparatuses have been distinguished in recent and extinct families, differing from each other in morphology, number of elements and rows, arrangement, and mineral composition of elements (Kielan-Jaworowska 1966, Orensanz 1990, Tzetlin and Purschke 2005, Paxton 2009). At least in onuphids, dorvilleids, and eunicids, sets of maxillae periodically shed and replace each other in ontogeny (Paxton 2005, 2006, Paxton and Safarik 2008, Paxton and Eriksson 2012). Currently, six major types of maxillae are recognized. Placognath (plate-jaw) maxillae are found exclusively in extinct families from the Paleozoic (Tab. 7.12.1.1). They lack carriers and have plate-like elements with two rows of denticles (Fig. 7.12.1.2A) (Kielan-Jaworowska 1966, Paxton 2009). Dorvilleidae and few extinct families (Tab. 7.12.1.1) carry ctenognath (comb-jaw) maxillae lacking carriers and having plate-like elements with four or more rows of denticles (Fig. 7.12.1.2B) (Kielan-Jaworowska 1966, Paxton 2009). Symmetrognath (symmetrical-jaw) maxillae (sensu Paxton 2009) are found in extant Lumbrineridae and Hartmaniellidae, which have short to moderately long stout carriers and symmetrical number of dentate elements (Fig. 7.12.1.2C). A number of extinct families possessed labidognath (pincer-jaw) maxillae, which are differentiated from symmetrognath mainly by right MxI reduced to basal plate (but still present as a separate element) and asymmetrical number of dentate elements (Fig. 7.12.1.2D) (Ehlers 1868, Struck et al. 2006). Paxton (2009) suggested a new type of labidognath jaws, so-called eulabidognath, found in extinct Paulinitidae and extant Onuphidae and Eunicidae. Eulabidognath jaws have a right MxI reduced

Tab. 7.12.1.1: Types of maxillae described for Eunicida, families in which they have been registered and the oldest known record for these families. In bold, extant families; ?, questionable record; —, no recognized fossil; *, jaw type questionable; #, jaw originally described as xenognath. [1]Paxton (2009). [2]Hints and Eriksson (2007). [3]Van Erve (1981). [4]Szaniawski and Wrona (1973). [5]Thompson and Johnson (1977). [6]Kozur (1970). [7]Szaniawski and Imajima (1996). [8]Mierzejewski (1984).

Jaw Type[1]	Family	Period of Oldest Known Fossil
Ctenognatha	Archaeoprionidae Mierzejewski & Mierzejewska, 1975*,#	Middle Ordovician (470–458 Ma)[2]
	Dorvilleidae	Early Jurassic (191–174 Ma)[3]
	Tetraprionidae Kielan-Jaworowska, 1966	?Late Cambrian (490–485 Ma)/Middle Ordovician (470–458 Ma)[2]
Labidognatha	Hadoprionidae Eriksson & Bergman, 1998	Late Ordovician (458–444 Ma)[2]
	Kalloprionidae Kielan-Jaworowska, 1966	Late Ordovician (458–444 Ma)[2]
	Kielanoprionidae Szaniawski, 1968	Late Devonian (363–359 Ma)[4]
	Polychaetaspidae Kielan-Jaworowska, 1966	Middle Ordovician (470–458 Ma)[1]
	Polychaeturidae Kielan-Jaworowska, 1966	Middle Ordovician (470–458 Ma)[2]
	Ramphoprionidae Kielan-Jaworowska, 1966	Middle Ordovician (470–458 Ma)[2]
	Tretoprionidae Hints, 1999	Late Ordovician (458–444 Ma)[2]
Eulabidognatha	**Eunicidae**	Carboniferous Pensilvanian (323–299 Ma)[5]
	Onuphidae	Late Triassic (237–201 Ma)[6]
	Paulinitidae Lange, 1947	Late Ordovician (458–444 Ma)[2]
Symmetrognatha	Conjungaspidae Hints, 1999	Early Ordovician (485–470 Ma)[2]
	Hartmaniellidae	Late Carboniferous Pensilvanian (307–299 Ma)[7]
	Lumbrineridae	—
	Symmetroprionidae Kielan-Jaworowska, 1966	Late Ordovician (458–444 Ma)[2]
Placognatha	Mochtyellidae Kielan-Jaworowska, 1966	Early Ordovician (485–470 Ma)[2]
	Rhytiprionidae Kielan-Jaworowska, 1966	Middle Ordovician (470–458 Ma)[2]
	Xanioprionidae Kielan-Jaworowska, 1966	?Late Cambrian (490–485 Ma)/Early Ordovician (485–470 Ma)[2]
Prionognatha	Atraktoprionidae Kielan-Jaworowska, 1966	Middle Ordovician (470–458 Ma)[2]
	Histriobdellidae*	—
	Oenonidae	Middle Silurian (433–427 Ma)[8]
	Skalenoprionidae Kielan-Jaworowska, 1966	Late Ordovician (458–444 Ma)[2]

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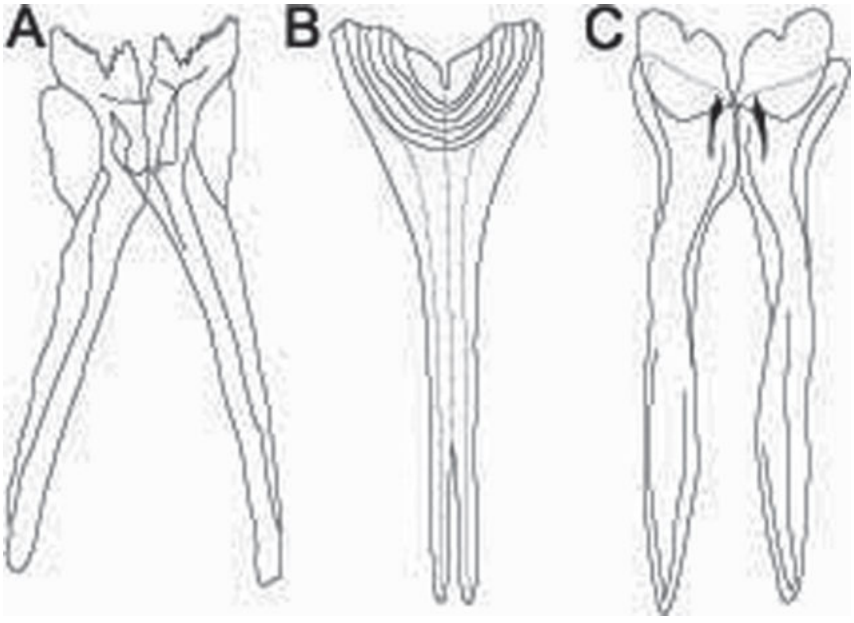


Fig. 7.12.1.1: Examples of mandibles in Eunicida families. A, Dorvilleidae: *Ophryotrocha adherensis* (modified from Paavo et al. 2000); B, Lumbrineridae: *Errano* sp. (modified from Budaeva 2005); C, Onuphidae: *Paradiopatra fauchaldi* (modified from Budaeva 2008).

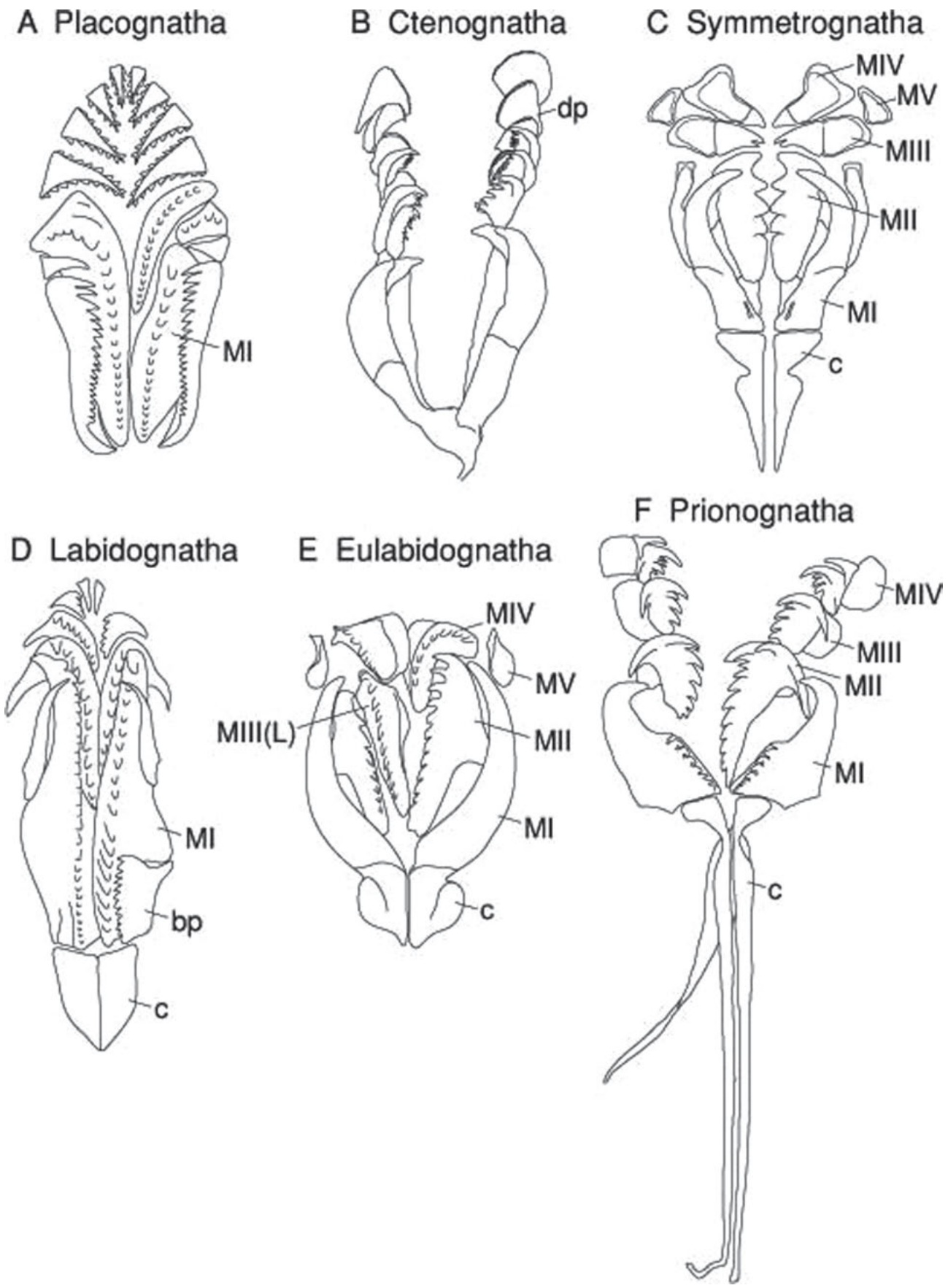
to a very small basal plate fused with the right forceps-like element (Fig. 7.12.1.2E). The recent eulabidognaths also have the articular locking structure of the forceps and lack most of attachment lamellae. Oenonidae and few extinct families (Tab. 7.12.1.1) carry prionognath (saw-jaw) maxillae with very long slender carriers, forceps-like elements, and a number of asymmetrical-shaped dentate elements (Ehlers 1868, Paxton 2009) (Tab. 7.12.1.1; Fig. 7.12.1.2F).

Besides jaw morphology, the monophyly of Eunicida is supported by a number of putative synapomorphies. Various prostomial and pharyngeal structures in eunicidan families have been shown to be homologous based on their topology and innervation (Orrhage 1995, Zanol 2010). Palps and antennae are best developed in onuphids and eunicids but also present in dorvilleids and oenonids. Onuphids and some dorvilleids have one apodous peristomial ring, whereas the rest of the families possesses two apodous peristomial rings that have been shown to be a subdivision of a single ring (Åkesson 1967, Müller and Westheide 2002). Generally, eunicidans have long cylindrical bodies consisting of a large number of segments, although presumably secondarily short-bodied species can be found in every family. Parapodia are subbiramous or uniramous with neuropodia well developed and notopodia reduced to dorsal cirri or absent. Many species have branchiae as dorsal extensions associated with dorsal parapodial (notopodial) cirri. In onuphids and eunicids, ventral cirri are modified into glandular pads producing mucous (Arias and Paxton 2015). Ventral cirri are generally absent in oenonids and lumbrinerids. All eunicidans possess lateral organs (also called dorsal cirrus organs) composed of bundles of cilia located between the dorsal cirrus and the neuropodium (Hayashi and Yamane 1994, Purschke et al. 2014). Chaetal-type diversity has been shown to increase during evolution of Eunicida, with Eunicidae and Onuphidae having significantly more types of chaetae than other families (Tilic et al. 2016).

The largest known polychaetes are found within Eunicida, some species of *Eunice* reach up to 6 m in length and consist of more than 1500 segments (Fauchald 1992). However, Eunicida also comprise small species, such as the dorvilleid *Neotenotrocha sterreri* Eibye-Jacobsen & Kristensen, 1994 described from Bermuda, which is only 255 µm long (Eibye-Jacobsen and Kristensen 1994).

All Eunicida have lecithotrophic development with various degrees of parental care from broadcast spawning to viviparity (Rouse 2006). Many tubicolous forms brood their young inside the parental tubes until late juvenile stages (Åkesson 1967, Paxton 1993, Budaeva and Fauchald 2010). Scissiparity, the process when existing segments are transformed into stolons, was reported in Oenonidae (Steiner and Amaral 2009), and architomy was described in Dorvilleidae (Åkesson and Rice 1992). The presence of

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the nurse cells attached to the oocytes was suggested as an apomorphy of Eunicida (Rouse 1992), although their arrangement may vary significantly even within a single family (Paxton 1986).

Eunicidans are widely distributed in the ocean, inhabiting various biotopes from intertidal to hadal depths (Paxton 2000, Rouse and Pleijel 2001, Struck et al. 2006). The majority of these bristle worms are free-living benthic sediment dwellers (epifaunal crawlers or tubicolous). Some species of the family Oenonidae are endoparasites of polychaetes and other marine invertebrates (Dean 1992, Hernándes-Alcántara and Solís-Weiss 1998, Martin and Britayev 1998), and all histriobdellids are obligatory ectosymbionts of marine and freshwater crustaceans (Steiner and Amaral 1999). Eunicidans have been reported to reach extremely high densities in some marine biotopes. For instance, an opportunistic dorvilleid *Ophryotrocha shieldsi* Paxton & Davey, 2010, inhabiting organically enriched sediments close to fish farms in Tasmania, Australia, occurs in numbers estimated as 100,000 ind/m^2 (Paxton and Davey 2010). A Hawaiian onuphid *Diopatra dexiognatha* Paxton & Bailey-Brock, 1986 forms dense intertidal aggregations of more than 21,000 ind/m^2, providing a special environment that supports a diverse community of marine invertebrates (Bailey-Brock 1984).

Some species of the order have cultural or economic value being used as traditional food, bait, or fish feed. *Palola viridis* Gray in Stair, 1847 (Eunicidae), the so-called "palolo worm", collected during the breeding season in South Pacific, is used as a source of local traditional food (Mondragón 2004, Schulze 2006). *Diopatra aciculata* Knox & Cameron, 1971 (Onuphidae) is commercially grown in aquaculture for recreational fishing and food supplies for breeding stock of local fish farming (Safarik et al. 2006). Lumbrinerids and oenonids in the Suez Canal (Osman et al. 2010), onuphids in Australia (Paxton 1979) and the eastern Atlantic (Cunha et al. 2005, Dağli et al. 2005), and eunicids in Adriatic and Mediterranean Coasts, Australia, Japan, and the United States (Gambi et al. 1994, Olive 1994, Bettoso et al. 1998) sustain local recreational and commercial fishing.

Eunicida together with Phyllodocida are the major groups within the annelid clade Errantia (Struck et al. 2011, Struck 2013, Weigert et al. 2014, Struck et al. 2015). Previously, both groups together with Amphinomida Lamarck, 1818 were a part of a large clade "Aciculata" (Rouse and Fauchald 1997, Rouse and Pleijel 2001); however, most recent phylogenomic studies provided high support for sister relationships between Amphinomida and Sipuncula (Weigert et al. 2014, Struck et al. 2015, Struck 2019). For a detailed discussion, refer to Chapter 2, Volume 1 on annelid phylogeny in general (Struck 2019).

Hypotheses of phylogeny of Eunicida based on genetic markers (Struck et al. 2006, 2015, Tilic et al. 2016) are congruent in recovering monophyletic Eunicidae, Onuphidae, Lumbrineridae, and Oenonidae (Fig. 7.12.1.3). Dorvilleidae status is contradictory, but it is most probably paraphyletic due to the placement of *Pettiboneia* Orensanz, 1973 in another clade supported by molecular data (Struck et al. 2006) and jaw structure (Paxton 2009). Hypotheses that lack *Pettiboneia* recovered monophyletic Dorvilleidae (Struck et al. 2015, Tilic et al. 2016). The monophyly of Histriobdellidae and Hartmaniellidae has not been assessed.

Eunicidae and Onuphidae are sister families sharing eulabidognath maxillae, five prostomial appendages, peristomial cirri, and subacicular hooks in median and posterior parapodia (Struck et al. 2006, 2015, Tilic et al. 2016). The relationship among the other families is uncertain. Ctenognath Dorvilleidae appears to be sister to the Eunicidae and Onuphidae clade (Struck et al. 2006), all other eunicidans (Struck et al. 2015), or Oenonidae (Tilic et al. 2016). In all analyses, dorvilleids have significantly longer branches than other eunicidan taxa, which potentially could cause uncertainty in their placement especially in analysis with limited taxon sampling (Struck et al. 2006). Prionognath Oenonidae, another clade that bears terminals with long branches, also displays alternative sister group relationships forming a clade with Eunicidae and Onuphidae, Dorvilleidae (Struck et al. 2006), Lumbrineridae (Struck et al. 2015), or Dorvilleidae (Tilic et al. 2016). Lumbrineridae is sister to all other eunicidans (Struck et al. 2006, Tilic et al. 2016) or Oenonidae (Struck et al. 2015).

◂ **Fig. 7.12.1.2**: Examples of different types of maxillae described for Eunicida. A, Placognatha: *Vistulella* (modified from Kielan-Jaworowska 1968); B, Ctenognatha: *Ophryotrocha adherens* (modified from Paavo et al. 2000); C, Symmetrognatha: *Lumbrineris latreilli* (modified from Carrera-Parra 2006); D, Labidognatha: *Rhamphoprion* (modified from Kielan-Jaworowska 1968); E, Eulabidognatha: *Paradiopatra lepta* (modified from Budaeva and Fauchald 2011); F, Prionognatha: *Arabella aracaensis* (modified from Steiner and Amaral 2009). bp, basal plate; c, carriers; dp, dentate plates; MI–MV, maxillary elements 1 to 5 (in Eulabidognatha, only the left MIII is present and the right MI combines forceps-like element and fused basal plate).

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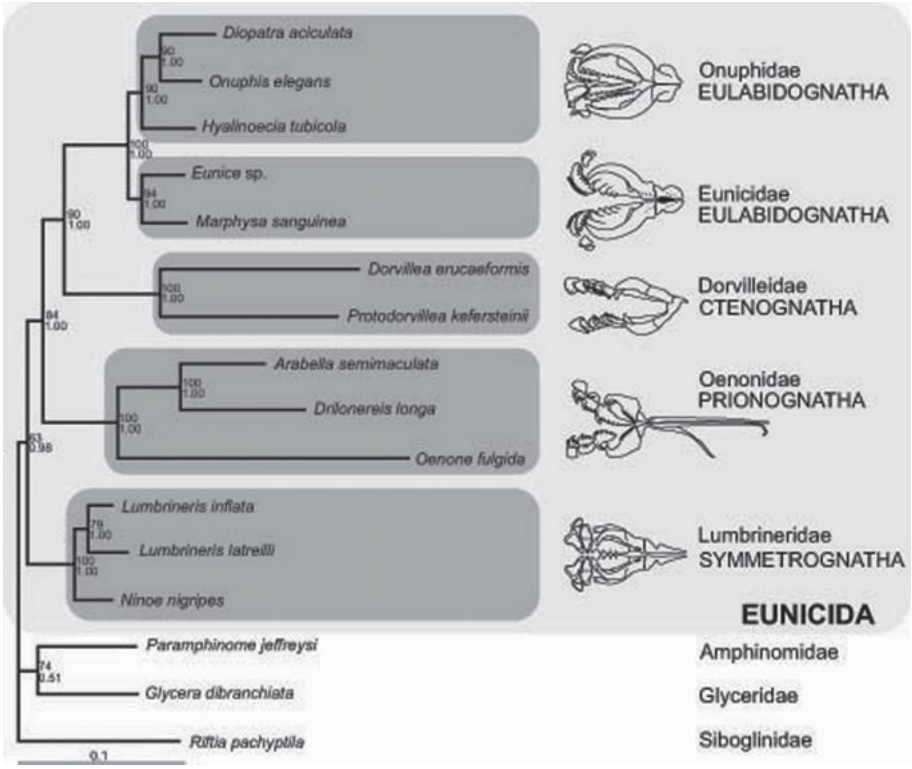


Fig. 7.12.1.3: Phylogenetic tree of Eunicida. ML tree of the four-gene analysis with 16 taxa (-ln L = 21,337.51). Bootstrap values above 50 are shown above posterior probabilities values from Bayesian inference right to the node (modified from Struck et al. (2006) following the classification of maxillae types by Paxton 2009; Onuphidae maxillae modified from Budaeva and Fauchald (2011); Eunicidae maxillae modified from Zanol et al. (2007); Dorvilleidae maxillae modified from Paavo et al. (2000); Oenonidae maxillae modified from Steiner and Amaral (2009); and Lumbrineridae maxillae modified from Carrera-Parra (2006)).

Several jawless minute polychaete genera, such as *Dinophilus* Schmidt, 1848 and *Diurodrilus* Remane, 1925, have been traditionally placed within Eunicida (Eibye-Jacobsen and Kristensen 1994, Rouse and Fauchald 1997, Paxton 2000). A detailed study of the anatomy of *Diurodrilus* in combination with molecular data placed it within Spiralia with a lack of strong evidence of its affiliation with Annelida (Worsaae and Rouse 2008). Nonetheless, the analysis of the mitochondrial genomic data supported the inclusion of *Diurodrilus* into Annelida with uncertain placement (Golombek et al. 2013). The reduction of parapodia and jaws together with a small size of individuals suggested the progenetic origin of *Dinophilus*. However, molecular analysis based on a single gene revealed that it is most likely not a member of Eunicida, lacking affiliation with any of the eunicidan families (Struck et al. 2002). In fact, phylogenomic analysis has shown that both genera are closely affiliated with Orbiniidae, a family of sedentarian bristle worms (Laumer et al. 2015, Struck et al. 2015). Morphologically, *Dinophilus* and *Diurodrilus* resemble orbiniid larvae in having only few segments and ciliary rings and lacking palps, parapodia, and chaetae, supporting the hypothesis of progenetic evolution within Sedentaria (Struck et al. 2015).

References

Åkesson, B. (1967): The embryology of the polychaete *Eunice kobiensis*. *Acta Zoologica* 48: 141–192.

Åkesson, B. & Rice, S.A. (1992): Two new *Dorvillea* species (Polychaeta, Dorvilleidae) with obligate asexual reproduction. *Zoologica Scripta* 21: 351–362.

Arias, A. & Paxton, H. (2015): *Paradiopatra* Ehlers, 1887 (Annelida: Onuphidae) from southwestern Europe with the description of a new species and new ultramorphological data for the genus. *Zootaxa* 4040: 149–168.

Bailey-Brock, J. (1984): Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg, 1865 (Onuphidae) in Hawaii: community structure, and sediment stabilizing properties. *Zoological Journal of the Linnean Society, London* 80: 191–199.

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Berthold, A.A. (1827): *Lareille's Natürliche Familien des Thierreichs. Aus dem Franzosischen, mit Anmerkungen und Zusätzen*. Verlage Landes-Industrie-Comptoirs, Weimar.

Bettoso, N., Faverio, G. & Orel, G. (1998): Note sulla biologia e sulla pesca del verme di Rimini (*Eunice aphroditois* Pallas) in Alto Adriatico. *Hydrores* 16: 25–34.

Budaeva, N.E. (2005): Lumbrineridae (Annelida: Polychaetae) from the Sea of Okhotsk. *Invertebrate Zoology* 2: 181–202. [in Russian]

Budaeva, N.E. (2008): *Paradiopatra kirkegaardi* is a new species name for *Paradiopatra fauchaldi* (Kirkegaard 1988, Polychaeta, Onuphidae). *Zoologicheskij Zhurnal* 87: 1034–1040. [in Russian]

Budaeva, N. & Fauchald, K. (2010): Larval development of *Mooreonuphis stigmatis* (Treadwell 1922) (Polychaeta: Onuphidae) from the north-east Pacific. *Marine Biology Research* 6: 6–24.

Budaeva, N. & Fauchald, K. (2011): Phylogeny of the *Diopatra* generic complex with a revision of *Paradiopatra* Ehlres, 1887 (Polychaeta: Onuphidae). *Zoological Journal of the Linnean Society, London* 163: 319–436.

Carrera-Parra, L.F. (2006): Revision of *Lumbrineris* de Blainville, 1828 (Polychaeta: Lumbrineridae). *Zootaxa* 1336: 1–64.

Chamberlin, R.V. (1919): The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48: 1–514.

Colbath, G.K. (1987): Evidence for shedding of maxillary jaws in eunicoid polychaetes. *Journal of Natural History* 21: 443–447.

Cunha, T., Hall, A. & Queiroga, H. (2005): Estimation of the *Diopatra neapolitana* annual harvest resulting from digging activity in Canal de Mira, Ria de Aveiro. *Fisheries Research* 76: 56–66.

Dağli, E., Ergen, Z. & Çinar, M.E. (2005): One-year observation on the population structure of *Diopatra neapolitana* Delle Chiaje (Polychaeta, Onuphidae) in Izmir Bay (Aegean Sea, eastern Mediterranean). *Marine Ecology* 26: 265–272.

Dales, R.P. (1962): The polychaete stomodeum and the interrelationships of the families of the Polychaeta. *Proceedings of the Zoological Society of London* 139: 289–328.

Dean, H.K. (1992): A new arabellid polychaete living in the mantle cavity of deep-sea wood boring bivalves (family Pholadidae). *Proceedings of the Biological Society of Washington* 105: 224–232.

Ehlers, E. (1868): Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Engelmann, Leipzig.

Eibye-Jacobsen, D. & Kristensen, R.M. (1994): A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 23: 107–131.

Eriksson, M. & Bergman, C.F. (1998): Scolecodont systematics exemplified by the polychaete *Hadoprion cervicornis* (Hinde, 1879). *Journal of Paleontology* 72: 477–485.

Fauchald, K. (1992): A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithsonian Contributions to Zoology* 523: 1–422.

Fauvel, P. (1923): Polychètes Errantes. *Faune de France* 5: 1–488.

Gambi, M.C., Castelli, A., Giangrande, A., Lanera, P., Prevedelli, D. & Zunarelli Vandini, R. (1994): Polychaetes of commercial and applied interest in Italy: an overview. *Mémoires du Muséum National d'Histoire Naturelle* 162: 593–603.

Golombek, A., Tobergte, S., Nesnidal, M.P., Purschke, G. & Struck, T.H. (2013): Mitochondrial genomes to the rescue — Diurodrilidae in the myzostomid trap. *Molecular Phylogenetics and Evolution* 68: 312–326.

Hartman, O. (1944): Polychaetous annelids. Part V. Eunicea. *Allan Hancock Pacific Expeditions* 10: 1–237.

Hayashi, I. & Yamane, S. (1994): On a probable sense organ newly found in some eunicid polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 74: 765–770.

Hernándes-Alcántara, P. & Solís-Weiss, V. (1998): Parasitism among polychaetes: a rare case illustrated by a new species: *Labrorostratus zaragozensis*, n. sp. (Oenonidae) found in the Gulf of California, Mexico. *Journal of Parasitology* 84: 978–982.

Hints, O. (1999): Two new polychaete families from the Upper Ordovician of Estonia. *Palaeontology (Oxford)* 42: 897–906.

Hints, O. & Eriksson, M.E. (2007): Diversification and biogeography of scolecodont-bearing polychaetes in the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245: 95–114.

Imajima, M. (1977): A new polychaete family, Hartmaniellidae, from Japan. In: Reish, D.J. & Fauchald, K. (eds.). *Essays on Polychaetous Annelids in Memory of De. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 211–216.

Kielan-Jaworowska, Z. (1966): Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica* 16: 1–152.

Kielan-Jaworowska, Z. (1968): Scolecodonts versus jaw apparatuses. *Lethaia* 1: 39–49.

Kinberg, J.G.H. (1865): Annulata nova. Öfversigt af Kongl. Vetenskaps-akademiens förhandlingar, Stockholm 21: 559–574.

Knox, G.A. & Cameron, D.B. (1971): Port Phillip Bay Survey 1957–1963, Victoria, Australia. Part 2(4) Polychaeta. *Memoirs of the National Museum of Victoria* 32: 21–42.

Kozur, H. (1970): Zur Klassifikation und phylogenetischen Entwicklung der fossilen Phyllodocida und Eunicida (Polychaeta). *Freiberger Forschungshefte Ser. C* 260: 35–81.

Lamarck, J.B. de (1818): Histoire naturelle des Animaux sans Vertèbres, préséntant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; precedes d'une Introduction offrant la determination des caracteres essentiels de l'Animal, sa distinction du vegetal et desautres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Deterville, Paris: 612 pp.

Lange, F.W. (1947): Annelidos poliquetos dos folhelhos devonianos do Parana. *Arquivos do Museu Paranaense* 6: 161–230.

Laumer, C.E., Bekkouche, N., Kerbl, A., Goetz, F., Neves, R.C., Sørensen, M. V., Kristensen, R.M., Hejnol, A., Dunn, C.W., Giribet, G. & Worsaae, K. (2015): Spiralian phylogeny informs the evolution of microscopic lineages. *Current Biology* 25: 2000–2006.

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Martin, D. & Britayev, T.A. (1998): Symbiotic polychaetes: Review of known species. *Oceanography and Marine Biology: An Annual Review* 36: 217–340.

Mierzejewski, P. (1984): *Synclinophora synclinalis* Eisenack — The oldest arabellid polychaete. *Review of Palaeobotany and Palynology* 43: 285–292.

Mierzejewski, P. & Mierzejewska, G. (1975): Xenognath type of polychaete jaw apparatuses. *Acta Palaeontologica Polonica* 20: 437–444.

Mondragón, C. (2004): Of winds, worms and mana: The traditional calendar of the Torres Islands, Vanuatu. *Oceania* 74: 289–308.

Müller, M.C.M. & Westheide, W. (2002): Comparative analysis of the nervous systems in presumptive progenetic dinophilid and dorvilleid polychaetes (Annelida) by immunohistochemistry and CLSM. *Acta Zoologica* 83: 33–48.

Olive, P.J.W. (1994): Polychaeta as a world resource: a review of patterns of exploitation as sea angling baits, and potential for aquaculture based production. *Mémoires du Muséum National d'Histoire Naturelle* 162: 603–610.

Orensanz, J.M. (1973): Los anelidos poliquetos de la provincia biogeogratica argentina. III. Dorvilleidae. *Physis* 3: 325–342.

Orensanz, J.M. (1990): The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Antarctic Research Series* 52: 1–183.

Orrhage, L. (1995): Appendages of the Eunicea (Polychaeta), with a tentative outline of the fundamental constitution of the cephalic nervous system of the polychaetes. *Acta Zoologica* 76: 229–248.

Osman, I.H., Gabr, H.R., Saito, H. & El-Etreby, S.Gh. (2010): Reproductive biology of the highly commercial polychaetes in the Suez Canal. *Journal of Marine Biological Association of the UK* 90: 281–290.

Paavo, B., Bailey-Brock, J.H. & Åkesson, B. (2000): Morphology and life history of *Ophryotrocha adherens* sp. nov. (Polychaeta, Dorvilleidae). *Sarsia* 85: 251–264.

Paxton, H. (1979): Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Onuphidae). *Australian Journal of Marine and Freshwater Research* 30: 265–294.

Paxton, H. (1986): Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). *Records of the Australian Museum* 38: 1–74.

Paxton, H. (1993): *Diopatra* Audouin and Milne Edwards (Polychaeta, Onuphidae) from Australia, with a discussion of developmental patterns in the genus. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 10: 115–154.

Paxton, H. (2000): Eunicida. In: Beesley, P.L., Ross, G.J.B., & Glasby, C.J., editors. *Polychaetes and Allies: The Southern Synthesis*. Vol. 4A*: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 89–106.

Paxton, H. (2005): Molting polychaete jaws — Ecdysozoans are not the only molting animals. *Evolution and Development* 7: 337–340.

Paxton, H. (2006): Replacement of adult maxillary jaws in Eunicida (Polychaeta). *Scientia Marina* 70S3: 331–336.

Paxton, H. (2009): Phylogeny of Eunicida (Annelida) based on morphology of jaws. *Zoosymposia* 2: 241–264.

Paxton, H. & Bailey-Brock, J.H. (1986): *Diopatra dexiognatha*, a new species of Onuphidae (Polychaeta) from Oahu, Hawaiian Islands. *Pacific Science* 40: 1–6.

Paxton, H. & Safarik, M. (2008): Jaw growth and replacement in *Diopatra aciculata* (Annelida: Onuphidae). *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 24: 15–21.

Paxton, H. & Davey, A. (2010): A new species of *Ophryotrocha* (Annelida: Dorvilleidae) associated with fish farming at Macquarie Harbour, Tasmania, Australia. *Zootaxa* 2509: 53–61.

Paxton, H. & Eriksson, M.E. (2012): Ghosts from the past – Ancestral features reflected in the jaw ontogeny of the polychaetous annelids *Marphysa fauchaldi* (Eunicidae) and *Diopatra aciculata* (Onuphidae). *GFF* 00: 1–8.

Purschke, G., Bleidorn, C. & Struck, T. (2014): Systematics, evolution and phylogeny of Annelida — A morphological perspective. *Memoirs of Museum of Victoria* 71: 247–269.

Remane, A. (1925): Diagnosen neuer Archianneliden (zugleich 3. Beitrag zur Fauna der Kieler Bucht). *Zoologischer Anzeiger* 65: 15–17.

Rouse, G.W. (1992): Oogenesis and larval development in *Micromaldane* spp. (Polychaeta, Capitellida, Maldanidae). *Invertebrate Reproduction & Development* 21: 215–230.

Rouse, G.W. (2006): Annelid larval morphology. In: Jamieson, B.G.M. (ed.), *Reproductive Biology and Phylogeny. Rouse G., Pleijel F, editors. Vol.4. Reproductive Biology and Phylogeny of Annelida.* Science Publishers, Enfield (NH), Jersey, Plymouth: 141–177.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

Rouse, G.W. & Pleijel, F. (2001): Polychaetes. Oxford University Press, Oxford: 354 pp.

Safarik, M., Redden, A.M. & Schreider, M.J. (2006): Density-dependent growth of the Polychaete *Diopatra aciculata*. *Scientia Marina* 70S3: 337–341.

Schmarda, L.K. (1861): *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Erster Band (zweite Hälfte) Turbellarien, Rotatorien und Anneliden.* Wilhelm Engelmann, Leipzig.

Schmidt, E.O. (1848): *Neue Beiträge zur Naturgeschichte der Würmer gesammelt auf einer Reise nach den Färor im Frühjahr 1848.* Friedrich Mauke, Jena: 44.

Schulze, A. (2006): Phylogeny and genetic diversity of palolo worms (*Palola*, Eunicidae) from the tropical North Pacific and the Caribbean. *Biological Bulletin* 210: 25–37.

Stair, J.B. (1847): An account of Palolo, a sea-worm eaten in the Navigator Islands, with a description by J.E. Gray. *Proceedings of the Zoological Society of London* 15: 17–18.

Steiner, T.M. & Amaral, A.C.Z. (1999): The family Histriobdellidae (Annelida, Polychaeta) including descriptions of two new species from Brazil and a new genus. *Contributions to Zoology* 68: 95–108.

Steiner, T.M. & Amaral, A.C.Z. (2009): *Arabella aracaensis*, a new species with growth rings on its mandibles, and some remarks on the endoparasitic *Labrorostratus prolificus* (Polychaeta: Oenonidae) from southeast Brazil. *Journal of Natural History* 43: 2537–2551.

Struck, T.H. (2013): The impact of paralogy on phylogenomic studies — A case study on annelid relationships. *PLoS ONE* 8, e62892

Struck, T.H. (2019): Phylogeny. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.) Handbook of Zoology. Annelida. Vol.1 Annelida, Basal groups and PListoannelida, Sedentaria I. Berlin, De Gruyter: 37–68.

Struck, T.H., Westheide, W. & Purschke, G. (2002): Progenesis in Eunicida ("Polychaeta," Annelida) — Separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution* 25: 190–199.

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Struck, T.H., Purschke, G. & Halanych, K.M. (2006): Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach. *Systematic Biology* 55: 1–20.
Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.
Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.
Szaniawski, H. (1968): Three new polychaete jaw apparatuses from the Upper Permian of Poland. *Acta Palaeontologica Polonica* 13: 255–281.
Szaniawski, H. & Wrona, R.M. (1973): Polychaete jaw apparatuses and scolecodonts from the upper Devonian of Poland. *Acta Palaeontologica Polonica* 18: 223–267.
Szaniawski, H. & Imajima, M. (1996): Hartmaniellidae — Living fossils among polychaetes. *Acta Palaeontologica Polonica* 41: 111–125.
Thompson, I. & Johnson, R.G. (1977): New fossil Polychaete from Essex, Illinois. *Fieldiana Geology* 44: 471–487.
Tilic, E., Bartolomaeus, T. & Rouse, G.W. (2016): Chaetal type diversity increases during evolution of Eunicida (Annelida). *Organisms Diversity and Evolution* 16: 105–119.
Tzetlin, A.B., & Purschke, G. (2005): Pharynx and Intestine. *Hydrobiolgia* 535/536: 199–225.
Uschakov, P.V. (1955): Polychaeta of the far eastern seas of the U.S.S.R. *Keys of the Fauna of the USSR* 56: 1–1445. [in Russian. Translated 1965 by Israel Program for Scientific Translations, Jerusalem.]
Vaillant, L. (1890): *Histoire neturelle des Annelés marins et d'eau douce. Lombriciniens, Hirudiniens, Bdellomorphes, Térétulariens et Planariens*. Librairie Encyclopédique de Roret, Paris.
Van Erve, A.W. (1981): Lower Jurassic scolecodonts from the Vicentinian Alps (northeastern Italy), representing the family Dorvilleidae Chamberlin, 1919. *Review of Palaeobotany and Palynology* 34: 225–235.
Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.
Williams, H.S., Nowlan, G.S., Barnes, C.R. & Batten, R.S.R. (1999): The Ledge section at Cow Head, western Newfoundland as a GSSP candidate for the lower boundary of the second stage of the Ordovician System: New data and discussion of the graptolite, conodont and chitinozoan assemblages. *A Report to the IUGS/ICS Subcommission on Ordovician Stratigraphy*. June 1999: 30.
Worsaae, K. & Rouse, G.W. (2008): Is *Diurodrilus* an annelid? *Journal of Morphology* 269: 1426–1455.
Zanol, J. (2010). Homology of prostomial and pharyngeal structures in Eunicida (Annelida) based on innervation and morphological similarities. *Journal of Morphology* 271: 1023–1043.
Zanol, J., Fauchald, K. & Paiva, P.C. (2007): A phylogenetic analysis of the genus *Eunice* (Eunicidae, Polychaete, Annelida). *Zoological Journal of the Linnean Society* 150: 413–434.

Helena Wiklund, Günter Purschke and Ascensao Ravara

7.12.2 Dorvilleidae Chamberlin, 1919

Introduction

The family Dorvilleidae Chamberlin, 1919 belongs to the order Eunicida and consists of 32 genera, 13 of which are monospecific. In total, 192 recent and 3 fossil species have been described. The three most species-rich genera are *Ophryotrocha* Claparède & Mecznikow, 1869, *Dorvillea* Parfitt, 1866, and *Schistomeringos* Jumars, 1974, with 77, 20, and 17 species, respectively, representing approximately 60% of the dorvilleid species.

Dorvilleids are present in all oceans from intertidal down to deep sea, sometimes in high abundance in the presence of organically enriched environments (e.g., *Ophryotrocha*, *Parougia* Wolf, 1986b). Some of the smallest genera (e.g., *Neotenotrocha* Eibye-Jacobsen & Kristensen, 1994) occur interstitially and are rarely found. Three dorvilleid genera (*Exallopus* Jumars, 1974, *Ophryotrocha*, and *Parougia*) are mainly represented by species described from deep waters. Some species of *Ophryotrocha* can be successfully cultured in aquaria environments.

The main distinguishing characters for the dorvilleids used to separate them from other families, but also to separate among and within genera, are the jaws. These are ctenognath (comb-jaws) in shape, and as they can be heavily sclerotinized, ctenognath jaw elements have been found in fossil records as old as early Ordovician (Hints and Eriksson 2007).

Morphology

External morphology

Dorvilleids range in sizes from about 250 µm in *Neotenotrocha* to several centimeters in *Dorvillea*. Their body is elongate and rounded in cross-section or dorsoventrally flattened (e.g., *Ophryotrocha*). The color in live animals varies from whitish to yellowish with bright red or dark pigmentation patterns (Fig. 7.12.2.1A, B). All segments have ciliary rings that are often well developed (Figs. 7.12.2.2B, 7.12.2.3A). Dorsal lobes may be present in the posterior region, close to the parapodia (e.g., *Ophryotrocha*) (Figs. 7.12.2.1E, 7.12.2.2D). The pygidium has two, three, or four anal cirri (Figs. 7.12.2.1B, C, 7.12.2.2E, F, 7.12.2.3F). When three anal cirri are present, the median one is usually smaller and may be reduced to a small papilla (Figs. 7.12.2.1C, 7.12.2.2F, 7.12.2.3F).

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The prostomium is anteriorly rounded, and sometimes dorsoventrally flattened (e.g., *Ophryotrocha*) (Figs. 7.12.2.1C, 7.12.2.2C). Paired antennae and paired palps may be present, absent or reduced to small papillae (Fig. 7.12.2.1B). Antennae, when present, are simple (Figs. 7.12.2.1C, 7.12.2.2C) or multiarticulated (Figs. 7.12.2.1A, 7.12.2.2A, B). Palps, when present, are simple (Figs. 7.12.2.1C, 7.12.2.2C) or biarticulated (Figs. 7.12.2.1D, 7.12.2.2A, B). Eyes may be present (Figs. 7.12.2.1A, 7.12.2.2A) or absent (Figs. 7.12.2.1B, C, E, 7.12.2.2B, C). Nuchal organs are located between the prostomium and the peristomium (Fig. 7.12.2.2B). Two apodous peristomial rings are always present (Figs. 7.12.2.1A, 7.12.2.2A, B).

Jaws may be absent (*Apodotrocha* Westheide & Riser, 1983, *Ikosipodoides* Westheide, 2000, and *Parapodrilus* Westheide, 1965) but are usually present as a pair of ventral mandibles of varied morphology (Figs. 7.12.2.4, 7.12.2.5) and a varying number of dorsal maxillary

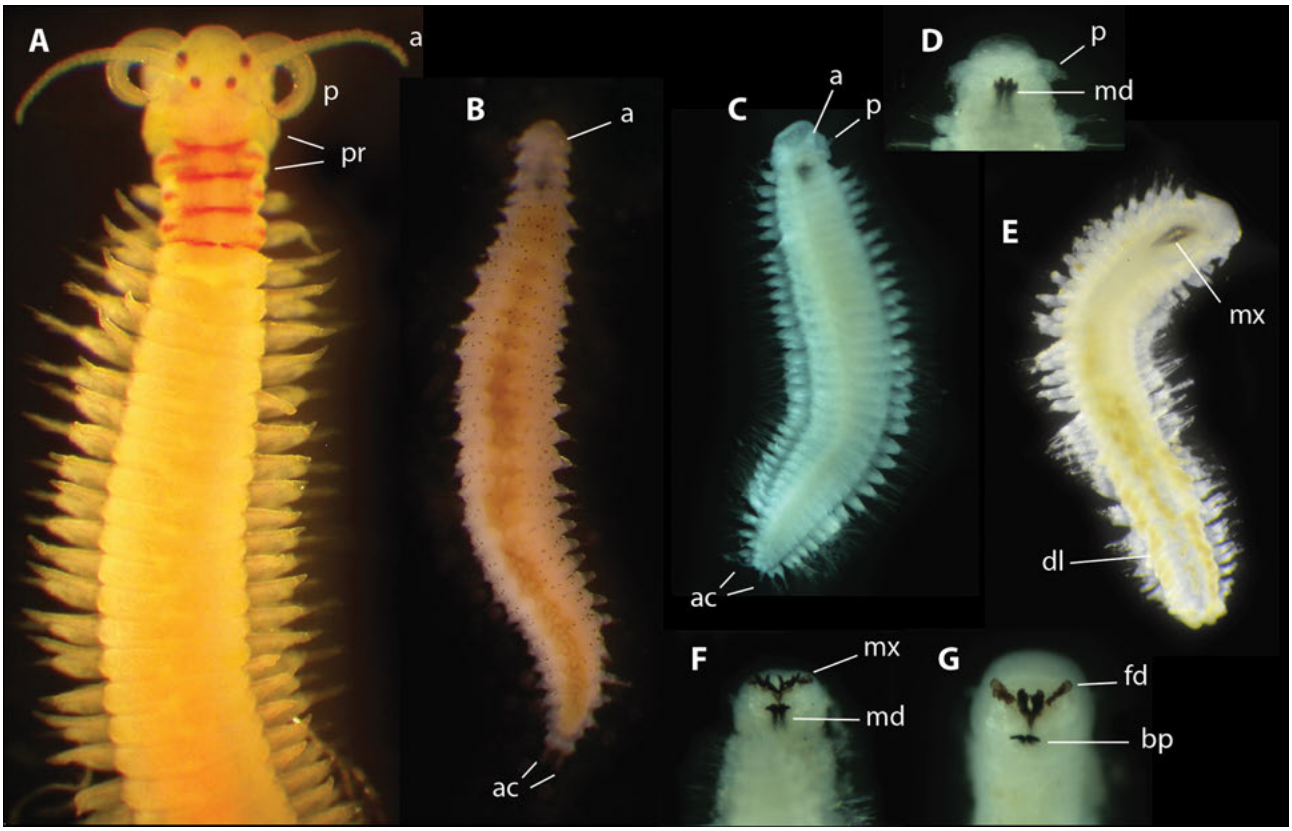
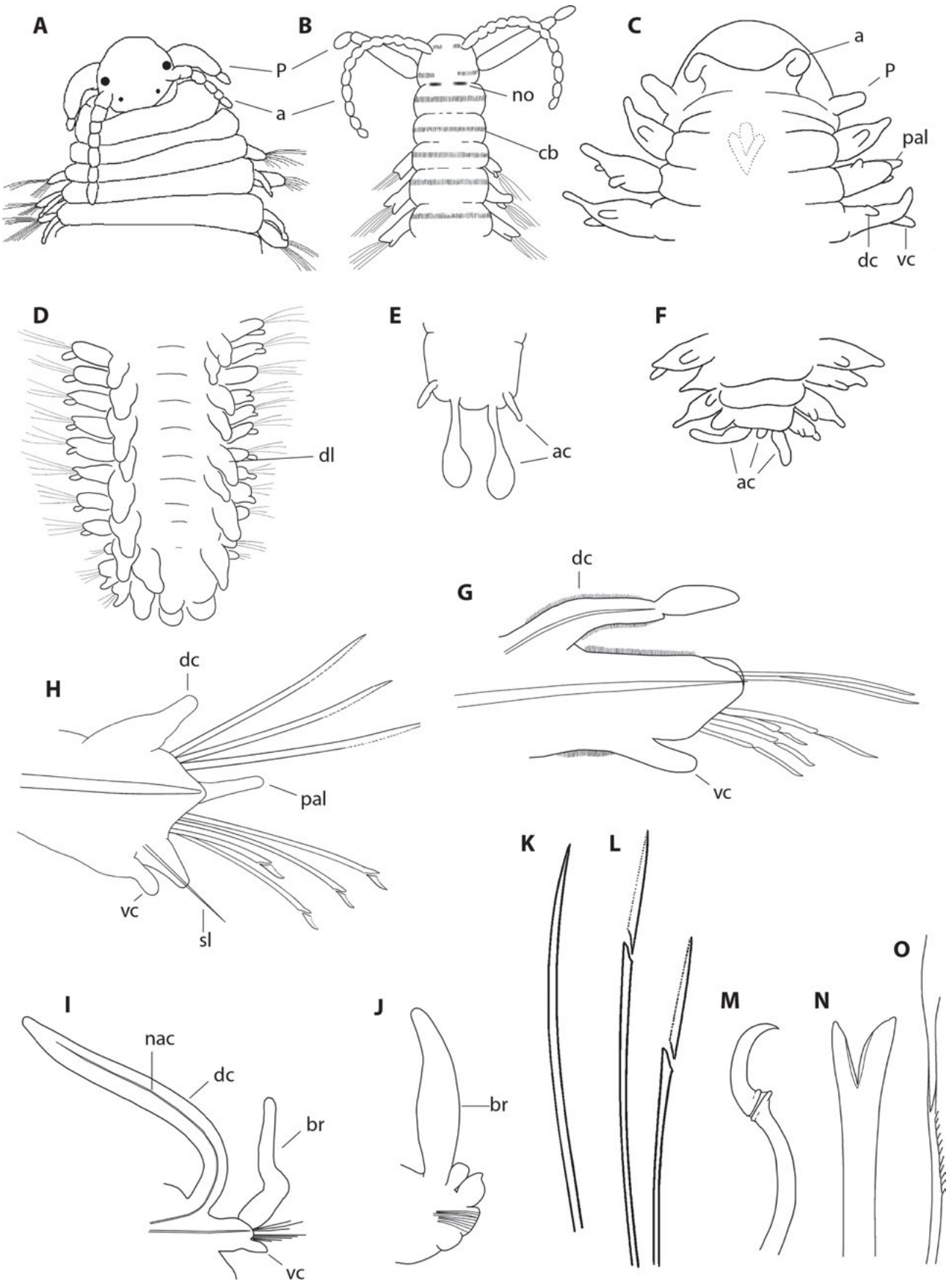


Fig. 7.12.2.1: General morphology. A, Undescribed dorvilleid species, living specimen, anterior end, dorsal view; B, *Ophryotrocha maculata* Åkesson, 1973, living specimen, dorsal view showing dark pigment spots; C, *Ophryotrocha lusa* Ravara, Marçal, Wiklund & Hilário, 2015, preserved specimen, entire worm, dorsal view; D, *Ophryotrocha mammillata* Ravara, Marçal, Wiklund & Hilário, 2015, preserved specimen, anterior end, ventral view; E, Same specimen, entire worm, dorsal view; F, G, *Ophryotrocha sadina* Ravara, Marçal, Wiklund & Hilário, 2015, preserved specimens, anterior end, ventral view showing everted pharynx with protruding mandibulae and maxillary apparatus. A, B © H. Wiklund; C–F, G © A. Ravara. a, antenna; ac, anal cirri; bp, basal plate; dl, dorsal lobes; fd, free denticles; md, mandibulae; mx, maxillae; p, palp; pr, peristomial rings.

▸ **Fig. 7.12.2.2**: General morphology (schematic figure). A–C, Anterior end of *Dorvillea largidentis* Wolf, 1986b, *Coralliotrocha natans* Westheide & von Nordheim, 1985, and *Ophryotrocha lusa*, dorsal view; D, Posterior region of *Ophryotrocha mammillata*, dorsal view; E, Pygidium of *Marycarmenia lysandrae* Nuñez, 1998, dorsal view; F, Posterior end of *O. lusa*, dorsal view; G, Parapodium from chaetiger 5 of *D. largidentis*, posterior view; H, Parapodium from midbody region of *O. lusa*, posterior view; I, Parapodium from midbranchiate region of *Diaphorosoma magnavena* Wolf, 1986a, anterior view; J, Parapodium from midbody region of *Iphitime sartorae* de Paiva & Nonato, 1991, posterior view; K and L, Simple supra-acicular and compound subacicular chaetae of *Ophryotrocha* sp.; M, Compound chaetae from first parapodia of *Exallopus cropion* Jumars, 1974; N and O, Forked chaeta of *Protodorvillea kefersteini* McIntosh, 1869 and *C. natans*. A, G, After Wolf 1986b; B–D, F, H, K, L, From Ravara et al. 2015; E, After Nuñez 1998; I, After Wolf 1986a; M, After Jumars 1974; J, After de Paiva and Nonato, 1991; N, After George and Hartmann-Schröder 1985; O, After Westheide and von Nordheim 1985. a, antenna; ac, anal cirri; at, accessory teeth; bp, basal plate; cb, ciliary bands; dc, dorsal cirrus; dl, dorsal lobes; fd, free denticles; inf, inferior row; mc, maxillary carriers; nac, notoacicula; no, nuchal organs; p, palp; pal, preacicular lobe; sup, superior row; vc, ventral cirrus.

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elements (Figs. 7.12.2.6, 7.12.2.7) attached to a muscular ventral proboscis that ends anteriorly in a ventrally placed mouth (Fig. 7.12.2.1F, G) (Purschke 1987, 1988, Purschke and Tzetlin 1996, Tzetlin and Purschke 2005). Maxillary elements consist of a number of plates organized in two or four rows (Fig. 7.12.2.6). Dorvilleids do not have the same kind of carriers as other eunicids; thus, their structures are called carrier-like (Purschke 1987, Paxton 2009). Dorsal carrier-like structures are present in *Dorvillea* and *Protodorvillea* Pettibone, 1961 (Fig. 7.12.2.6A), whereas ventral carrier-like structures are present in *Parougia* and *Ophryotrocha* (Fig. 7.12.2.8B, D) and absent in *Diaphorosoma* Wolf, 1986. Different jaw types may occur during ontogeny, e.g., in some species of *Ophryotrocha* where the "P-type" (from German: primitiv, primitive) maxillae (Fig. 7.12.2.8B) in juveniles are replaced with "K-type" (from German: kompliziert, complicated) maxillae, with the basal plates enlarged and resembling ice tongs (Fig. 7.12.2.8D), in the adult stage. Shedding, replacement, and growth of maxillae and in part of mandibles have been described by Paxton (2004) as well as by Tzetlin and Purschke (2005). In transmission electron microscopy (TEM), dorvilleid jaws appear as electron-dense homogenous structures (*Ophryotrocha gracilis* Huth, 1933, *Ophryotrocha puerilis* Claparede & Mecznikow, 1869, and *Protodorvillea kefersteini* McIntosh, 1869). This material is secreted into a preformed cuticular grid of collagen (Damas 1986, Purschke 1987, 1988) and, according to Damas (1986), mainly comprises calcium carbonate.

Parapodia are subbiramous (Fig. 7.12.2.2G), uniramous (Fig. 7.12.2.2H), or even absent (*Apodotrocha* and *Neotenotrocha*), with or without dorsal and/or ventral cirri. Dorsal cirri may be simple (Fig. 7.12.2.2H, I) or biarticulated (Fig. 7.12.2.2G), with or without an internal acicula. More or less developed prechaetal and postchaetal lobes may be present or absent (Figs. 7.12.2.2H, 7.12.2.3B). When present, parapodial cirri and lobes often have cilia at their tips (Fig. 7.12.2.3B). Branchiae occur in some genera and may dorsally be attached to the neuropodia (*Diaphorosoma*) (Fig. 7.12.2.2I) or the dorsal cirri (*Iphitime* Marenzeller, 1902) (Fig. 7.12.2.2J). Chaetae may be present or absent (*Apodotrocha*, *Neotenotrocha*). When present, supra-acicular chaetae are normally simple (Figs. 7.12.2.2K, 7.12.2.3C) and subacicular chaetae may be compound (Figs. 7.12.2.2L, 7.12.2.3D) or simple. Modified chaetae may be present in some genera (e.g., *Exallopus*; Fig. 7.12.2.2M). Supra-acicular furcate chaetae of various shape are present (Fig. 7.12.2.2N, O) or absent. Some genera have a subacicular retractable lobe (e.g., *Ophryotrocha*), with a simple or a compound chaeta (Figs. 7.12.2.2H, 7.12.2.3E).

Body wall and cuticle. Studies on the structure of the body wall and cuticle are scarce, and data on epidermis and cuticle are often only available in connection with studies on other structures (e.g., Purschke 1988, 1997, Rhode 1989, Schlawny et al. 1991a, Purschke and Nowak 2015). The most complete study has been carried out by Westheide and Riser (1983) on *Apodotrocha progenerans* Westheide & Riser, 1983, describing epidermal supportive cells, various types of gland cells, and cuticle in detail. As typical of annelids (Hausen 2005, Purschke et al. 2014), the dorvilleid cuticle is composed of an amorphous to filamentous matrix traversed by microvilli. Smaller species, such as *A. progenerans* and *Ophryotrocha* spp., lack the layers of parallel collagen fibers, which, however, are present in larger species, such as *Protodorvillea kefersteini* or *Schistomeringos neglecta*.

Nervous system and sense organs. The nervous system has been studied in *Parapodrilus psammophilus* Westheide, 1965, *Ophryotrocha gracilis*, *Ophryotrocha* sp., and *Dorvillea bermudensis* Åkesson & Rice, 1992 (see Evdonin and Bubko 1983, Müller and Westheide 2002, Müller and Henning 2004). In all species studied, the nervous system comprises a prostomial brain and a ventral nerve cord with segmental ganglia. The ventral cord communicates with the brain via the circumoesophageal connectives, which are split up into dorsal and ventral roots. These roots form two intracerebral commissures each. The dorsal neuropil gives rise to two pairs of nuchal nerves innervating the two pairs of nuchal organs in *D. bermudensis*. In each segment, a number of segmental nerves are present, the parapodial nerve always being the largest. The regeneration of the nervous system has been investigated in *D. bermudensis* and *Ophryotrocha puerilis* (see Pfannenstiel 1984, Müller 2004, Müller and Henning 2004). During regeneration, the ventral nerve cord plays an important role during segment proliferation and in signaling positional information (Pfannenstiel 1984). Neurosecretory substances and activities as well as certain transmitters have mainly been studied in *Ophryotrocha* spp. (Grothe 1982, Grothe et al. 1987, Schlawny et al. 1991b, c, Müller and Westheide 2002, Müller 2004, Müller and Henning 2004, Franchini 2008). Among these, FMRFamide-like molecules are present from the very beginning of ontogenesis, suggesting an important role of this substance during nervous system development (Franchini 2008).

Several dorvilleid species possess two pairs of pigmented eyes such as *Dorvillea rubrovittata* Grube, 1855 or *Schistomeringos rudolphi* (delle Chiaje, 1828). In these, the eyes are almost of equal size or the anterior ones being the largest. For instance, *Schistomeringos*

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neglecta Fauvel, 1923 possesses only one pair of eyes. Whereas *Protodorvillea kefersteini* is usually reported to possess only one pair of eyes (e.g., George and Hartmann-Schröder 1985), recent TEM investigations have shown that there exists an often overlooked anterior pair of minute eyes as sometimes reported (Rouse and Pleijel 2001) (Fig. 7.12.2.4C, D). In all of these cases, the eyes are positioned on the prostomium at the level of the palps and antennae (Figs. 7.12.2.1A, 7.12.2.2A, 7.12.2.4C, D). Ultrastructural investigations have been carried out in a few species so far (*S. neglecta* and *P. kefersteini*), revealing that, irrespective their size, these eyes are typical adult annelid eyes (Purschke et al. 2014, Purschke and Nowak 2015). In contrast, the eyes present in certain *Ophryotrocha* species are deeper embedded into the epidermal tissues and are situated more posteriorly and usually behind the nuchal organs (e.g., Åkesson 1973a, 1976, Rhode 1990). These eyes strongly reflect incident light and appear dark gray in transmitted light (Åkesson 1976). Besides supportive and sensory cells, these eyes comprise cells equipped with crystalline reflective platelets in all species studied by electron microscopy so far (*Ophryotrocha puerilis*, *Ophryotrocha dimorphica* Zavarzina & Tzetlin, 1986, and *Ophryotrocha gracilis*) (see Zavarzina and Tzetlin 1986, Zavarzina 1987, Rhode 1990, Purschke 2005, Purschke et al. 2006). Moreover, these eyes lack shading pigment; therefore, they have been regarded as independently evolved (Purschke et al. 2006).

Nuchal organs form oval ciliated pits, and there may be one or two pairs (Purschke 1997). For instance, two pairs have been found in *P. kefersteini, O. puerilis, O. gracilis*, and *D. bermudensis* (Dohle 1967, Rhode 1989, Purschke 1997, Müller and Henning 2004). TEM studies have been conducted for these three species (Rhode 1989, Purschke 1997). Three types of primary sensory cells have been described for *O. puerilis* as well (Schlawny et al. 1991a). These are uniciliated or multiciliated and predominantly occur on the appendages, but about 20 receptor cells are present on each trunk segment as well.

Musculature and body cavity. Ontogenetic muscle formation and structure of the body musculature have been studied in *Ophryotrocha diadema* Åkesson, 1976 by Bergter et al. (2008). The musculature comprises three main compartments: prostomial/peristomial, trunk, and parapodial musculature. The trunk musculature mainly comprises pairs of strong ventral and dorsal bands, whereas true circular fibers are lacking; these may functionally be replaced by dorsal transverse and diagonal (bracing) muscle fibers. The musculature of the anterior end and parapodia are comparatively complex.

The structure of the body cavity is known for *Ophryotrocha labronica* La Greca & Bacci, 1962, *Ophryotrocha dimorphica* Zavarzina & Tzetlin, 1986, *Ophryotrocha puerilis, Dorvillea sociabilis* Webster, 1879, and *Parougia caeca* Webster & Benedict, 1884 (as *Schistomeringos caeca*), both of which possess a coelom with partial peritoneal lining (see Fransen 1980, Pfannenstiel and Grünig 1982a, Smith and Ruppert 1988, Zavarzina and Tzetlin 1990). The smallest dorvilleids possess protonephridia (e.g., *Apodotrocha progenerans*) (see Westheide and Riser 1983, Westheide 1985). The terminal cells exhibit unique features, such as an unusual terminal cell with pedicel-like filtration structures, which borders directly to the greatly reduced coelomic space; a blood vascular system is reported to be lacking (Westheide and Riser 1983). The slightly larger species, such as *Dorvillea sociabilis*, *Ophryotrocha puerilis*, and *Ophryotrocha dimorphica*, possess metanephridial systems, including the coelom and blood vascular system (Pfannenstiel and Grünig 1982a, b, Zavarzina and Tzetlin 1987, Smith and Ruppert 1988). In the former species, the sites of ultrafiltration, i.e., the podocytes forming part of the coelomic lining at the blood vessels, have been described by Smith and Ruppert (1988).

Biology and ecology

Worms from the dorvilleid family can be found worldwide in marine habitats from intertidal to the deep sea. The majority of the dorvilleid species are free-living, crawling around at the seafloor or with a burrowing (*Meiodorvillea* Jumars, 1974) lifestyle, but some are symbiotic (e.g., species in *Iphitime* and two species of *Ophryotrocha* living in crab gill chambers) or presumed parasitic (*Veneriserva* Rossi, 1984 living in the coelom of aphroditid polychaetes). Dorvilleids can surround themselves with mucus, and some species have been observed to construct mucus tubes (Jumars et al. 2015 and references therein). Populations of *Ophryotrocha* species are often infected by apicomplexan parasites (*Grellia* spp.), and host specificity and cross-infection experiments have been carried out by Åkesson (1968, 1977).

Some species are reported to be carnivorous (e.g., *Schistomeringos neglecta* and *Protodorvillea kefersteini*), whereas others have been observed grazing algae or bacterial mats or living off detritus (Fauchald and Jumars 1979, Jumars et al. 2015). Studies from coral reefs suggest that species of *Schistomeringos* Jumars, 1974

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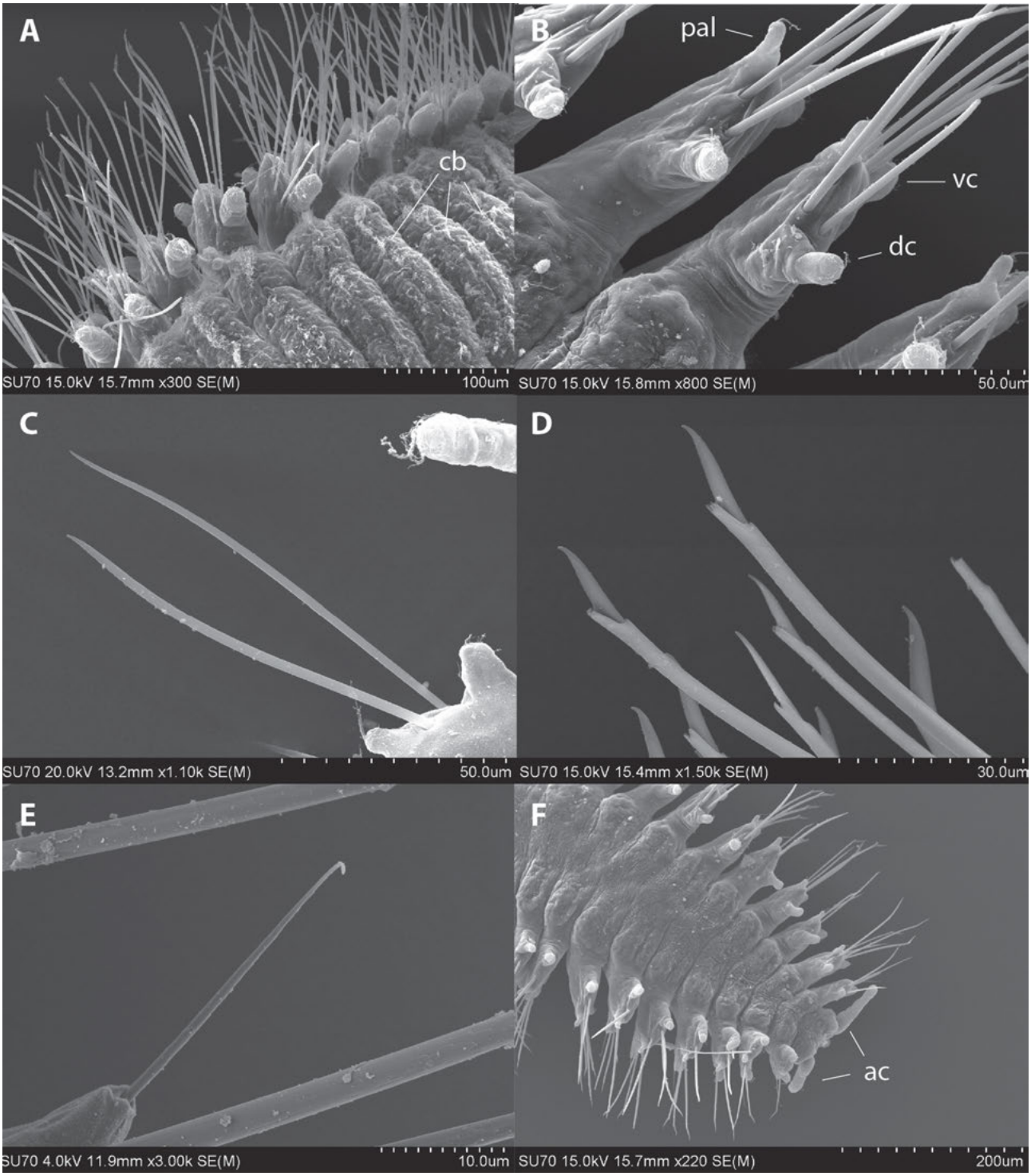


Fig. 7.12.2.3: Scanning electronic microscopy (SEM) images of dorsal cilia, parapodia, chaetae, and pygidium. A, *Ophryotrocha sadina* Ravara, Marçal, Wiklund & Hilário, 2015, midbody region showing parapodia and ciliary bands, dorsal view; B, *Ophryotrocha lusa* Ravara, Marçal, Wiklund & Hilário, 2015, midbody parapodia, dorsal view; C, D, *O. lusa*, simple supra-acicular and compound subacicular chaetae; E, *O. lusa*, simple chaetae from the subacicular lobe; F, *O. lusa*; posterior end showing pygidium and anal cirri, dorsal view. A–F, © A. Ravara. ac, anal cirri; cb, ciliary bands; dc, dorsal cirrus; pal, preacicular lobe; vc, ventral cirrus.

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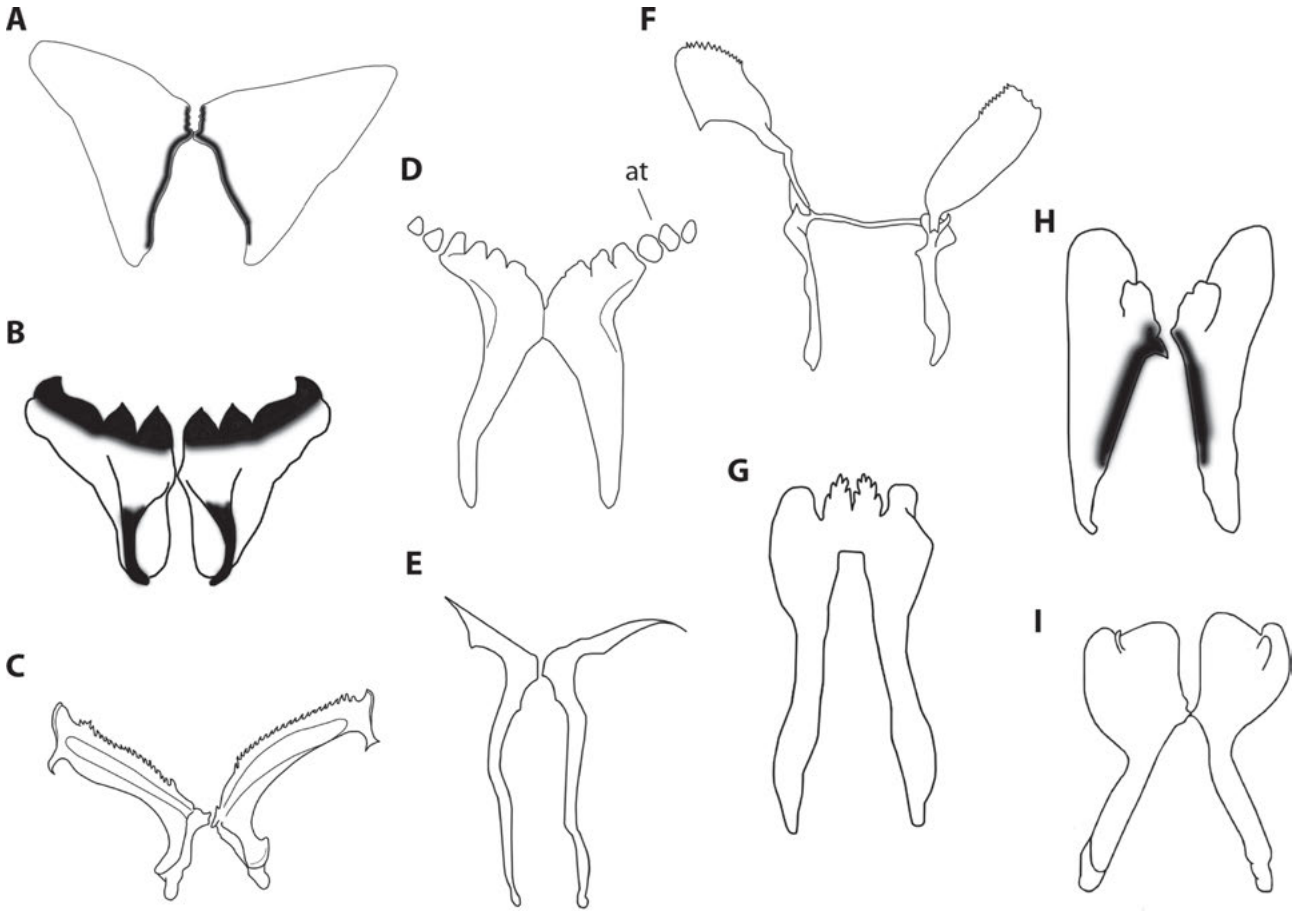


Fig. 7.12.2.4: Schematic drawings of different mandibulae. A, *Arenotrocha lanzarotensis* Brito & Nunez, 2003; B, *Petrocha notogaea* von Nordheim, 1987; C, *Exallopus intermedius* Hilbig & Blake, 1991; D, *Protodorvillea kefersteini* McIntosh, 1869; E, *Ikosipodus carolensis* Westheide, 1982; F, *Pseudophryotrocha serrata* Hilbig & Blake, 1991; G, *Pinniphitime pinnognatha* Orensanz, 1990; H, *Diaphorosoma magnavena* Wolf, 1986a; I, *Ougia tenuidentis* Wolf, 1986a. A, After Brito and Nunez 2003; B, After von Nordheim 1987; C, F, After Hilbig and Blake 1991; D, After George and Hartmann-Schroder 1985; E, After Westheide 1982; G, After Orensanz 1990; H, I, After Wolf 1986a.

(e.g., *Schistomeringos loveni* Kinberg, 1865) can both feed on detritus and bore into corals (Hutchings and Peyrot-Clausade 1988). Many *Ophryotrocha* species seems to be opportunistic, grazing on algae, bacterial mats, or detritus (Jumars et al. 2015); in organically enriched environments, several species may co-occur, reaching high densities (e.g., Wiklund et al. 2012, Ravara et al. 2015, Taboada et al. 2017). These enriched environments include marine mammal remains, which repeatedly have been shown to be colonized rapidly by *Ophryotrocha* species in high abundances (Ravara et al. 2015). This kind of opportunistic nutrition may be the most important clue why *Ophryotrocha* spp. can comparatively easily been kept in laboratory cultures and fed with frozen spinach (see Åkesson 1970). Therefore, in combination with a comparatively short generation time, *Ophryotrocha* spp. may be suitable candidates as test or model organisms for various kinds of studies (Åkesson 1967, 1970, 1973b, 1977, 1980, 1984, Åkesson and Costlow 1978, Dahlgren et al. 2001). Unfortunately, these animals did not make into the exclusive group of model organisms of this century and were even not considered in a recent contribution suggesting annelid model systems (Weigert and Bleidorn 2016).

Dorvilleids are generally small and have historically not been an important commercial group. However, recently *Ophryotrocha craigsmithi* Wiklund, Glover & Dahlgren, 2009 has been evaluated as a component in a coupled aquaculture experiment (Nederlof et al. 2019). The authors suggested that *O. craigsmithi* can be an important marine resource by being fed with fish feces and in turn being fed to the fish (Nederlof et al. 2019).

Reproduction and development in Dorvilleidae have been reviewed by Richards (1967), Westheide (1982), Paxton (2000), and Sella (2006). Sexes are usually

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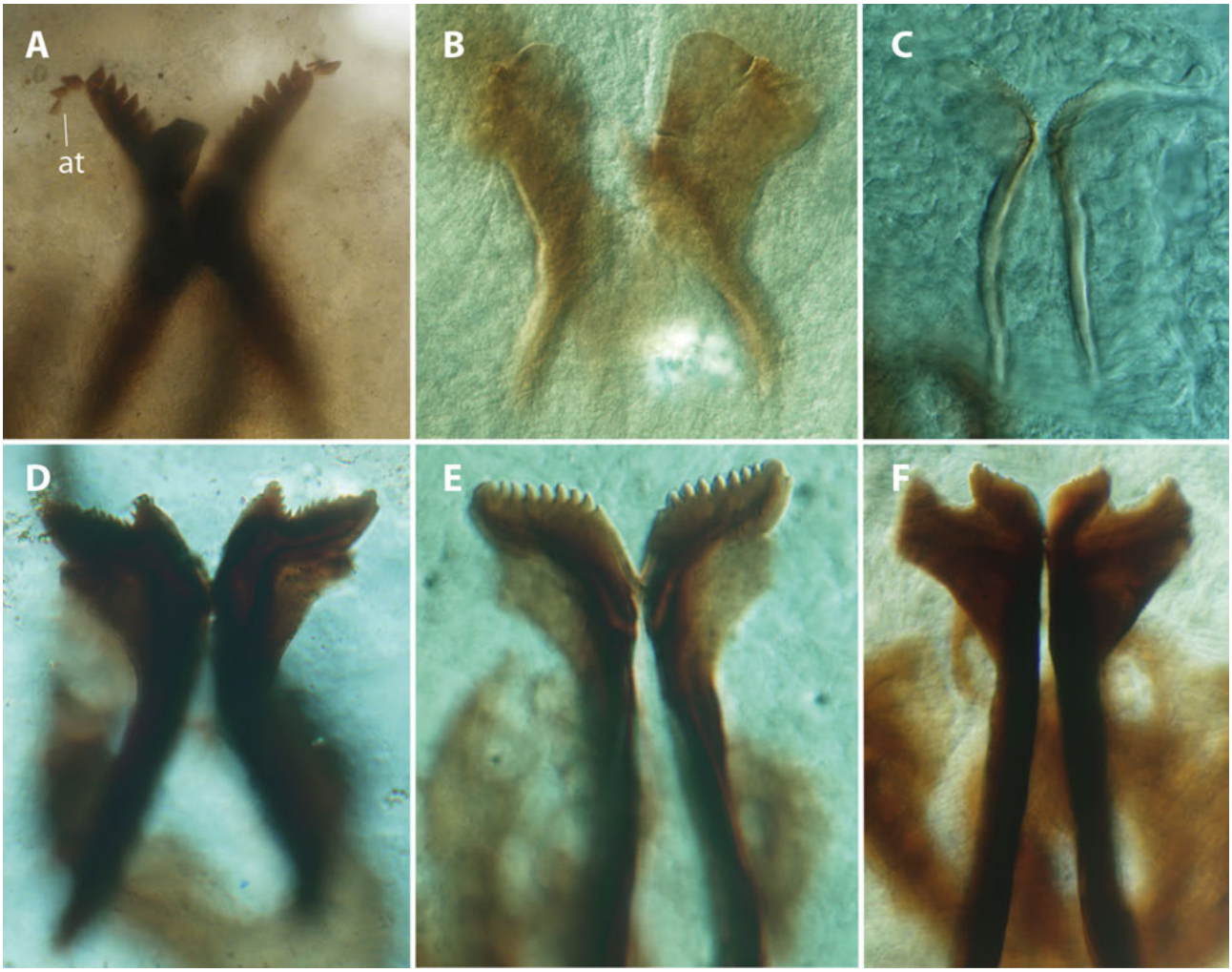


Fig. 7.12.2.5: Microscopy photographs of different mandibulae. A, *Dorvillea* sp. from the Gulf of Cadiz, ventral view; B, *Parougia* sp. from the Gulf of Cadiz, ventral view; C–F, *Ophryotrocha* sp. from the Gulf of Cadiz, ventral view. A–F c A. Ravara. ac, accessory teeth.

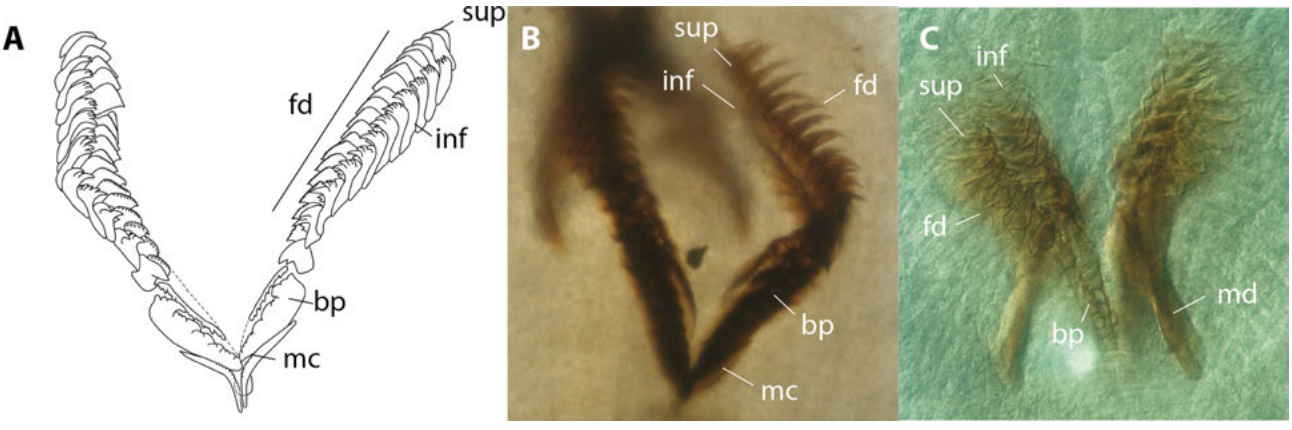


Fig. 7.12.2.6: Schematic figure and microscopy photographs of maxillary apparatus. A, *Protodorvillea bifida* Perkins, 1979, dorsal view; B, *Dorvillea* sp. from the Gulf of Cadiz, dorsal view; C, *Parougia* sp. from the Gulf of Cadiz, dorsal view. A, After Perkins 1979; B, C, c A. Ravara. bp, basal plate; fd, free denticles; inf, inferior row; mc, maxillary carriers; sup, superior row.

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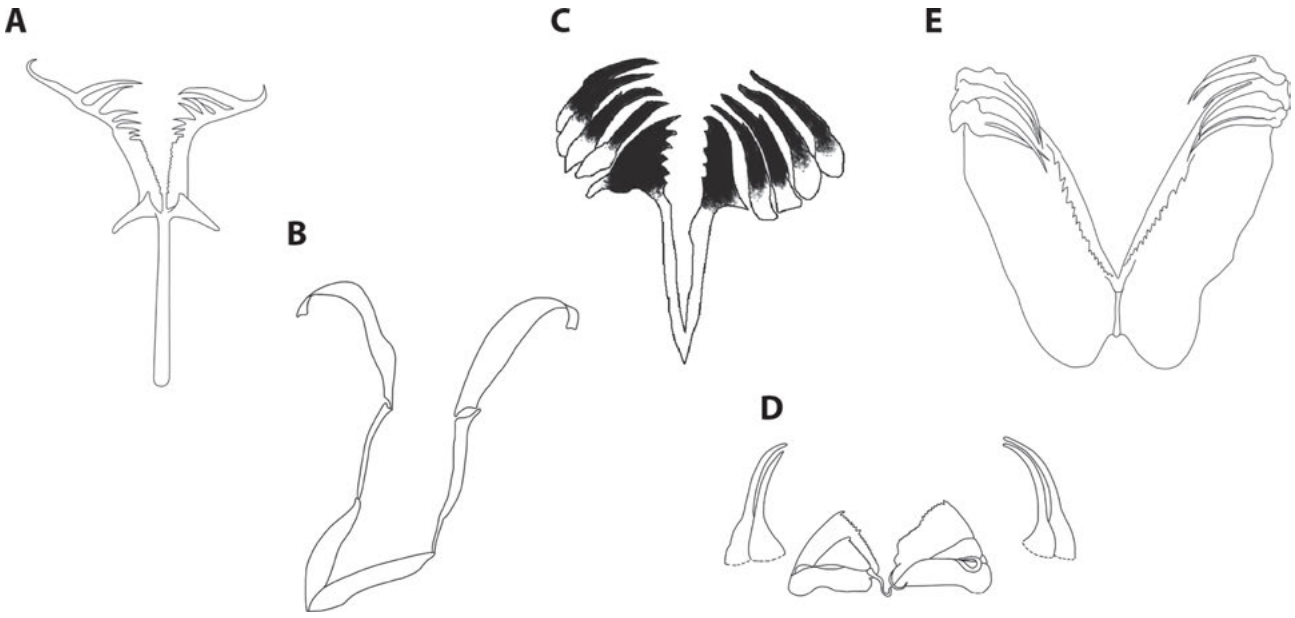


Fig. 7.12.2.7: Schematic drawings of different maxillary apparatus. A, *Westheideia minutimala* Wolf, 1986b; B, *P. serrata* Hilbig & Blake, 1991; C, *Anchidorvillea moniliformis* Hilbig & Blake, 1991; D, *Neotenotrocha sterreri* Eibye-Jacobsen & Kristensen, 1994; E, *Ikosipodus carolensis* Westheide, 1982. A, After Wolf 1986b; B, C, After Hilbig and Blake 1991; D, After Eibye-Jacobsen and Kristensen 1994; E, After Westheide 1982.

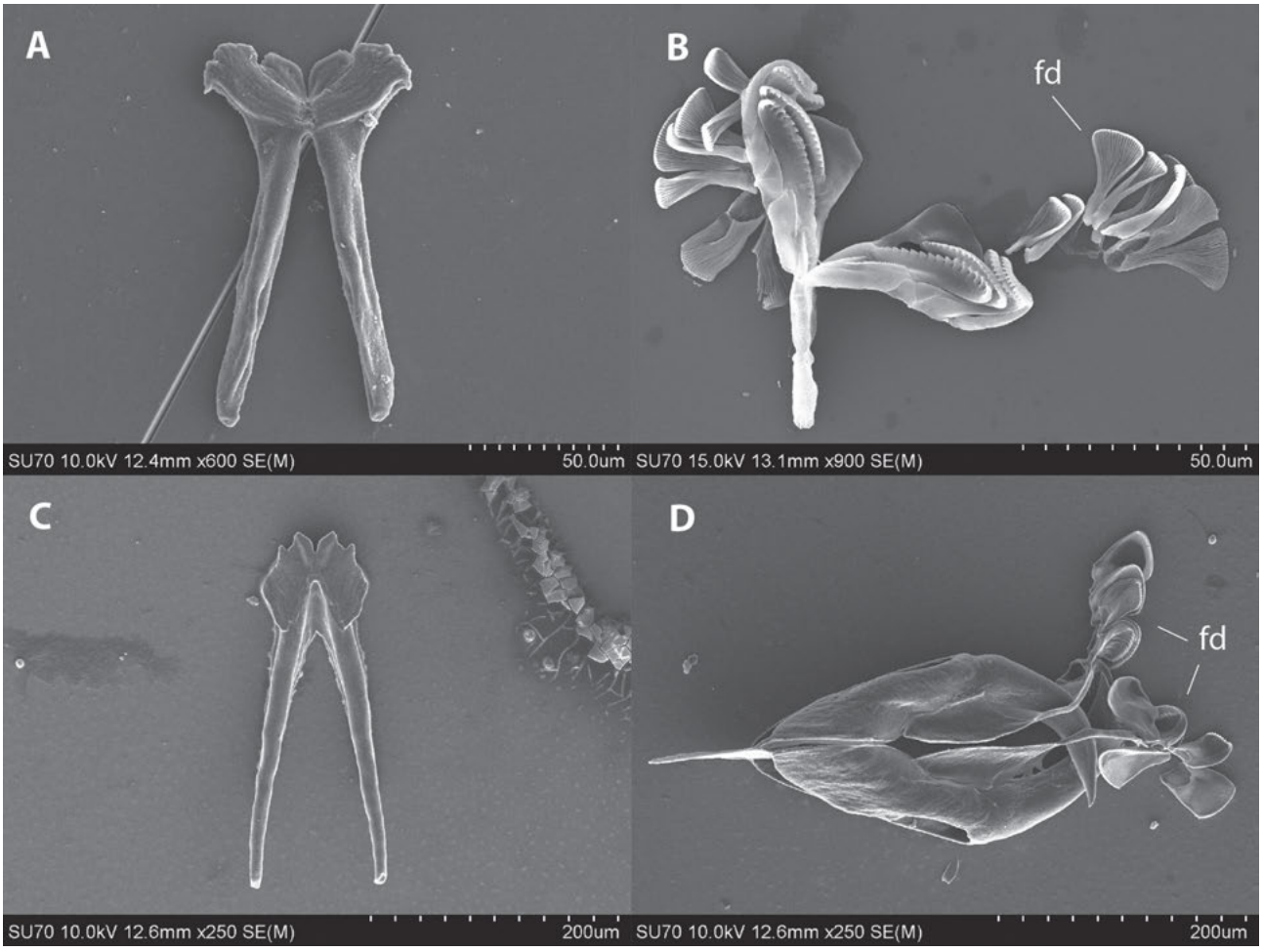


Fig. 7.12.2.8: Scanning Eletronic Microscopy images of mandibulae and maxillary apparatus of two *Ophryotrocha* species. **A**, **B**, *O. lusa* Ravara, Marçal, Wiklund & Hilário, 2015, mandibulae and P-type maxillae; **C**, **D**, *O. mammillata* Ravara, Marçal, Wiklund & Hilário, 2015, mandibulae and K-type maxillae. **A – D** © A. Ravara.

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separate and lack sexual dimorphism, except in certain *Ophryotrocha* species (Richards 1967, Åkesson 1975, Westheide 1982, Paxton 2000). Epitokal modification has been observed in *Dorvillea*, *Ougia*, *Parougia*, and *Protodorvillea* with enlarged eyes (Richards 1967, Oug 1978, Paxton 2000, Purschke and Nowak 2015) and in *Parougia* and *Protodorvillea* with longer chaetae (Oug 1978) (Fig. 7.12.2.9A-D). Asexual reproduction has been reported in *Parougia*, where fragments as small as two segments are able to regenerate into a whole worm (Åkesson and Rice 1992). Gonochorism, consecutive, and simultaneous hermaphroditism all occur in *Ophryotrocha*.

Oocytes and primordial germ cells and oogenesis have been studied in *O. puerilis* (see Pfannenstiel and Grünig 1982b, c). Sperm ultrastructure has been described in a number of *Ophryotrocha* species, which

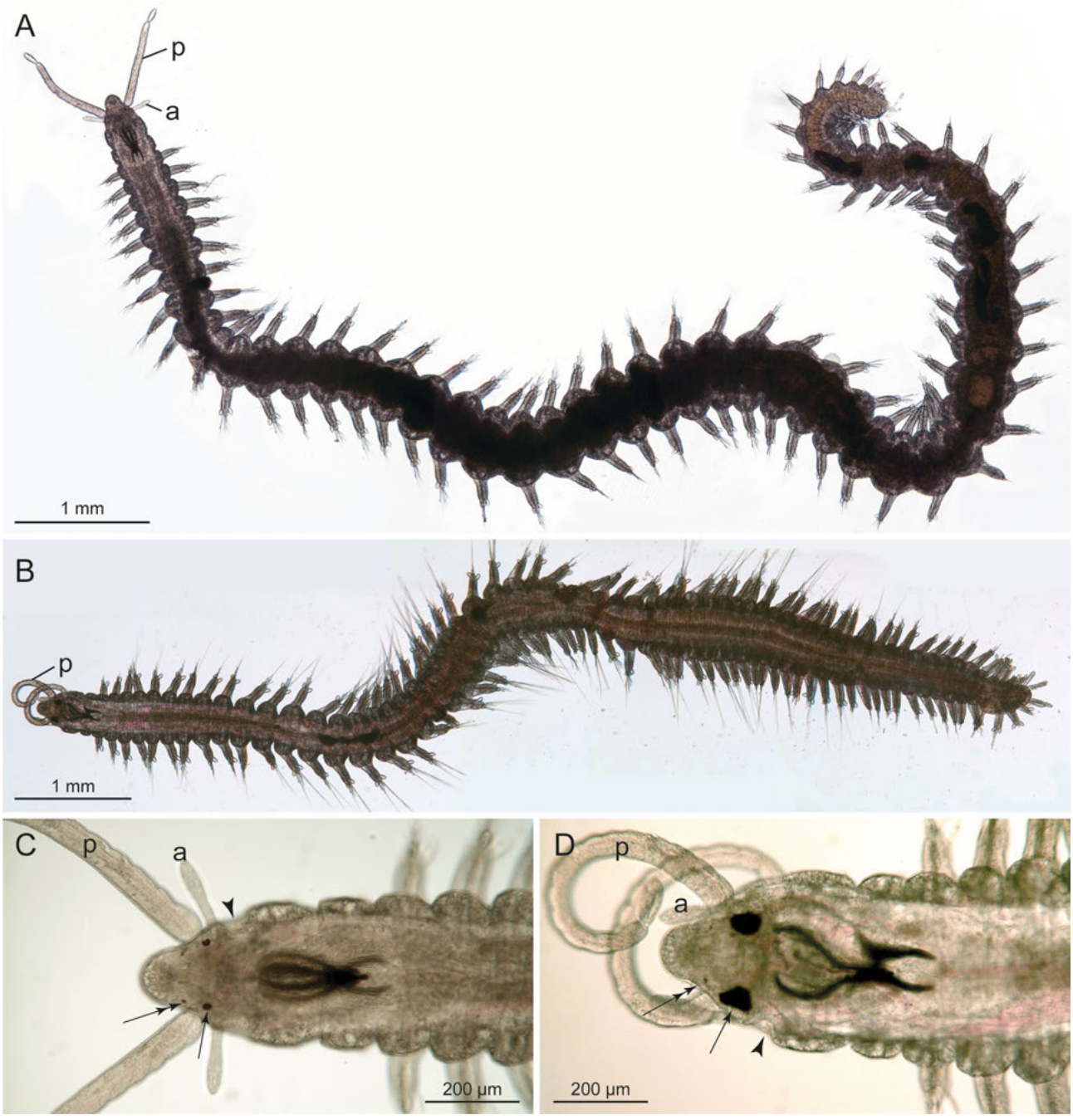


Fig. 7.12.2.9: Epitokous modification in Dorvilleidae. *Protodorvillea kefersteini* McIntosh, 1869 from Roscoff, France. Light micrographs of living specimens. A, B, Comparison of entire atoke and epitoke; eyes hardly visible; A, Atoke with shorter and fewer nonswimming chaetae; B, Epitoke with longer chaetae starting in chaetiger 3; C, D. Enlarged anterior ends to show the eyes; C, Atoke with small posterior eyes (arrow) and minute anterior eye (double arrow), arrowhead points to nuchal organ; D, Epitoke with enlarged posterior eyes (arrow), whereas the anterior eyes remained unchanged (double arrow), arrowhead: nuchal organs. a, antenna; p, palp.

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have first been described as aflagellate in *O. puerilis* (see Berruti et al. 1978). Subsequent studies, however, showed that the sperm are in fact presumably immotile but still possess a flagellum-like process, called flagellar equivalent (Troyer and Schwager 1979, Pfannenstiel and Grünig 1990). Preliminary data of spermatozoa are available for the interstitial dorvilleids *A. progenerans* and *I. carolensis* Westheide, 1982 (see Westheide 1982, 1988), both of which have been described from the receptacula semines and show characteristics typical of internal fertilization (Jamieson and Rouse 1989, Rouse 2006). Interestingly, in the former example, sperm are not fully mature when transferred to the female, and they finish spermatogenesis within the receptacles (Westheide 1988). The immotile introsperms in all studied *Ophryotrocha* species suggest internal fertilization or pseudocopulation, that is, release into egg case or cocoon (Jamieson and Rouse 1989). In some *Ophryotrocha* species, a mating behavior called egg trading has been observed, where two ovigerous hermaphrodites form a pair and then take turns in being an egg spawner and an egg fertilizer (Sella and Ramella 1999). Brooding has been observed in many cultured *Ophryotrocha* species, where eggs are released into a gelatinous egg mass that is protected by both parents (Fig. 7.12.2.10A, B) (Åkesson 1973b). The fertilized eggs develop to juveniles inside the egg mass (Fig. 7.12.2.10C). Viviparity occurs in a few *Ophryotrocha* species, which indicates that internal fertilization might take place (Jamieson and Rouse 1989). Although brooding is common for *Ophryotrocha* species, other dorvilleids have shown broadcast spawning after a brief swarming phase (Richards 1967). Studies by Richards (1967) on *S. rudolphi* delle Chiaje, 1828 showed that males spawn first, releasing sperms through segmental openings, and females normally begin their spawning activity as soon as some sperms are present. Larvae form within the first 24 hours and spend a week as lecithotrophic planktonic larvae before settling (Richards 1967).

Phylogeny and taxonomy

The first species in what is now Dorvilleidae was described by delle Chiaje in 1828 as *Nereis rudolphi* delle Chiaje, 1828. Some years later, Grube (1855) erected a new genus, *Staurocephalus* Grube, 1855 for the new species *Staurocephalus rubrovittatus* Grube, 1855. Kinberg (1865) described two more *Staurocephalus* species and placed all of them in a new family named Staurocephalea Kinberg, 1865. However, the genus name *Staurocephalus* was preoccupied in Crustacea, and Verrill (1900) replaced it with *Stauronereis* and moved it to a new family, Stauronereidae. In doing this, Verrill (1900) also changed the type species to *Stauronereis rudolphi* (delle Chiaje, 1828), which violated a nomenclatural rule in ICZN (Jumars 1974). Parfitt (1866) had described a new genus, *Dorvillea* Parfitt, 1866, seemingly placing it in Nereidae, and McIntosh (1910) synonymized Parfitt's species *Dorvillea lobata* Parfitt, 1866 with *S. rubrovittatus*. Chamberlin (1919) delved into the nomenclatural problems and suggested that *Staurocephalus* and *Stauronereis* should be synonymized

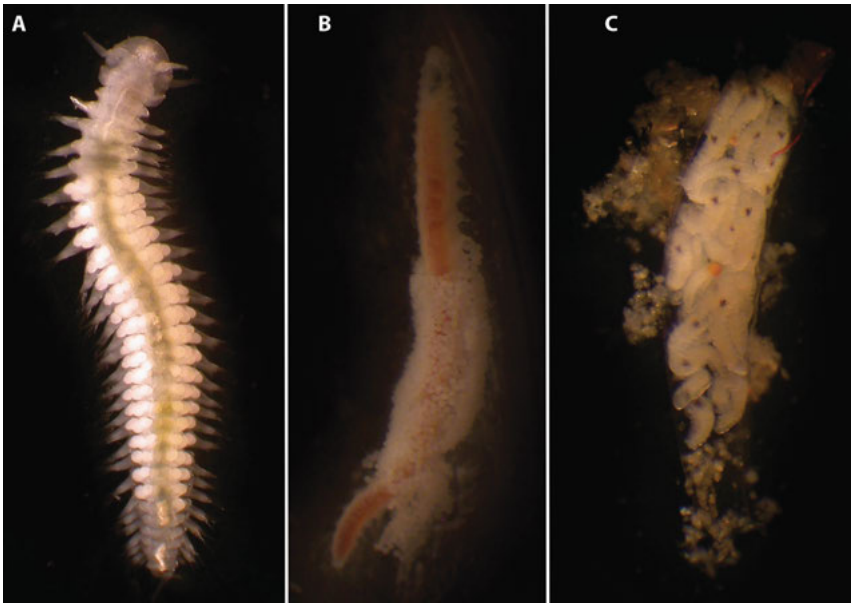


Fig. 7.12.2.10: Reproductive stages. A, *Ophryotrocha scutellus* Wiklund, Glover & Dahlgren, 2009, living specimen, dorsal view showing eggs present from chaetiger 5; B, *Ophryotrocha eutrophila* Wiklund, Glover & Dahlgren, 2009, living specimen, female with egg mass; C, *Ophryotrocha* sp., living specimens, juveniles ready to leave egg mass. A–C, © H. Wiklund.

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with *Dorvillea* Parfitt, 1866, as that was the next name applicable to the genus, and he erected the family name Dorvilleidae with *Dorvillea rubrovittata* (Grube, 1855) as type species for the genus *Dorvillea*. However, the nomenclature problems continue as the genus name *Dorvillea* Parfitt, 1866 is a junior homonym of the mollusc genus name *Dorvillea* Leach in Gray, 1852 (Read and Fauchald 2020).

Chamberlin (1919) listed only two genera in Dorvilleidae: *Dorvillea* and *Ophryotrocha*. Not until 1961 were more genera added by Pettibone (1961), who did a revision of the family and divided *Dorvillea* into four genera: *Dorvillea* Parfitt, 1866, *Papilliodorvillea* n. gen., *Protodorvillea* n. gen., and *Stauronereis* Verrill, 1900. *Papilliodorvillea* was later synonymized with *Dorvillea*, whereas species described within *Stauronereis* have been moved to several other dorvilleid genera: *Dorvillea, Parougia, Protodorvillea*, and *Schistomeringos*.

Three new genera, *Parapodrilus* Westheide, 1965, *Parophryotrocha* Hartmann-Schröder, 1971, and *Pettiboneia* Orensanz, 1973, were described within Dorvilleidae before Jumars (1974) embarked on the next family revision. Jumars returned to the earliest taxonomic questions and erected a new genus, *Schistomeringos* Jumars, 1974, for the dorvilleids with furcate chaetae, moving many species from the former genus *Stauronereis*, including the type species *S. rudolphi*. In addition to *Schistomeringos*, Jumars (1974) also erected three new genera in his revision, *Apophryotrocha* Jumars, 1974, *Exallopus* Jumars, 1974, and *Meiodorvillea* Jumars, 1974.

Iphitimidae Fauchald, 1970 was erected for the branchiate genus *Iphitime* Marenzeller, 1902, which was previously placed under the now unaccepted family name Lysaretidae Kinberg, 1865 (Fauchald 1970). However, when Armstrong and Jumars (1978) discovered two dorvilleid species in the North Pacific whose morphology was similar to iphitimids, they suggested that *Iphitime* belongs within Dorvilleidae, and Gaston and Benner (1981) formally synonymized Iphitimidae with Dorvilleidae. When Orensanz (1990) did a study of Antarctic eunicemorph polychaetes, he argued that the two families should be separated, and he erected several new genera within Iphitimidae in addition to moving *Exallopus*, *Ophryotrocha*, *Parophryotrocha*, and *Veneriserva* from Dorvilleidae to Iphitimidae. His new genera *Mammiphitime* Orensanz, 1990, *Palpiphitime* Orensanz, 1990, and *Pinniphitime* Orensanz, 1990 contain both some newly described species and some species and specimens formerly identified as *Ophryotrocha*. Furthermore, he raised a hypothesis that Dorvilleidae, Iphitimidae, and Dinophilidae Macalister, 1876 form a clade based on maxillary characters (Orensanz 1990). Eibye-Jacobsen and Kristensen (1994) did a phylogenetic analysis of those families using 38 morphological characters, and based on their results, they proposed that both Iphitimidae and Dinophilidae belong within Dorvilleidae (Eibye-Jacobsen and Kristensen 1994). However, subsequent molecular analyses did not place Dinophilidae close to Dorvilleidae (e.g., Struck et al. 2005), and according to Struck et al. (2015), Dinophilidae is sister to Nerillidae in a group called Orbiniida (Struck et al. 2015). This view is followed here in the handbook; thus, Dinophilidae are placed within Orbiniida now (see Struck 2019, Westheide 2019, chapters phylogeny and Dinophilidae, respectively). Within Dorvilleidae, molecular phylogenetic analyses have been presented for the genus *Ophryotrocha* only by Dahlgren et al. (2001) and Heggøy et al. (2007).

The family Dorvilleidae needs a revision, preferably combining morphological characters with molecular data. Wiklund et al. (2012) synonymized Orensanz's *Palpiphitime* with *Ophryotrocha*, as the type species, which was originally described as an *Ophryotrocha*, fell well within that clade using three genes. Species from other genera that also fall within *Ophryotrocha* in molecular analyses include *Exallopus* and *Iphitime* (Wiklund et al. 2012, Taboada et al. 2013), although formal synonymy has not been possible due to the lack of molecular data from the respective type species of the two genera. The genera *Mammiphitime* and *Pinniphitime* erected by Orensanz (1990) might also belong to *Ophryotrocha*. The genus *Mammiphitime* was justified by the large dorsal lobes in median and posterior segments (Orensanz 1990), but since then another species with similar lobes has been described, *O. mammillata* Ravara et al. 2015, and molecular data placed it within *Ophryotrocha*. As such, the unique character used by Orensanz (1990) is not informative, and in the key to dorvilleid genera in this chapter, *Ophryotrocha* and *Mammiphitime* fall on the same line. Furthermore, molecular data might be needed to separate cryptic species of dorvilleids. Within the genus *Ophryotrocha*, morphological species have been found to consist of genetically divergent lineages that might represent different species, e.g., *O. puerilis* Claparède & Mecznikow, 1869 (Taboada et al. 2017) and *O. labronica* La Greca & Bacci, 1962 (Cossu et al. 2015).

Jaws of dorvilleids fossilize well and three species have been formally described from jaw elements. *Schistomeringos expectatus* Szaniawski & Gaździcki, 1978 was described from Upper Jurassic material in Poland based on maxilla I (MI) elements. Van Erve (1981) later found jaws that he identified as this species in material from Lower Jurassic in northeastern Italy, with similar MI

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elements, but additionally with maxilla II (MII) elements that resemble those of recent *Schistomeringos* species. In the same paper, Van Erve mentioned jaw forms that he assigned to *Dorvillea* from Middle Cretaceous in southeastern France; he cited this as "in preparation" but seemingly never published the results (Van Erve 1981). Two *Ophryotrocha* species have been described from fossil records, and other materials have been assigned to the genus level only. The two described species are *Ophryotrocha antarctica* Szaniawski & Wrona, 1987 from Lower Miocene material at King George Island in Antarctica and *Ophryotrocha lukowensis* Szaniawski, 1974 from Middle Jurassic material in eastern Poland. Intermediate to these in time is *Ophryotrocha* sp. from Upper Cretaceous material in southern Sweden (Eriksson and Lindström 2000).

Dorvilleidae Chamberlin, 1919
Type genus: *Dorvillea* Parfitt, 1866
Diagnosis: (After Chamberlin 1919, emended by Jumars 1974, Hilbig 1995) Body slender and cylindrical in shape. Prostomium with or without one or two pairs of eyes, paired antennae and palps. When present, antennae and palps can be simple or articulated. Eversible pharynx usually with well-developed jaws consisting of a pair of mandibles and numerous maxillary plates, reduced or absent in some genera. Peristomium comprised two achaetous rings, no true segments. Parapodia subbiramous with notopodia consisting of dorsal cirrus with an internal acicula, uniramous or absent. Neuropodium sometimes have conical, retractable ventral lobe in addition to acicular lobe. Branchiae present or absent. Supra-acicular chaetae smooth or serrated capillaries and spines, sometimes furcate. Subacicular chaetae homogomph or heterogomph falcigers or spinigers. Some genera have only simple or only compound chaetae. Pygidium with central or dorsal anus and often one or two pairs of anal cirri.

Anchidorvillea Hilbig & Blake, 1991
Type species: *Anchidorvillea moniliformis* Hilbig & Blake, 1991
This genus is monospecific.
Diagnosis: (After Hilbig and Blake 1991) Body cylindrical and slender, with slightly reduced segmental ciliation. Prostomium with two long, multiarticulate antennae and two cirriform smooth palps of subequal length. Jaws with elongate mandibles with short anterior cutting edge. Maxillae consisting of five pairs of heavy denticles, the posteriormost pair joined by a ligament and slightly resembling P-type forceps of *Ophryotrocha*, other denticles free, fang-shaped, distally pointed or bidentate, arranged in two rows. Parapodia uniramous with short and papilliform dorsal cirri, and long cirriform ventral cirri extending well beyond acicular lobe. Supra-acicular chaetae simple, shorter in anterior chaetigers, initially bifid, then gradually changing to long capillaries. Subacicular chaetae compound, heterogomph falcigers. Subacicular chaetal lobe supported by inferiormost compound chaeta.

Apodotrocha Westheide & Riser, 1983
Type species: *Apodotrocha progenerans* Westheide & Riser, 1983
This genus is monospecific.
Diagnosis: (After Westheide and Riser 1983) Prostomium without appendages, no muscular pharynx, jaws absent. Six segments lacking parapodia, appendages, and chaetae. The pygidium is fused with the last segment and bears three appendages; the unpaired one is located ventrally.

Apophryotrocha Jumars, 1974
Type species: *Apophryotrocha mutabiliseta* Jumars, 1974
This genus is monospecific.
Diagnosis: (After Jumars 1974) Prostomium roughly hemispherical with very long and cirriform antennae and well-developed subulate palps, shorter than antennae. Jaws with both pairs of carrier-like structures and all four basal plates fused in an ice-tong shape, no free denticles. Parapodia uniramous with simple capillary and heterogomph compound chaetae.

Arenotrocha Westheide & von Nordheim, 1985
Type species: *Ophryotrocha minuta* Lévi, 1954 accepted as *Arenotrocha minuta* (Lévi, 1954)
This genus contains two species.
Diagnosis: (After Westheide and von Nordheim 1985) Prostomium with two broad palps and two slender antennae, palps and antennae of approximately equal length and without articulations. Jaws with simple butterfly-wing-shaped mandibles and two rows of a few delicate maxillary plates, the anterior with few fang-like denticles. Four nuchal organs. Two anterior apodous rings followed by homonomous chaetigers, parapodia uniramous without cirri. Chaetae simple serrate capillaries and heterogomph falcigers. Pygidium with two slender terminal anal appendages and ventrally a short median cirrus.

Coralliotrocha Westheide & von Nordheim, 1985
Type species: *Coralliotrocha natans* Westheide & von Nordheim, 1985
This genus contains two species.

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Diagnosis: (After Westheide and von Nordheim 1985) Conspicuous ciliary rings on all parts of the body. Prostomium with two biarticulate palps with long palpophores and two multiarticulate long antennae. Jaw apparatus with wing-shaped mandibles and four rows of delicate maxillary elements, two of which have posterior basal plates, anterior plates bowl-shaped with serrated margins. Two apodous anterior rings, parapodia uniramous with dorsal and ventral cirri, except in the first chaetiger. Chaetae include serrate geniculate capillaries, furcate chaetae with very fine tines, and compound heterogomph falcigers. Two slender dorsal and one short ventral anal appendages.

Diaphorosoma Wolf, 1986

Type species: *Diaphorosoma magnavena* Wolf, 1986

This genus is monospecific.

Diagnosis: (After Wolf 1986a) Prostomium with long, articulated antennae and biarticulated palps. Jaws with maxillae in four rows, each row composed entirely of free denticles, basal plates lacking. Maxillary carriers absent. Parapodia with long anterior notopodia, slender with internal acicula, and small posterior ones without internal acicula. Branchiae present on anterior parapodia. Supra-acicular chaetae simple, tapering to bidentate tips. Furcate chaetae absent. Subacicular chaetae bidentate compound and pseudocompound falcigers.

Dorvillea Parfitt, 1866

Type species: *Dorvillea lobata* Parfitt, 1866 accepted as *Dorvillea rubrovittata* (Grube, 1855)

This genus contains 20 species.

Diagnosis: (After Hilbig 1995) Prostomium with well-developed antennae and palps, antennae usually moniliform, palps biarticulate. Jaws with dark triangular mandibles with few large teeth along cutting edge and often several lateral free conical teeth. Maxillae heavily sclerotized, visible through body wall, consisting of maxillary carrier-like structures and four rows of denticles, the posterior ones fused to form superior and inferior basal plates. Parapodia subbiramous throughout, except for chaetiger 1, with notopodium consisting of dorsal cirrus and acicula projecting into the cirrostyle. Chaetae simple capillaries and heterogomph falcigers.

Eliberidens Wolf, 1986

Type species: *Eliberidens forceps* Wolf, 1986

This genus contains two species.

Diagnosis: (After Wolf 1986a) Prostomium with palps and antennae similar to each other in size and shape, each simple, smooth, digitiform. Maxillae in four rows, each row with superior and inferior basal plates only, free denticles entirely lacking. Maxillary rows fused posteriorly to very small and thin, reduced maxillary carrier-like structures apparently fused to posteriorly directed ligament. Parapodia uniramous. Supra-acicular chaetae include simple, serrate, tapering forms with or without furcate chaetae. Subacicular chaetae compound, unidentate falcigers.

Exallopus Jumars, 1974

Type species: *Exallopus cropion* Jumars, 1974

This genus contains five species.

Diagnosis: (After Jumars 1974, emended by Hilbig 1991, Hilbig and Blake 1991) Body cylindrical and slender or dorsoventrally compressed and stout, sometimes incompletely ciliated or lacking cilia. Prostomium with two cirriform smooth or annulated antennae and two cirriform or biarticulated palps, about equal in length to antennae. Jaws with L-shaped mandibles with cutting edge as long as or longer than handle. Maxillae with fused carrier-like structures and basal plates resembling P-type forceps in *Ophryotrocha* and four to seven pairs of free denticles. Parapodia uniramous, usually with ventral chaetal lobe in addition to acicular lobe. With or without dorsal and ventral cirri, when present cirri short, never extending beyond acicular lobe. Supra-acicular chaetae simple, subacicular chaetae homogomph or heterogomph falcigers or spinigers. Chaetae in anterior 10 chaetigers modified in size and shape, change between modified and unmodified chaetae abrupt. Subacicular chaetal lobe with simple chaeta.

Gymnodorvillea Wainwright & Perkins, 1982

Type species: *Gymnodorvillea floridana* Wainwright & Perkins, 1982

This genus is monospecific.

Diagnosis: (After Wainwright and Perkins 1982) Body minute and slender with about 20 to 30 chaetigers. Prostomium pear-shaped with two encircling bands of cilia, lacking antennae and palps. Jaws with mandibles and two rows of maxillary denticles with reduced basal plates, carrier-like structures reduced if present. Denticle rows fused posteriorly with denticles of three types: rounded serrate, serrate with principal tooth, and spinous. Mandibles without free lateral teeth. Parapodia uniramous without dorsal cirri, ventral cirri beginning on chaetiger 2. Chaetae including serrate capillary, furcate, geniculate, and cultriform simple chaetae and heterogomph falcigers.

Ikosipodoides Westheide, 2000

Type species: *Ikosipodoides seychellensis* Westheide, 2000

This genus is monospecific.

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Diagnosis: (After Westheide 2000) Prostomium with one pair of ventrolateral palps, muscular pharyngeal bulb without jaws. Two apodous rings followed by seven chaetigerous segments. Parapodia uniramous with compound chaetae. Pygidium with three anal appendages.

Ikosipodus Westheide, 1982
Type species: *Ikosipodus carolensis* Westheide, 1982
This genus is monospecific.
Diagnosis: (After Westheide 1982) Prostomium with one pair of lateroventral palps, jaws with small mandibles, and maxillary elements consist of one pair of carrier-like structures, one pair of basal plates, and several denticles on each side. Two apodous rings and 10 segments with uniramous parapodia and compound chaetae. Pygidium with a pair of anal appendages.

Iphitime Marenzeller, 1902
Type species: *Iphitime doederleini* Marenzeller, 1902
This genus contains seven species.
Diagnosis: (After Marenzeller 1902, emended by Fauchald 1970) Prostomium with two small antennae, without palps and eyes. Jaws with mandibles fused medially over nearly half their length, maxillae with carrier-like structures fused to maxillae I. Parapodia are uniramous with large postchaetal and shorter prechaetal lobes. Simple and compound falcate chaetae present. Branchiae always present, simple or branched.

Mammiphitime Orensanz, 1990
Type species: *Mammiphitime tridentata* Orensanz, 1990
This genus contains two species.
Diagnosis: (After Orensanz 1990) Prostomium with two antennae, without palps. Jaws with mandibles not fused, maxillae of P- or K-type with eight pairs of maxillary elements. Parapodia uniramous, distally partitioned into two lobes, a round prechaetal acicular lobe and a ventral retractile lobe. Median and posterior segments with well-developed dorsal lobes. Supra-acicular chaetae simple, subacicular chaetae compound spinigers, subacicular retractable lobe with a simple chaeta.

Marycarmenia Nuñez, 1998
Type species: *Protodorvillea gaspeensis* Pettibone, 1961 accepted as *Marycarmenia gaspeensis* (Pettibone, 1961)
This genus contains two species.
Diagnosis: (After Nuñez 1998) Body minute and slender, with up to 30 chaetigers. Prostomium pear-shaped, with two short and smooth dorsal antennae and two biarticulate ventrolateral palps. Jaws with elongated mandibles denticled anteriorly, two rows of maxillary structures and free denticles. Maxillary carriers absent. Parapodia uniramous, dorsal cirri absent, ventral cirri not extending beyond neuropodial lobe. Branchiae absent. Supra-acicular fascicle with serrate capillary and furcate chaetae, subacicular fascicle with heterogomph falcigers and occasionally inferior simple chaeta. Pygidium with four anal cirri.

Meiodorvillea Jumars, 1974
Type species: *Protodorvillea minuta* Hartman, 1965 accepted as *Meiodorvillea minuta* (Hartman, 1965)
This genus contains three species.
Diagnosis: (After Jumars 1974) Prostomium roughly pear shaped. Palps very small or absent. When present, either simple or biarticulate. Antennae small and clavate, longer than the palps when both pairs of appendages are found. Jaws with carrier-like structures and two rows of denticles always present, although rows of denticles may be represented by only basal plates. Parapodia with or without small dorsal cirri. Three kinds of chaetae, capillary, furcate or geniculate, and compound heterogomph.

Microdorvillea Westheide & von Nordheim, 1985
Type species: *Microdorvillea otagensis* Westheide & von Nordheim, 1985
This genus contains two species.
Diagnosis: (After Westheide and von Nordheim 1985) All parts of the body with ciliary rings. Prostomium with paired biarticulate palps and paired slender inarticulate antennae. Jaws with paddle-shaped mandibles and four rows of delicate maxillary elements comprising two posterior basal plates, plates with numerous distinct denticles and two anterior plates on each side with larger fang-like denticles. Uniramous parapodia without dorsal or ventral cirri. Chaetae including capillaries and compound heterogomphs.

Neotenotrocha Eibye-Jacobsen & Kristensen, 1994
Type species: *Neotenotrocha sterreri* Eibye-Jacobsen & Kristensen, 1994
This species is monospecific.
Diagnosis: (After Eibye-Jacobsen and Kristensen 1994) Prostomium with row of rectangular ciliophores, an apical ciliary tuft, and an adhesive apparatus. Lacking antennae, palps, and eyes. Peristomium with row of ciliophores and lateral nuchal organs. Jaws with mandibles, maxillary apparatus consisting only of superior basal plates and two pairs of superior denticles. Parapodia, parapodial cirri, and chaetae absent. Adults with complete trochae, including retained prototroch, metatroch, and telotroch; neurotroch present in adults. Pygidium with three anal cirri.

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Ophryotrocha Claparède & Mecznikow, 1869
Type species: *Ophryotrocha puerilis* Claparède & Mecznikow, 1869
This genus contains 75 extant and 2 fossil species.
Diagnosis: (After Hilbig and Blake 1991) Body cylindrical, slender or dorsoventrally compressed, usually with segmental ciliary bands or tufts. Prostomium with or without two antennae and two palps, both appendages either simple or biarticulated; papilliform or cirriform. Mandibles rod-like with short anterior cutting edge or L-shaped with cutting edge about as long as shaft. Maxillae composed of forceps, formed of fused maxillary carrier-like structures and basal plates, and at least five pairs of free denticles of variable shapes arranged in two or four rows, sometimes reduced. Parapodia uniramous, with or without subacicular lobe in addition to acicular lobe. With or without dorsal and ventral cirri. Supra-acicular chaetae simple, capillary to cultriform, smooth to coarsely serrated. Subacicular chaetae mostly compound, blades falcigerous or spinigerous. Subacicular lobe supported by simple or compound inferiormost chaeta.

Ougia Wolf, 1986
Type species: *Ougia tenuidentis* Wolf, 1986
This genus contains two species.
Diagnosis: (After Wolf 1986a) Prostomium with two long antennae, sometimes articulated, and long biarticulated palps. Jaws with maxillae in four rows, superior rows with basal plates and free denticles, and inferior rows without basal plates, with free denticles. Maxillary carrier-like structures present. Notopodia with or without distal article, with internal acicula throughout. Supra-acicular chaetae simple, with or without furcate chaetae. Subacicular chaetae include compound falcigers and occasionally inferior simple chaetae in far posterior chaetigers.

Parapodrilus Westheide, 1965
Type species: *Parapodrilus psammophilus* Westheide, 1965
This genus contains two species.
Diagnosis: (After Westheide 1965) Slender body with rounded conical prostomium, lacking antennae and palps. No muscular pharynx or jaws. Two apodous rings followed by four chaetigers, an apodous segment and pygidium.

Parophryotrocha Hartmann-Schröder, 1971
Type species: *Ophryotrocha isochaeta* Eliason, 1962 accepted as *Parophryotrocha isochaeta* (Eliason, 1962)
This genus contains four species.
Diagnosis: (After Hilbig and Blake 1991, emended by Oug 2006) Body cylindrical and slender, completely ciliated. Prostomium with simple antennae, with or without palps. Jaws with elongate mandibles with short cutting edge. Maxillae composed of P- or K-type forceps and five to seven pairs of free denticles arranged in four rows. Parapodia uniramous with or without dorsal and ventral cirri, subacicular chaetal lobes present or absent. Chaetae all simple.

Parougia Wolf, 1986
Type species: *Schistomeringos nigridentata* Oug, 1978 accepted as *Parougia nigridentata* (Oug, 1978)
This genus contains 11 species.
Diagnosis: (After Wolf 1986b) Prostomium with well-developed, articulated antennae. Palps well-developed, stout, biarticulate, shorter than antennae. Jaws with mandibles dentate anteriorly and maxillae in four rows. Superior maxillary rows with basal plates and free denticles, basal plates composed of five to seven fused free denticles. Inferior maxillary rows without basal plates, with free denticles. Maxillary carriers absent. Parapodia with well-developed, biarticulate notopodia, with internal notoacicula. Supra-acicular chaetae include simple minutely bidentate forms, furcate chaetae, when present, with long thin tines. Subacicular chaetae compound, bidentate falcigers. Pygidium with two dorsal anal cirri and single midventral cirrus.

Petrocha von Nordheim, 1987
Type species: *Petrocha notogaea* von Nordheim, 1987
This species is monospecific.
Diagnosis: (After von Nordheim 1987) Prostomium with two digitiform simple lateral palps. Jaws with mandibles semicircularly arranged with anterior region crown-shaped and four rows of maxillary plates. Maxillae distally well denticulated and sclerotized and basally fused to weakly sclerotized undenticulated lateral plates. Some of the lateral plates are connected posteriorly to a very reduced carrier-like element. Two anterior apodus rings followed by homonomous chaetigers. All parts of the body encircled by complete ciliary rings. Parapodia uniramous without any cirri or lobes. Chaetae simple capillaries and compound heterogomph falcigers. Pygidium with two digitiform pygidial appendages caudolaterally and a very small median process ventrally.

Pettiboneia Orensanz, 1973
Type species: *Pettiboneia sanmatiensis* Orensanz, 1973
This genus contains 12 species.
Diagnosis: (After Blake 1979, Orensanz 1990) Prostomium with simple antennae and well-developed, biarticulated palps. Jaws with mandibles and seven pairs of denticle rows, no carriers. Parapodia with small elongated dorsal

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cirri bearing notoacicula anteriorly, dorsal cirri missing in posterior body. Chaetae serrated capillaries, furcate and compound.

Pinniphitime Orensanz, 1990
Type species: *Pinniphitime pinnognatha* Orensanz, 1990
This species is monospecific.
Diagnosis: (After Orensanz 1990) Prostomium without conspicuous appendages. Jaws with fused mandibles with distal pinnate inner lobes, three pairs of elongate maxillae. Parapodia uniramous, supra-acicular chaetae simple and subacicular chaetae compound falcigers. Subacicular retractable lobe with simple chaeta. Pygidium with two anal cirri.

Protodorvillea Pettibone, 1961
Type species: *Staurocephalus kefersteini* McIntosh, 1869 accepted as *Protodorvillea kefersteini* (McIntosh, 1869)
This genus contains nine species.
Diagnosis: (After Pettibone 1961) Prostomium with two short antennae, antennae sometimes absent, and two longer palps. Jaws with elongated mandibles, flared and denticled anteriorly. Maxillae four longitudinal rows of numerous denticled plates (two rows on each side). Parapodia uniramous, with short dorsal and ventral cirri. Supra-acicular chaetae simple capillaries or furcate, subacicular chaetae compound heterogomphs.

Pseudophryotrocha Hilbig & Blake, 1991
Type species: *Pseudophryotrocha serrata* Hilbig & Blake, 1991
This genus contains three species.
Diagnosis: (After Hilbig and Blake 1991) Prostomium with or without two short, clavate antennae, palps lacking. Jaws with elongate mandibles with short cutting edge or L-shaped with cutting edge as long as handle, weakly sclerotized. Maxillae consisting of three pairs of elongate, unsclerotized, smooth plates. Proximal pair of plates basally linked by ligament, the other two pairs free. Parapodia uniramous, without dorsal and ventral cirri. Supra-acicular chaetae simple, subacicular chaetae mostly compound, homogomph or heterogomph falcigers. Subacicular lobe with simple chaeta.

Pusillotrocha Westheide & von Nordheim, 1985
Type species: *Pusillotrocha akessoni* Westheide & von Nordheim, 1985
This species is monospecific.
Diagnosis: (After Westheide and von Nordheim 1985) Prostomium with two digitiform simple palps, no antennae. Jaws with shoulder-blade-shaped mandibles and a few delicate maxillary elements, comprising serrated posterior plates, anterior plates with long denticles and carrier-like elements. Two anterior apodous rings followed by homonomous chaetigers. Uniramous parapodia without dorsal or ventral cirri. Supra-acicular chaetae simple serrate capillaries and subacicular chaetae compound heterogomphs. Pygidium with two digitiform anal appendages.

Schistomeringos Jumars, 1974
Type species: *Nereis rudolphi* delle Chiaje, 1828 accepted as *Schistomeringos rudolphi* (delle Chiaje, 1828)
This genus contains 16 extant and 1 fossil species.
Diagnosis: (After Jumars 1974) Prostomium with well-developed multiarticulate antennae and biarticulate palps of approximately equal lengths. Jaws with maxillary carrier-like structures that may be fused with basal plates of superior rows of denticles, but four distinct denticle rows always apparent. Basal plates of inferior denticle rows free. Parapodia with dorsal and ventral cirri, dorsal cirri biarticulate with acicula. Three kinds of chaetae, simple capillary and furcate, and compound heterogomphs.

Veneriserva Rossi, 1984
Type species: *Veneriserva pygoclava* Rossi, 1984
This species is monospecific.
Diagnosis: (After Rossi 1984) Prostomium without appendages. Jaws with mandibles completely fused medially into a single structure. One pair of maxillae, fused basally with carrier-like structures that are fused medially. Parapodia uniramous with simple chaetae.

Westheideia Wolf, 1986
Type species: *Westheideia minutimala* Wolf, 1986
This species is monospecific.
Diagnosis: (After Wolf 1986a) Prostomium with indistinctly articulated antennae similar in lengths to the biarticulated palps. Jaws with maxillae in two rows, each row composed of single plate, serrate posteriorly, with denticles anteriorly. Maxillary carrier-like structures fused to posteriorly directed ligament. Parapodia with notopodia on anterior chaetigers only, each without distal article but with internal acicula. Branchiae present on anterior parapodia. Supra-acicular chaetae simple including long, evenly tapered forms and furcate forms. Subacicular chaetae compound, unidentate falcigers.

Key for the genera of Dorvilleidae (adapted from Eibye-Jacobsen and Kristensen 1994):

1. Notopodia with notoaciculae present (except *Parougia diapason* Taboada, Bas & Avila, 2015) **2**
   —Notopodia with notoaciculae absent **8**

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2. Notopodia on anterior chaetigers only; neuropodial branchiae usually present **3**
—Notopodia on most chaetigers; neuropodial branchiae absent **5**
3. Maxillary carriers and superior basal plates present ***Westheideia***
—Maxillary carriers and superior basal plates absent **4**
4. Antennae simple; inferior free denticles absent; furcate chaetae present ***Pettiboneia***
—Antennae articulated; inferior free denticles present; furcate chaetae absent ***Diaphorosoma***
5. Anterolateral accessory mandibular teeth present (Fig. 7.12.2.4D, 7.12.2.5A); pygidium with four anal cirri; furcate chaetae present or absent **6**
—Mandibles without accessory teeth; pygidium with three anal cirri; furcate chaetae usually present **7**
6. Furcate chaetae absent ***Dorvillea***
—Furcate chaetae present ***Schistomeringos***
7. Maxillary carriers present; ventral neuropodial chaetal lobe absent ***Ougia***
—Maxillary carriers absent; ventral neuropodial chaetal lobe present (except *Parougia macilenta*) (Oug, 1978) ***Parougia***
8. Furcate chaetae present **9**
—Furcate chaetae absent **14**
9. Maxillary apparatus with more than eight superior free denticles; pygidium with four anal cirri **10**
—Maxillary apparatus with eight or fewer superior free denticles; pygidium with two or three anal cirri **12**
10. Antennae and palps simple; mandibles without accessory teeth; maxillary inferior basal plates and free denticles absent ***Meiodorvillea***
—Palps biarticulated; anterolateral accessory mandibular teeth present; maxillary inferior basal plates and free denticles present **11**
11. Antennae multiartculated; dorsal cirri present ***Protodorvillea***
—Antennae simple; dorsal cirri absent ***Marycarmenia***
12. Antennae and palps articulated; dorsal cirri present; three anal cirri ***Coralliotrocha***
—Antennae and palps simple or absent; dorsal cirri absent; two anal cirri **13**
13. Antennae and palps simple; free denticles absent; subacicular lobe absent; ventralmost chaeta compound ***Eliberidens***
—Antennae and palps absent; free denticles present; subacicular lobe present; ventralmost chaeta simple ***Gymnodorvillea***
14. Adults with more than 20 chaetigers; chaetae present **15**
—Adults with 20 or fewer chaetigers; chaetae present or absent **21**
15. Compound chaetae and anal cirri absent **16**
—Subacicular compound chaetae and anal cirri present **17**
16. Simple antennae and free maxillary denticles present; neuropodia with one acicula; free-living species ***Parophryotrocha***
—Antennae and free maxillary denticles absent; neuropodia with more than one acicula; known only as endoparasites in species of *Aphrodita* Linnaeus, 1758 ***Veneriserva***
17. Maxillary apparatus reduced to five or six thin, unsclerotized strips (Fig. 7.12.2.7B) ***Pseudophryotrocha***
—Maxillary apparatus sclerotized, including at least large posterior elements and free denticles **18**
18. One or a few anterior chaetigers with chaetae differing from those of following chaetigers, change abrupt; antennae usually articulated **19**
—Change between chaetae of anterior and following chaetigers, if present, gradual; antennae simple **20**
19. Inferiormost chaeta compound; ventral neuropodial chaetal lobe absent or very weakly developed; ventral cirri elongate, extending beyond neuropodia; all free denticles elongate, falcate (Fig. 7.12.2.7C) ***Anchidorvillea***
—Inferiormost chaeta usually simple, supporting ventral neuropodial chaetal lobe; ventral cirri short, not extending beyond neuropodia; free denticles include plate-like elements ***Exallopus***
20. Ventral neuropodial chaetal lobes absent; commensal species on gills of brachyuran crabs ***Iphitime***
—Ventral neuropodial chaetal lobes present or absent; posterior segments may have prominent, dorsolateral lobes; mainly free-living species ***Ophryotrocha/Mammiphitime***
21. Ventral neuropodial chaetal lobe present, with simple seta; other subacicular chaetae compound ***Pinniphitime***
—Ventral neuropodial chaetal lobe absent; subacicular chaetae, if present, of only one type **22**
22. Compound and simple chaetae present **23**
—Chaetae, if present, either all compound or all simple **27**
23. Antennae present **24**
—Antennae absent **26**
24. Palps biarticulated ***Microdorvillea***
—Palps simple **25**
25. Dorsal and ventral cirri present ***Apophryotrocha***
—Dorsal and ventral cirri absent ***Arenotrocha***
26. Three anal cirri ***Petrocha***
—Two anal cirri ***Pusillotrocha***
27. Chaetae present **28**
—Chaetae absent **30**

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28. All chaetae simple; four chaetigers; jaws apparatus absent ***Parapodrilus***
—All chaetae compound; more than four chaetigers **29**
29. Jaws apparatus present; 10 chaetigers ***Ikosipodus***
—Jaws apparatus absent; 7 chaetigers ***Ikosipodoides***
30. Jaw apparatus present; three segments ***Neotenotrocha***
—Jaw apparatus absent; at least four segments ***Apodotrocha***

References

Åkesson, B. (1967): On the biology and larval morphology of *Ophryotrocha puerilis* Claparéde and Metschnikov (Polychaeta). *Ophelia* 4: 111–119.

Åkesson, B. (1968): The parasite-host relation between *Eucoccidium ophryotrochae* Grell and *Ophryotrocha labronica* La Greca & Bacci. *Oikos* 19: 158–163.

Åkesson, B. (1970): *Ophryotrocha labronica* as test animal for the study of marine pollution. *Helgoländer wissenschaftliche Meeresuntersuchungen* 20: 293–303.

Åkesson, B. (1973a): Morphology and life history of *Ophryotrocha maculata* sp.n. (Polychaeta, Dorvilleidae). *Zoologica Scripta* 2: 141–144.

Åkesson, B. (1973b): Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zoologica Scripta* 2: 145–155.

Åkesson, B. (1975): Reproduktion in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *Pubblicazioni della stazione zoologica di Napoli* 39: 377–398.

Åkesson, B. (1976): Morphology and life cycle of *Ophryotrocha diadema*, a new polychaete species from California. *Ophelia* 15: 23–35.

Åkesson, B. (1977): Parasite-host relationships and phylogenetic systematics. The taxonomic position of dinophilids. In: Sterrer, W. & Ax, P. (eds.): *The meiofauna species in space and time. Workshop Symposium Bermnuda Biological Station 1975. Mikrofauna des Meeresbodens* 61: 19–28.

Åkesson, B. (1980): The use of certain polychaetes in bioassay studies. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*. 179: 315–321.

Åkesson, B. (1984): Speciation in the genus *Ophryotrocha*. *Fortschritte der Zoologie* 29: 299–316.

Åkesson, B. & Costlow, J.D. (1978): Effects of temperature and salinity on the life cycle of *Ophryotrocha diadema* (Polychaeta, Dorvilleidae). *Ophelia* 17: 215–229.

Åkesson, B. & Rice, S.A. (1992): Two new *Dorvillea* species (Polychaeta, Dorvilleidae) with obligate asexual reproduction. *Zoologica Scripta* 21: 351–362.

Armstrong, J.W. & Jumars, P. A. (1978): Branchiate Dorvilleidae (Polychaeta) from the North Pacific. *Bulletin Southern California Academy of Sciences* 77: 133–138.

Blake, J.A. (1979): A redescription of *Pettiboneia sanmatiensis* Orensanz (Polychaeta: Dorvilleidae) and a revised key to the genera of the Dorvilleidae. *Bulletin Southern California Academy of Sciences* 78: 136–140.

Bergter, A., Brubacher, J.L. & Paululat, A. (2008): Muscle formation during embryogenesis of the polychaete *Ophryotrocha diadema* (Dorvilleidae) — New insights into annelid muscle patterns. *Frontiers in Zoology* 5: 1.

Berruti, G., Ferraguti, M. & Lora Lamina Donin, C. (1978): The aflagellate spermatozoon of *Ophryotrocha*: a line of evolution of fertilization among polychaetes. *Gamete Research* 1: 287–292.

Brito, M.C. & Nuñez, J. (2003): Three new interstitial dorvilleids (Annelida: Polychaeta) from the *Cymodocea nodosa* meadows of the Canary Islands. *Hydrobiologia* 496: 27–34.

Chamberlin, R.V. (1919): *The Annelida Polychaeta* [*Albatross Expedition*]. Memoirs of the Museum of Comparative Zoology, Harvard: 48: 1–514.

Claparède, É. & Mecznikow, E. (1869): Beiträge zur Kenntnis der Entwicklungsgeschichte der Chaetopoden. *Zeitschrift für wissenschaftliche Zoologie* 163–205.

Cossu, P., Maltagliati, F., Pannacciulli, F.G., Simonini, R., Massamba-N'Siala, G., Casu, M., Lardicci, C., Prevedelli, D. & Castelli, A. (2015): Phylogeography of *Ophryotrocha labronica* (Polychaeta, Dorvilleidae) along the Italian coasts. *Marine Ecology* 36: 1088–1097.

Dahlgren, T.G., Åkesson, B., Schander, C., Halanych, K.M. & Sundberg, P. (2001): Molecular phylogeny of the model annelid *Ophryotrocha*. *The Biological Bulletin* 201: 193–203.

Damas, D. (1986): Étude cytologique, histochimique et microanalytique des pieces maxillaires d'*Ophryotrocha puerilis* (Annèlide, Polychéte, Eunicidae). *Bulletin de la Société zoologique de France* 111: 61–74.

de Paiva, P.C. & Nonalo, E.F. (1991): On the genus *Iphitime* (Polychaeta: Iphitimidae) and description of *Iphitime sartorae* sp. nov. a commensal of Brachyuran crabs. *Ophelia* 34: 209–215.

delle Chiaje, S. (1828): *Memorie sulla storia e notomia degli animali senza vertebre del Regno di Napoli. Volume 3*. Stamperia della Societa' Tipografica. Napoli: 1–232.

Dohle, W. (1967): Zur Moprhologie und Lebensweise von *Ophryotrocha gracilis* Huth 1934 (Polychaeta, Eunicidae). *Kieler Meeresforschungen* 23: 68–74.

Eibye-Jacobsen, D. & Kristensen, R.M. (1994): A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 23: 107–131.

Eliason, A. (1962): Die Polychaeten der Skagerak-Expedition 1933. *Zoologiska bidrag från Uppsala* 33: 207–293.

Eriksson, M. & Lindström, S. (2000): *Ophryotrocha* sp., the first report of a jawed polychaete from the Cretaceous of Skåne, Sweden. *Acta Palaeontologica Polonica* 45: 311–315.

Evdonin, L.A. & Bubko, O.V. (1983): The architectonics of nervous system in *Ophryotrocha* sp. (Eunicemorpha, Dorvilleidae). *Zoologiceskij Zhurnal* 62: 201–206. [in Russian]

Fauchald, K. (1970): Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in Marine Biology* 5: 1–335.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Reviews* 17: 193–284.

Fauvel, P. (1923): Revision de quelques Euniciens (*Staurocephalus neglectus* n. sp.). *Bulletin de la Société Zoologique de France* 48: 300–312.

Franchini, A. (2008): Distribution of cells containing FMRFamide-related molecules in the embryonic development of *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *Invertebrate Biology* 127: 327–335.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphologie* 95: 235–249.

Gaston, G.R. & Benner, D.A. (1981): On Dorvilleidae and Iphitimidae (Annelida: Polychaeta) with a redescription of *Eteonopsis geryonicola* and a new host record. *Proceedings of the Biological Society of Washington* 94: 76–87.

George, J. D. & Hartmann-Schröder, G. (1985): Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synopses of the British Fauna (New Series)* 32: 1–221.

Gray, J.E. (1852): *Molluscorum Britanniae. Synopsis of the Mollusca of Great Britain*. John van Vorst, London: xvi. 376 pp.

Grothe, C.B. (1982): Axon terminals with unusual vesicles in the brain of the polychaete *Ophryotrocha puerilis. Cell and Tissue Research* 226: 237–240.

Grothe, C., Seidl, K. & Pfannenstiel, H.D. (1987): Cytochemical and biochemical characterization of neurosecretory material in the brain of an annelid *Ophryotrocha puerilis* (Polychaeta). *General and Comparative Endocrinology* 68: 1–5.

Grube, A.E. (1855): Beschreibungen neuer oder wenig bekannter Anneliden. *Arkiv für Naturgeschichte, Berlin* 21: 81–136.

Hausen, H. (2005): Comparative structure of the epidermis in polychaetes (Annelida). *Hydrobiologia* 535/536: 25–35.

Hartman, O. (1965): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation* 28: 1–384.

Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. In: Dahl, C.F.T. (ed.), *Die Tierwelt Deutschlands*, vol. 58. Gustav Fischer Verlag, Jena, Germany: 594 pp.

Heggøy, K.K., Schander, C., Åkesson, B. (2007): The phylogeny of the genus *Ophryotrocha* (Dorvilleidae). *Marine Biology Research* 3: 412–420.

Hilbig, B. (1991): Reconsideration of the genus *Exallopus* with description of two new species. In Petersen, M.J. & Kirkegaard, J. (eds.), *Proceedings of the 2nd International Polychaete Symposium, Copenhagen, 1986. Ophelia (Suppl.)*

Hilbig, B. (1995): 13. Family Dorvilleidae Chamberlin, 1919. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Santa Barbara Museum of Natural History, Santa Barbara: 341–364.

Hilbig, B. & Blake, J.A. (1991): Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with generic revision of *Ophryotrocha*. *Zoologica Scripta* 20: 147–183.

Hints, O. & Eriksson, M. (2007): Diversification and biogeography of scolecodont-bearing polychaetes in the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245: 95–114.

Hutchings, P. & Peyrot-Clausade, M. (1988): Macro-infaunal boring communities of Porites a biogeographical comparison. *Proc. 6th Int. Coral Reef Symp., Australia*. Vol. 3.

Jamieson, B.G.M. & Rouse G.W. (1989): The spermatozoa of the Polychaeta (Annelida): An ultrastructural review. *Biological Reviews* 64: 93–157.

Jumars, P.A. (1974): A generic revision of the Dorvilleidae (Polychaeta), with six new species from the deep Pacific. *Zoological Journal of the Linnean Society* 54: 101–135.

Jumars, P.A., Dorgan, K.M. & Lindsay S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Kinberg, J.G.H. (1865): Annulata nova. Öfversigt af Kongl. Vetenskaps-akademiens forhandlingar 21: 559–574.

La Greca, M. & Bacci, G. (1962): Una nuova specie di *Ophryotrocha* delle coste tirreniche (Annelida, Polychaeta). *Bollettino di Zoologia* 29: 3–18.

Lévi, C. (1954): *Ophryotrocha minuta* nov. sp. nouveau polychète mésopsammique. *Bulletin de la Société Zoologique de France* 79: 466–469.

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata [10th revised edition], vol. 1: 824 pp. Laurentius Salvius: Holmiae.

Macalister, A. (1876): *An Introduction to Animal Morphology and Systematic Zoology. Part I — Invertebrata.* Longmans Green, London, 462 pp.

Marenzeller, E. von. (1902): Südjapanische Anneliden. III. *Aphroditea*, *Eunicea*. *Denkschriften der Akademie der Wissenschaften, Wien* 72: 563–582.

McIntosh, W.C. (1869): On the structure of the British nemerteans, and some new British annelids. *Transactions of the Royal Society of Edinburgh* 25: 305–433.

McIntosh, W.C. (1910): A monograph of the British annelids. Polychaeta. Syllidae to Ariciidae. *Ray Society of London* 2: 233–524.

Müller, M.C.M. (2004): Immunohistochemical analysis of nervous system regeneration in chimeric individuals of *Dorvillea bermudensis* (Polyxchaeta, Dorvilleidae). *Development, Growth and Differentiation* 46: 131–138.

Müller, M.C.M. & Westheide, W. (2002): Comparative analysis of the nervous systems in presumptive progenetic dinophilid and dorvilleid polychaetes (Annelida) by immunohistochemistry and cLSM. *Acta Zoologica (Stockholm)* 83: 33–48.

Müller, M.C.M. & Henning, L. (2004): Ground plan of the polychaete brain — I. Patterns of nerve development during regeneration in *Dorvillea bermudensis* (Dorvilleidae). *The Journal of Comparative Neurology* 471: 49–58.

Nederlof, M.A.J., Jansen, H.M., Dahlgren, T.G., Fang, J., Meier, S., Strand, Ø., Sveier, H., Verdegem, M.C.J. & Smaal, A.C. (2019): Application of polychaetes in (de)coupled integrated aquaculture: Production of a high-quality marine resource. *Aquaculture Environment Interactions* 11: 221–237.

Nuñez, J. (1998): *Marycarmenia lysandrae*, a new genus and interstitial species (Polychaeta: Dorvilleidae) from Madeira. *Bulletin of Marine Science* 62: 115–119.

Orensanz, J.M. (1973): Los anelidos poliquetos de la provincia biogeographica Argentina. III. Dorvilleidae. *Physis* 32A: 325–342.

Orensanz, J.M. (1990): The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Antarctic Research Series* 52: 1–183.

Oug, E. (1978): New and lesser known Dorvilleidae (Annelida, Polychaeta) from Scandinavian and northeast American waters. *Sarsia* 63: 285–303.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Oug, E. (2006): Redescription of *Parophryotrocha isochaeta* (Eliason, 1962) and a new species of *Parophryotrocha* (Polychaeta: Dorvilleidae) from the Skagerrak and North Sea. *Scientia Marina* 70: 151–155.

Parfitt, E. (1866): Description of a *Nereis* new to science. *The Zoologist, London* 1: 113–114.

Paxton, H. (2000): Family Dorvilleidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 91–94.

Paxton, H. (2004): Jaw growth and replacement in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Zoomorphology* 123: 147–154.

Paxton, H. (2009): Phylogeny of Eunicida (Annelida) based on morphology of jaws. *Zoosymposia* 2: 241–264.

Perkins, T.H. (1979): Lumbrineridae, Arabellidae, and Dorvilleidae (Polychaeta), principally from Florida, with descriptions of six new species. *Proceedings of the Biological Society of Washington* 92: 415–465.

Pettibone, M.H. (1961): New species of polychaete worms from the Atlantic Ocean, with a revision of the Dorvilleidae. *Proceedings of the Biological Society of Washington* 74: 167–186.

Pfannenstiel, H.-D. (1984): The ventral nerve cord signals positional information during segment formation in an annelid (*Ophryotrocha puerilis*, Polychaeta). *Roux's Archives of Developmental Biology* 194: 32–36.

Pfannenstiel, H.-D. & Grünig, C. (1982a): Structure of the nephridium in *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Zoomorphology* 101: 187–195.

Pfannenstiel, H.-D. & Grünig, C. (1982b): Primordial germ cells and early stages of oogenesis in *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Zoomorphology* 101: 187–195.

Pfannenstiel, H.-D. & Grünig, C. (1982c): Yolk formation in an annelid (*Ophryotrocha puerilis*, Polychaeta). *Tissue and Cell* 14: 669–680.

Pfannenstiel, H.-D. & Grünig, C. (1990): Spermatogenesis and sperm ultrastructure in the polychaete genus *Ophryotrocha* (Dorvilleidae). *Zoomorphology* 44: 159–171.

Purschke, G. (1987): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). IV. The pharynx and jaws of the Dorvilleidae. *Acta Zoologica* 68: 83–105.

Purschke, G. (1988): Pharynx. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of Polychaeta. Mikrofauna Marina* 4: 177–197.

Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) — New results and review. *Acta Zoologica (Stockholm)* 78: 123–143.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 535/536: 53–78.

Purschke, G. & Nowak, K. (2015): Ultrastructure of pigmented eyes in Dorvilleidae (Annelida, Errantia, Eunicida) and their importance for understanding the evolution of eyes in polychaetes. *Acta Zoologica (Stockholm)* 96: 67–81.

Purschke, G. & Tzetlin, A.B. (1996): Dorsolateral ciliary folds in the polychaete foregut: Structure, prevalence and phylogenetic significance. *Acta Zoologica (Stockholm)* 77: 33–49.

Purschke, G., Arendt, D., Hausen, H. & Müller, M.C.M. (2006): Photoreceptor cells and eyes in Annelida. *Arthropod Structure & Development* 35: 211–230.

Purschke, G., Bleidorn, C. & Struck, T. (2014): Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Memoirs of Museum Victoria* 71: 247–269.

Ravara, A., Marçal, A.R., Wiklund, H. & Hilário, A. (2015): First account on the diversity of *Ophryotrocha* (Annelida, Dorvilleidae) from a mammal-fall in the deep-Atlantic Ocean with the description of three new species. *Systematics and Biodiversity* 13: 555–570.

Read, G. & Fauchald, K. (eds.) (2020). World Polychaeta database. *Dorvillea* Parfitt, 1866. Accessed through: http://www.marinespecies.org/polychaeta/aphia.php?p=taxdetails&id=129261 (Accessed on 2020-01-30).

Rhode, B. (1989): Ultrastructural investigations on the nuchal organs of the protandric polychaete, *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Zoomorphology* 108: 315–322.

Rhode, B. (1990): Eye structure of *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Journal of Morphology* 205: 147–154.

Richards, T.L. (1967): Reproduction and development of the polychaete *Stauronereis rudolphi*, including a summary of development in the superfamily Eunicea. *Marine Biology* 1: 124–133.

Rossi, M.M. (1984): A new genus and species of iphitimid parasitic in an aphroditid (Polychaeta), with an emendation of the family Iphitimidae. *Bulletin Southern California Academy of Sciences* 83: 163–166.

Rouse, G.W. (2006): Annelid sperm and spermiogenesis. In: Rouse, G.W. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield: 45–76.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford, New York: 354 pp.

Schlawny, A., Grünig, C. & Pfannenstiel, H.-D. (1991a): Sensory and secretory cells of *Ophryotrocha puerilis* (Polychaeta). *Zoomorphology* 110: 209–215.

Schlawny, A., Hamann, T., Müller, A.M. & Pfannenstiel, H.-D. (1991b): The catecholaminergic system of an annelid (*Ophryotrocha puerilis*, Polychaeta). *Cell and Tissue Research* 265: 175–184.

Schlawny, A., Hamann, T., Müller, A.M. & Pfannenstiel, H.-D. (1991c): Cytophysiology of neurosecretory axon terminals in the brain of an annelid (*Ophryotrocha puerilis*, Polychaeta). *Cell and Tissue Research* 265: 339–345.

Sella, G. (2006): Sexual strategies and mating systems. In: Rouse, G.W. & Pleijel, F. (eds.), *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield: 77–92.

Sella, G. & Ramella, L. (1999): Sexual conflict and mating systems in the dorvilleid genus *Ophryotrocha* and the dinophilid genus *Dinophilus*. *Hydrobiologia* 402: 203–213.

Smith, P.R. & Ruppert, E.E. (1988): Nephridia. In: Westheide, W. & Hermans, C.O. (eds.), *The Ultrastructure of Polychaeta. Mikrofauna Marina* 4: 231–262.

Struck, T.H. (2019): Phylogeny. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology. Annelida. Volume 1: Basal Groups and Pleistoannelida, Sedentaria I*. De Gruyter, Berlin: 37–68.

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Struck, T.H., Halanych, K.M. & Purschke, G. (2005): Dinophilidae (Annelida) is most likely not a progenetic Eunicida: Evidence from 18S and 28S rDNA. *Molecular Phylogenetics and Evolution* 37: 619–623.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Szaniawski, H. (1974): Some Mesozoic scolecodonts congeneric with recent forms. *Acta Palaeontologica Polonica* 19: 179–199.

Szaniawski, H. & Gaździcki, A. (1978): A reconstruction of three Jurassic polychaete jaw apparatuses. *Acta Palaeontologica Polonica* 23: 3–29.

Szaniawski, H. & Wrona, R. (1987): Polychaete jaws from the Cape Melville formation (Lower Miocene) of King George Island, West Antarctica. *Acta Palaeontologica Polonica* 49: 105–125.

Taboada, S., Wiklund, H., Glover, A.G., Dahlgren, T.G., Cristobo, J. & Avila, C. (2013): Two new Antarctic *Ophryotrocha* (Annelida: Dorvilleidae) described from shallow-water whale bones. *Polar Biology* 36: 1031-1045.

Taboada, S., Bas, M. & Avila, C. (2015): Parougia species (Annelida, Dorvilleidae) associated with eutrophic marine habitats in Antarctica. *Polar Biology* 38(4): 517–527.

Taboada, S., Leiva, C., Bas, M., Schult, N. & McHugh, D. (2017): Cryptic species and colonization processes in *Ophryotrocha* (Annelida, Dorvilleidae) inhabiting vertebrate remains in the shallow-water Mediterranean. *Zoologica Scripta* 46: 611–624.

Troyer, D. & Schwager, P. (1979): Ultrastructure and evolution of a sperm: Phylogenetic implications of altered motile machinery in *Ophryotrocha puerilis* spermatozoon. *European Journal of Cell Biology* 20: 174–176.

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535/536: 199–225.

Van Erve, A.W. (1981): Lower Jurassic scolecodonts from the vicentinian Alps (northeastern Italy), representing the family Dorvilleidae Chamberlin, 1919. *Review of Palaeobotany and Palynology* 34: 225–235.

Verrill, A.E. (1900): Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species. *Transactions of the Connecticut Academy of Arts and Sciences* 10: 595–671.

von Nordheim, H. (1987): *Petrocha notogaea* gen. et sp. n., a neotenic interstitial polychaete (Dorvilleidae) from the Hauraki Gulf, New Zealand. *Zoologica Scripta* 16: 33–38.

Wainwright, S.C. & Perkins, T.H. (1982): *Gymnodorvillea floridana*, a new genus and species of Dorvilleidae (Polychaeta) from southeastern Florida. *Proceedings of the Biological Society of Washington* 95: 694–701.

Weigert, A. & Bleidorn, C. (2016): Current status of annelid phylogeny. *Organisms, Diversity and Evolution* 16: 345–362.

Westheide, W. (1965): *Parapodrilus psammophilus* nov. gen., nov. spec., eine neue Polychaeten-Gattung aus den Mesopsammal der Nordsee. *Helgoländer wissenschaftliche Meeresuntersuchungen* 12: 207–212.

Westheide, W. (1982): *Ikosipodus carolensis* gen. et sp. n., an interstitial neotenic polychaete from North Carolina, U.S.A., and its phylogenetic relationships within Dorvilleidae. *Zoologica Scripta* 11: 117–126.

Westheide, W. (1985): The systematic position of the Dinophiliidae and the Archiannelid problem. In: Morris, C. S., George, D., Gibson, R. & Platt, H. M. (eds.), *The origins and relationships of lower invertebrates*. Oxford University, Oxford: 310–326.

Westheide, W. (1988): Genital organs. In: Westheide, w. & Hermans, C.O. (eds.) *The Ultrastructure of Polychaeta. Microfauna Marina* 4: 263–279.

Westheide, W. (2000): *Ikosipodoides seychellensis*, a new genus and species of interstitial polychaetes (Dorvilleidae) from the island of Mahé, Indian Ocean. *Cahiers de Biologie Marine* 41: 15–23.

Westheide, W. (2019): Dinophilidae Verrill, 1892. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *Handbook of Zoology. Annelida. Volume 1: Basal Groups and Pleistoannelida, Sedentaria I*. De Gruyter, Berlin: 217–234.

Westheide, W. & Riser, N.W. (1983): Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n. gen., n. sp. (Annelida). *Zoomorphology* 103: 67–87.

Westheide, W. & von Nordheim, H. (1985): Interstitial Dorvilleidae (Annelida, Polychaeta) from Europe, Australia and New Zealand. *Zoologica Scripta* 14: 183–199.

Wiklund, H., Glover, A.G. & Dahlgren, T.G. (2009): Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the north-east Atlantic. *Zootaxa* 2228: 43–56.

Wiklund, H., Altamira, I.V., Glover, A.G., Smith, C.R., Baco, A.R. & Dahlgren, T.G. (2012): Systematics and biodiversity of *Ophryotrocha* (Annelida, Dorvilleidae) with descriptions of six new species from deep-sea whale-fall and wood-fall habitats in the north-east Pacific. *Systematics and Biodiversity* 10: 243–259.

Wolf, P.S. (1986a): Four new genera of Dorvilleidae (Annelida: Polychaeta) from the Gulf of Mexico. *Proceedings of the Biological Society of Washington* 99: 616–626.

Wolf, P.S. (1986b): Three new species of Dorvilleidae (Annelida: Polychaeta) from Puerto Rico and Florida and a new genus for dorvilleids from Scandinavia and North America. *Proceedings of the Biological Society of Washington* 99: 627–638.

Zavarzina, E.G. (1987): New data on photoreceptor structure in *Ophryotrocha dimorphica* (Polychaeta, Eunicida). *Doklady Akademia NAUK SSSR* 294: 224–227. [in Russian]

Zavarzina, E.G. & Tzetlin, A.B. (1986): Biology of *Ophryotrocha dimorphica* sp.n. (Polychaeta, Eunicida) from the Peter the Great Bay (The Japan Sea). *Zoologiceskij Zhurnal* 65: 1808–1817. [in Russian]

Zavarzina, E.G. & Tzetlin, A.B. (1987): Structure of the excretory system in *Ophryotrocha dimorphica* sp.n. (Polychaeta, Eunicida). *Doklady Akademia NAUK SSSR* 297: 498–500. [in Russian]

Zavarzina, E.G. & Tzetlin, A.B. (1990): Structure of the body cavity of some annelids, preliminary results. *Zoologiceskij Zhurnal* 69: 31–41. [in Russian]

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Nataliya Budaeva

7.12.3 Onuphidae Kinberg, 1865

Introduction

Onuphidae is a family of mainly tubicolous sediment dwellers with worldwide distribution. They have well-characterized external morphology and can be easily recognized by clearly delimited frontal lips on the anterior prostomial margin and five occipital appendages, three antennae and a pair of palps on the multiringed ceratophores (Fig. 7.12.3.1). As other members of Eunicida, onuphids possess complex jaws in the ventral muscular pharynx that can protrude from the mouth and are used for feeding. Currently, the family comprises ~330 species grouped into 22 accepted genera (Budaeva et al. 2016).

Morphology

Onuphids vary greatly in size, the deep-sea quill worms *Leptoecia* Chamberlin, 1919 can be as small as about one cm long (Budaeva et al. 2014), whereas intertidal beachworms *Australonuphis* Paxton, 1979 (see Paxton 1986a) may reach up to 300 cm (Paxton 1979). Several genera (e.g., *Anchinothria* Paxton, 1986, *Nothria* Malmgren, 1866, and *Leptoecia*) are relatively short-bodied with not more than 100 segments, whereas most species consist of ~200 segments and are about 5 to 10 cm long. The body appears to be homonymously segmented, however, the shape of parapodia and the distribution of different types of chaetae can vary significantly between the body regions (Fig. 7.12.3.2). Several anteriormost segments are usually cylindrical, accommodating the large muscular pharynx. The rest of the body is more or less dorsoventrally flattened, usually slender and uniform.

The prostomium is oval or rounded, sometimes with an anterior extension. Two frontal lips are located at the anterior margin of the prostomium usually well separated from each other and directed anteriorly or anteroventrally. Frontal lips are typically ovoid, oval, subulate, or spherical in shape and often are covered by numerous sensory buds (Fig. 7.12.3.3A, C, D). In *Leptoecia*, the frontal lips are reduced to short semispherical swellings or even to a conical or pointed prostomium without any apparent projections (Fig. 7.12.3.3E). Three antennae and a pair of palps are located in the occipital zone of the prostomium (Fig. 7.12.3.3A, B). They are morphologically similar, consisting of proximal ringed ceratophores and distal elongated and pointed ceratostyles (Fig. 7.12.3.3A–C). Ceratophores can consist of only two rings like in some species of *Hyalinoecia* Malmgren, 1866 and *Leptoecia* but also can be extremely annulated, reaching up to 60 rings in *Heptaceras* Ehlers, 1868 (Fig. 7.12.3.19B). In some species of *Diopatra* Audouin & Milne Edwards, 1833, ceratophores of antennae may bear lateral projections on the basalmost rings (Fig. 7.12.3.16A). Ceratostyles are covered by sensory ciliated buds that can be scattered (Fig. 7.12.3.3C) or form longitudinal rows like in many *Diopatra* species. Ventrally, the prostomium bears a pair of upper lips that are usually of oval shape or can have an additional distal lobe (Fig. 7.12.3.3C–E). Eyes, if present, are located between the bases of lateral antennae and palps. Juvenile eyes can be retained on the anterior margin of the prostomium in adults. So far, the ultrastructure of the eyes is only known in one species, *Aponuphis bilineata* (Baird, 1870) (see von Palubitzki and Purschke 2020). A pair of nuchal organs represented by ciliated grooves is located at the posterior margin of the prostomium (Fig. 7.12.3.3B). In most of the species, the nuchal organs are straight or slightly curved; they can almost meet at the midline of the prostomium or be widely separated from each other. In some *Diopatra* species, the nuchal organs can be crescentic or almost circular (Fig. 7.12.3.16A).

The first apodous ring is formed by the peristomium, which is dorsally complete in most of the genera (Fig. 7.12.3.3A, B, D). However, in *Australonuphis*, *Hartmanonuphis* Paxton, 1986, and *Hirsutonuphis* Paxton, 1986, the anterior peristomial fold is missing and the peristomium extends toward the median antenna (Figs. 7.12.3.18B, 7.12.3.20B). In *Heptaceras,* the peristomium has a middorsal notch and a median ridge (Fig. 7.12.3.19B). Ventrally, the peristomium forms the wide ventral lip (Fig. 7.12.3.3C, E), which, together with the prostomial upper lips, surrounds the mouth. In some genera, the ventral lip can have a distinct median section. Dorsally, the peristomium can bear a pair of cirri, which are usually located distally or subdistally (Fig. 7.12.3.3A, B); however, in *Americonuphis* Fauchald, 1973, they are situated in the middle of the peristomium. Several genera (*Aponuphis* Kucheruk, 1978, *Hyalinoecia*, *Hyalospinifera* Kucheruk, 1979, and *Leptoecia*) lack peristomial cirri.

Parapodia are subbiramous with well-developed neuropodia, whereas notopodia are reduced to a dorsal cirrus with embedded notoaciculae. Two to eight anterior pairs of parapodia are modified (Figs. 7.12.3.2B, 7.12.3.3C, D), often directed anteroventrally (e.g., *Americonuphis*) or anterolaterally (e.g., *Onuphis* Audouin & Milne Edwards, 1833 and *Kinbergonuphis* Fauchald, 1982) to dorsally (e.g., *Hirsutonuphis*). In some genera (e.g., *Kinbergonuphis, Mooreonuphis* Fauchald, 1982, *Onuphis*, and

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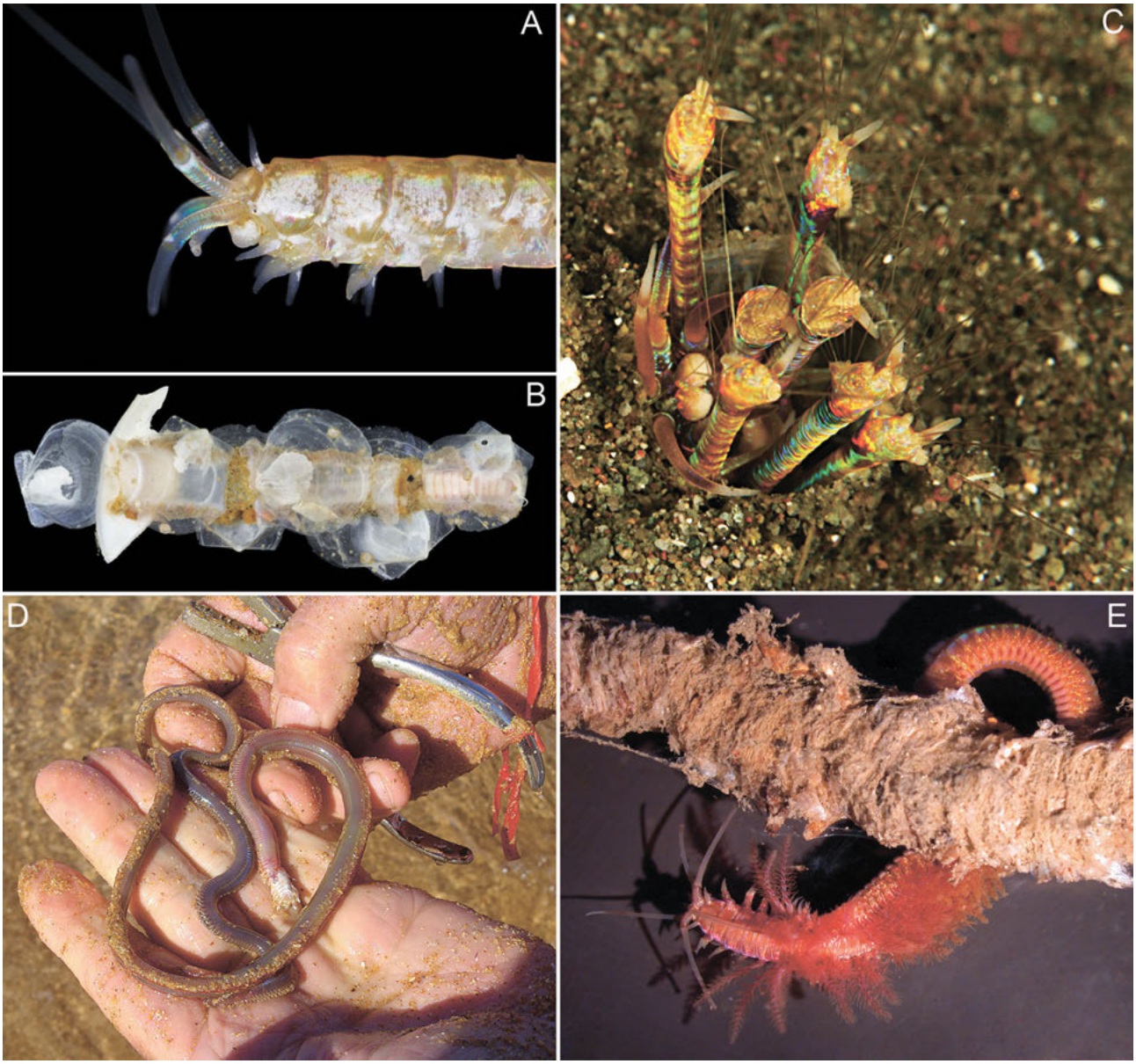


Fig. 7.12.3.1: Photographs of live onuphids. A, *Onuphis* sp. from Lizard Island, Great Barrier Reef, Australia, anterior part of body (© A. Semenov); B, *Nothria conchylega* (Sars, 1835) from the North Sea inside its tube built of bivalve shells (© K. Kongshavn); C, *Longibrachium* sp. from Rinca Island, Indonesia, inside its borrow with anterior parapodia and chaetae sticking out (© S. Mamaev); D, *Australonuphis* sp. caught on a sandy beach off Sydney, Australia, with a pair of pliers, used by local fishermen to catch this species as bait; E, *Diopatra ornata* from San Juan Island, Washington, USA, crawling around its tube (© M. Boyle).

Paradiopatra Ehlers, 1887), the anterior parapodia are not enlarged and only differ from the subsequent parapodia in the presence of well-developed subulate ventral cirri and specific chaetae (Figs. 7.12.3.21A, B, 7.12.3.23A, B, 7.12.3.24A, B, 7.12.3.25B, C). In other genera, the anterior parapodia can be significantly enlarged and strengthened (e.g., *Hyalinoecia*, *Nothria*, and *Hartmanonuphis*) (Figs. 7.12.3.8B, C, 7.12.3.11A, B, 7.12.3.18A) or elongated (e.g., *Fauchaldonuphis* Paxton, 2005, *Hirsutonuphis*, *Longibrachium* Paxton, 1986, and *Rhamphobrachium* Ehlers, 1887) (Figs. 7.12.3.1C, 7.12.3.17A, 7.12.3.22A, B). Subsequent parapodia are similar in size and shape, with ventral cirri modified into glandular pads (Figs. 7.12.3.2B, 7.12.3.3C, D). The pads are usually rounded or oval in shape with the small openings of glands producing mucous. Usually, the gland openings are randomly scattered over the pad, but in some species they make specific patterns: honeycomb-like pattern (*Leptoecia* spp.) or single or multiple transverse rows of pores (*Paradiopatra* spp.) (Arias and Paxton 2015b). The dorsal cirri are subulate and present in all

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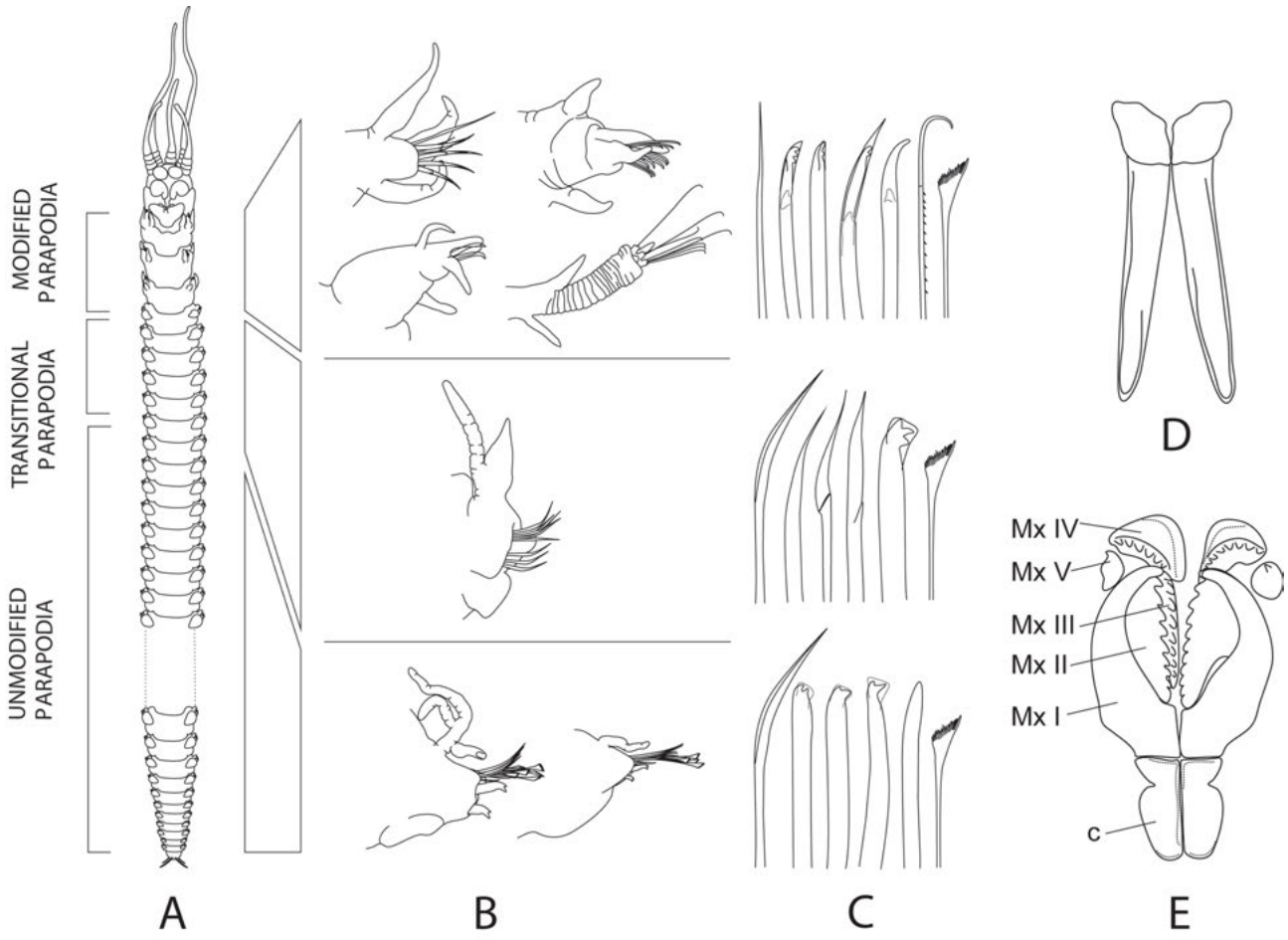


Fig. 7.12.3.2: Schematic drawing of the generalized body plan of Onuphidae. A, Onuphid worm, ventral view; B, Parapodia of the three body regions; C, Different chaetal types found in the three body regions; D, Mandibles; E, Maxillae. c, carriers; MxI–MxV, conventional labeling of maxillary plates.

parapodia, sometimes becoming shorter posteriorly. In *Hirsutonuphis*, anterior dorsal cirri may be extremely long, almost covering the dorsal part of the worm. Parapodia typically have acicular, prechaetal, and postchaetal lobes; however, additional parapodial lips, lobes, and papillae may be also present. For example, in *Diopatra*, the second postchaetal and the ventral lobes can be recognized in some species. The prechaetal lobe is located anterior to the acicular lobe and is usually short and conical but may also be bilobed or trilobed, gradually becoming smaller and eventually disappearing posteriorly. In *Hyalinoecia, Leptoecia*, and *Nothria*, the prechaetal lobes on the first two pairs of the parapodia are extended, having an auricular shape forming a hood over the chaetae (Figs. 7.12.3.8C, 7.12.3.10E, 7.12.3.11C). The extremely modified anterior parapodia of *Brevibrachium* Paxton, 1986, *Longibrachium*, and *Rhamphobrachium* lack prechaetal lobes (Figs. 7.12.3.15A–C, 7.12.3.22A, B, 7.12.3.28A, B). Postchaetal lobes are typically subulate to triangular in shape, well developed in the anterior parapodia, gradually becoming smaller posteriorly. In some genera, they disappear in the posterior region of the body, whereas in others they are present as small papillae even in posteriormost segments. Branchiae are located at the bases of the dorsal cirri and can start from the first chaetiger or more posteriorly. In many species, they start from chaetiger 6 or 7. All species of *Leptoecia* and *Hyalospinifera* as well as some species from other genera lack branchiae; however, branchiated species are the majority. Branchiae can be as single filaments often quite long and flat; in most onuphids, branchiae are pectinate with 3 to 15 branchial filaments arranged in a comb-like structure. In *Anchinothria*, branchiae are dichotomously branched; in *Diopatra*, they are spiral (Figs. 7.12.3.1E, 7.12.3.16A, C).

The notochaetae are reduced to internal chaetae embedded into the dorsal cirri; in some species of *Paradiopatra*, they may be completely absent. The neurochaetae consist of aciculae and two bundles of chaetae

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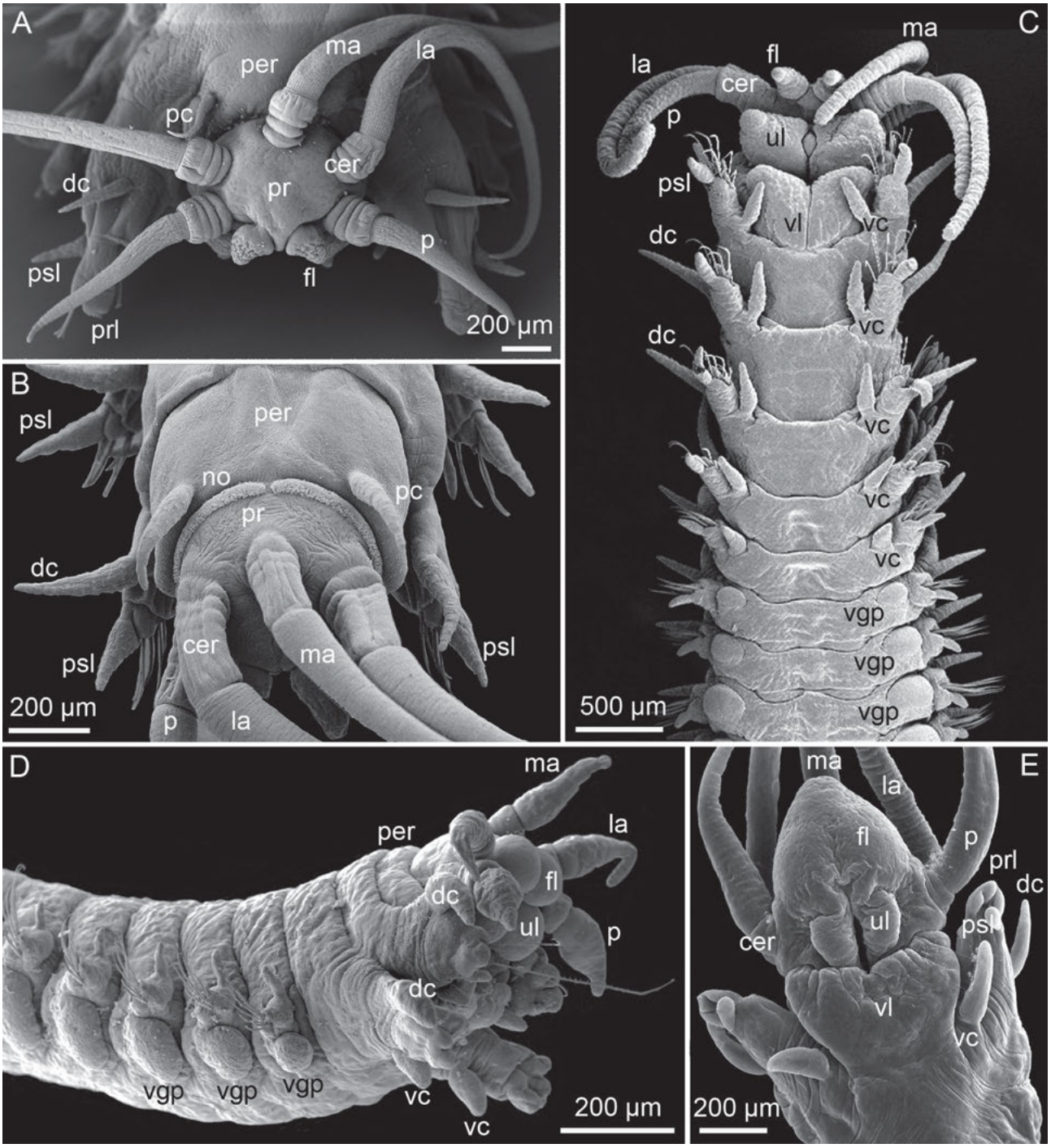


Fig. 7.12.3.3: Scanning electron microscopy micrographs of anterior ends of various Onuphidae. A, *Nothria otsuchiensis* Imajima, 1986, frontal view; B, *Mooreonuphis stigmatis*, dorsal view (modified from Budaeva and Fauchald 2010); C, *Diopatra tuberculantennata* Budaeva & Fauchald, 2008, ventral view (modified from Budaeva and Fauchald 2008); D, *Rhamphobrachium nutrix* Paxton & Budaeva, 2015, lateral view (modified from Paxton and Budaeva 2015); E, *Leptoecia midatlantica* Budaeva, 2012, ventral view (modified from Budaeva 2012). cer, ceratophore; dc, dorsal parapodial cirrus; fl, frontal lip; la, lateral antenna; ma, median antenna; no, nuchal organ; p, palp; pc, peristomial cirrus; per, peristomium; pr, prostomium; prl, prechaetal lobe; psl, postchaetal lobe; ul, upper lip; vc, ventral cirrus; vgp, ventral glandular pad; vl, ventral lip.

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that may differ in composition along the body. The upper limbate chaetae may appear from chaetiger 1 and be present throughout the whole body. In the modified parapodia, they are sometimes called capillary chaetae because of the very narrow limbation. In highly modified parapodia of *Rhamphobrachium*, *Longibrachium*, *Hyalinoecia*, *Leptoecia*, *Nothria*, and *Anchinothria*, the upper limbate chaetae may be absent on the first one to two chaetigers. The pectinate chaetae emerge in the upper bundle of chaetae and have the comb-like shape with numerous (from 3 to 30) denticles distally. The pectinate chaetae can be with straight or oblique distal margin and are usually flat (Figs. 7.12.3.16F, 7.12.3.18F, 7.12.3.19F). In *Anchinothria* and *Nothria*, they are scoop-shaped with lateral margins rolled up toward the middle (Figs. 7.12.3.7E, 7.12.3.11G). In many species, the pectinate chaetae start from chaetiger 1, whereas in others they appear more posteriorly.

Falcigers are present in the lower bundle of chaetae in modified parapodia. Typically, they are pseudocompound with distinct pseudoarticulation dividing the chaeta into the proximal shaft and the distal appendage. The distal appendage is usually bidentate to quadridentate, sometimes falcate, with a pair of lateral hoods covering the dental tip. The hoods vary in length from being very short (e.g., in *Leptoecia* or *Nothria*) (Figs. 7.12.3.10G, 7.12.3.11E) to being extremely long and pointed (e.g., in *Paradiopatra*) (Fig. 7.12.3.25E). The shafts of falcigers are typically smooth or can possess spines of different lengths and morphologies. The spines can be scattered or form two to four longitudinal rows (*Diopatra*, *Fauchaldonuphis*, and *Rhamphobrachium*) (Figs. 7.12.3.16D, 7.12.3.17C). In some genera, anterior falcigers are highly modified. *Anchinothria* and *Hyalinoecia* possess simple short and thick, falcate, or indistinctly bidentate falcigers (Figs. 7.12.3.7D, 7.12.3.8E, F). Falcigers of *Brevibrachium*, *Longibrachium*, and *Rhamphobrachium* are extremely long and retractable with the bundles of shafts enclosed in chaetal sacks extending backward to chaetigers 4 to 60 in the body cavity. In *Brevibrachium*, the falcigers range from recurved to tridentate (Fig. 7.12.3.15D), whereas in *Longibrachium* and *Rhamphobrachium* they become simple recurved hooks with extremely long and movable spines on the shafts (Figs. 7.12.3.22D, 7.12.3.28D).

Two genera, *Kinbergonuphis* and *Mooreonuphis*, show the presence of so-called "large median tridentate hooks" that appear in modified parapodia and are usually retained in the midbody segments until the start of the subacicular hooks (Figs. 7.12.3.21E, 7.12.3.23E). Lower limbate chaetae replace the anterior falcigers in unmodified parapodia. They have well-developed limbation on one or both sides. Typically, the surface of the limbate chaetae is covered by numerous tiny spikes. In *Diopatra*, these spikes may significantly increase in size, becoming large scales and forming coarse serration in the middle part of a chaeta (Fig. 7.12.3.16E). In some genera (e.g., *Mooreonuphis* and *Rhamphobrachium*), lower limbate chaetae become compound or pseudocompound, forming so-called "spinigers" found in the middle body segments (Figs. 7.12.3.23F, 7.12.3.28F). Subacicular hooks are present in all onuphids and can occur in the ventral or median position in the lower bundle of chaetae. In Hyalinoeciinae, where the hooks are in a median position, the lower limbate chaetae are present until the end of the body (Fig. 7.12.3.7C), whereas in Onuphinae, where the hooks are ventral, they replace the lower limbate chaetae completely (Figs. 7.12.3.23C, 7.12.3.25D). The hooks are usually simple paired and bidentate, with short hoods covering the distal dental part. In *Australonuphis*, they are distally entire lacking hoods (Fig. 7.12.3.14E). In *Rhamphobrachium*, up to six subacicular hooks can be found in a single parapodium. Subacicular hooks quite often start on chaetiger 9 but can originate as far back as on chaetiger 80.

All onuphids possess jaws in the ventral muscular pharynx. The ventral mandibles consist of two plates connected by a ligament forming two long shafts with anterior cutting plates (Fig. 7.12.3.2D). The cutting plate is covered by calcareous deposits on the ventral side. The dorsal maxillary jaw apparatus is of the eulabidognath type consisting of several sclerotized and calcified elements (Fig. 7.12.3.2E). The posterior carriers are a pair of plates of oval or triangular shape connected in the middle. Maxillae (Mx) I form a pair of forceps with falcate tips that are attached to the carriers. MxII and MxIII are denticulated plates with about 7 to 12 teeth on each element lying between the forceps plates. MxII are subsymmetrical, with elements on both sides, whereas only the left MxIII are present. MxIV are curved subsymmetrical denticulated plates with wide sclerotized attachment lamellae. They are positioned anterior to MxII and MxIII. MxV are small plates of irregular shape with a single tooth each, present in most of the genera but absent in *Leptoecia*. MxVI are present only in few genera (e.g., *Americonuphis*, *Paxtonia* Budaeva & Fauchald, 2011 and *Rhamphobrachium*) as small rounded plates without denticles.

The pygidium is a small, conical lobe with dorsal anus and one or two pairs of anal cirri. In some genera (e.g., *Hyalinoecia* and *Leptoecia*), the pygidium can be enlarged with numerous glandular openings.

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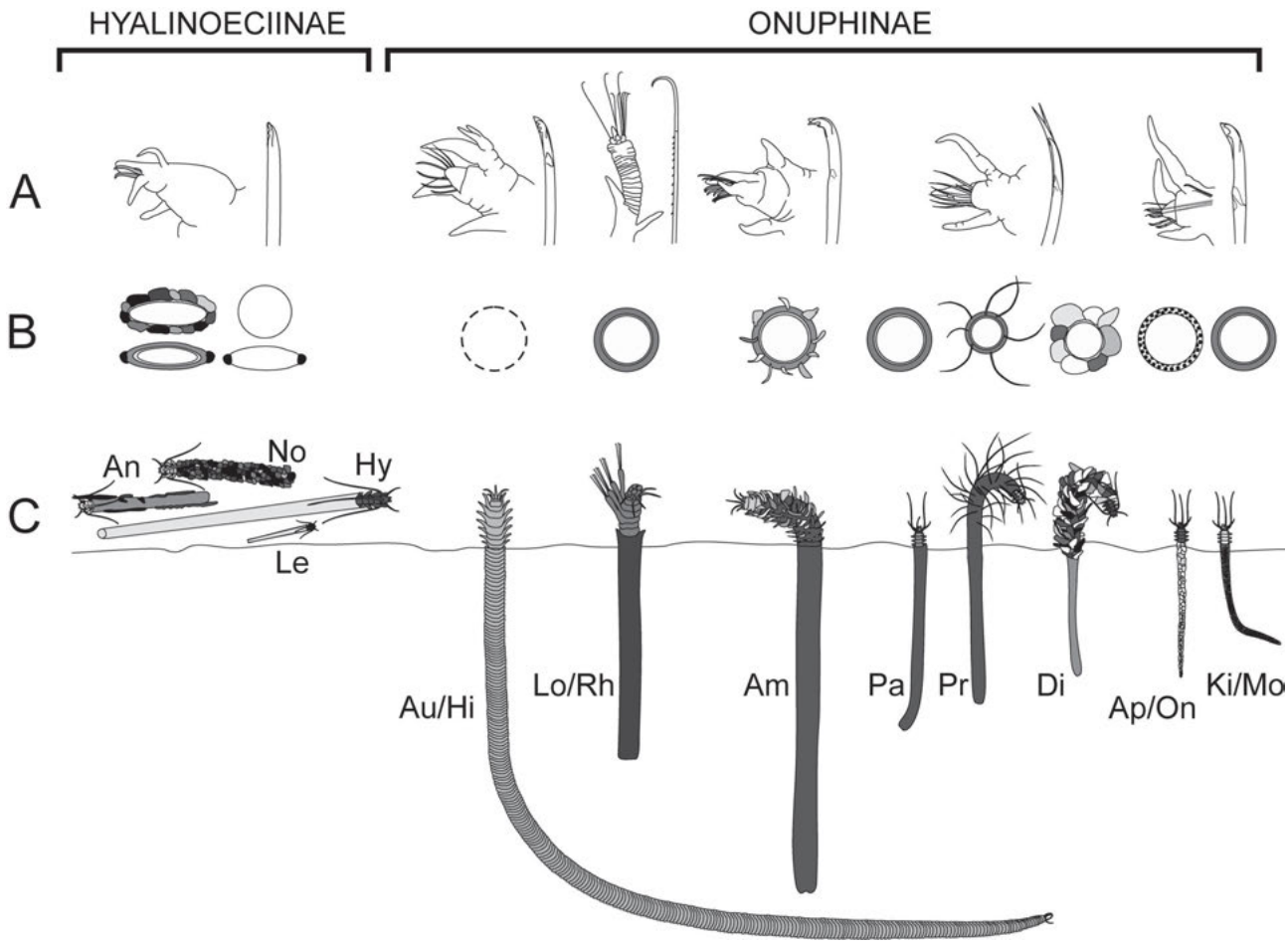


Fig. 7.12.3.4: Lifestyle and adaptive morphological characters in Onuphidae. A, Anterior modified parapodia and chaetae; B, Cross-sections of tubes; C, Schematic drawings of various genera and their position in/on the sediment. Am, *Americonuphis*; An, *Anchinothria*; Ap, *Aponuphis*; Au, *Australonuphis*; Di, *Diopatra*; Hi, *Hirsutonuphis*; Hy, *Hyalinoecia*; Ki, *Kinbergonuphis*; Le, *Leptoecia*; Lo, *Longibrachium*; Mo, *Mooreonuphis*; No, *Nothria*; On, *Onuphis*; Pa, *Paradiopatra*; Pr, *Protodiopatra*; Rh, *Rhamphobrachium*.

Onuphidae display outstanding diversity in shapes and composition of tubes. *Hyalinoecia*, *Leptoecia*, and *Hyalospinifera* build organic, totally secreted tubes. The quill-like tubes are slightly longer than their inhabitants and transparent. *Hyalinoecia* species have tubes with internal valves on the both ends, whereas some species of *Leptoecia* strengthen their tubes with lateral longitudinal ribs. *Nothria* construct dorsoventrally flattened short tubes composed of small stones or fragments of bivalve shells and foraminiferans (Fig. 7.12.3.1B). *Anchinothria* inhabit also dorsoventrally flattened tubes covered with mud with various long objects such as elongated shells of foraminiferans or sponge spicules attached to both longitudinal margins. Species of *Onuphis*, *Kinbergonuphis*, *Mooreonuphis*, and *Paradiopatra* are known to build long cylindrical tubes consisting of an inner parchment-like layer and an outer layer composed of mud or sand particles. These tubes are often considerably longer than their inhabitants. Many *Diopatra* build vertical tubes with the anterior part sticking out from the sediment and ornamented with debris (fragments of plants, shells, etc.), referred to as the "tube cap". *Protodiopatra* Budaeva & Fauchald, 2011 construct vertical muddy, distally curved tubes with very long and thin spines coated with mud (Fig. 7.12.3.27H). Such tubes can be quite large reaching up to 40 cm long and 1 cm in diameter (Imajima 1999). Several large-bodied intertidal onuphids (e.g., *Australonuphis*) live in temporary borrows and do not construct permanent tubes.

Biology and ecology

Distribution and abundance

Onuphidae occur worldwide from littoral to abyssal depths. Many species are very common in the intertidal

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zone (Fauchald 1973, 1980). At the same time, Onuphidae are the fourth most diverse polychaete family in the deep sea (Paterson et al. 2009). *Paradiopatra ehlersi* (McIntosh, 1885) and *Leptoecia ultraabyssalis* (Kucheruk, 1977) have been recorded from depths below 6000 m. Despite their wide distribution, only two genera of onuphids, *Nothria* and *Paradiopatra*, have been reported from the Arctic Ocean (Jirkov 2001).

Onuphids may reach remarkably high densities in some habitats. The Hawaiian *Diopatra dexiognatha* Paxton & Bailey-Brock, 1986 forms mounds on the reef flat built of densely aggregated vertical tubes, with up to 21,800 individuals/m^2. These mounds affect the local environment, accumulating sediment and providing a specific tridimensional biotope for rich local fauna (Bailey-Brock 1984). Being large in body size (up to 10–20 cm long), hyalinoecians can be quite abundant in slope areas. Meyer et al. (2016) reported *Hyalinoecia artifex* Verrill, 1880 reaching up to 70 individuals/m^2 in the Baltimore Canyon at 400 m water depth. Another quill worm, *Hyalinoecia tubicola* (Müller, 1776), reached up to 272 individuals/m^2 at 365 m offshore of Chesapeake Bay (Wigley and Emery 1967).

Feeding modes and lifestyles

Onuphidae are very diverse in their life strategies and feeding modes. Such diversity presumably was achieved by developing a range of the anterior body region modifications as well as great variation in tube shape and composition (Fig. 7.12.3.4A–C). Onuphids are believed to be mostly omnivores or scavengers; however, some species have been shown to have primarily a plant diet (Fauchald and Jumars 1979). *Hyalinoecia* and *Leptoecia* are motile epibenthic dwellers constructing very light organic tubes that are being dragged by a worm on the bottom surface (Meyer et al. 2016). They are called "quill worms", referring to the type of tube resembling a quill of a bird feather. Both genera have enlarged and enhanced anterior parapodia and robust simple falcigers, allowing the worm to crawl on the sediment surface in search for food objects (Fig. 7.12.3.4A–C, Hy, Le). Baited monster camera experiments performed at a 2000-m-deep site in Baja California demonstrated that hundreds of specimens of *Hyalinoecia* can accumulate in 5 hours after the bait (rotten fish) has been deployed (Dayton and Hessler 1972), suggesting the scavenging feeding mode in the deep-sea large-bodied species. Meyer et al. (2016) analyzed the stable isotope content in *Hyalinoecia artifex* tissues, confirming its secondary consumer status. Their results supported earlier observations on the gut content of the same species by Gaston (1987), showing the presence of the remains of various benthic invertebrates.

Many species of *Diopatra*, common in intertidal and shallow subtidal zones, construct peculiar tubes in which the lower thinner mucous part is covered by sand or silt particles and the upper thicker part of an inner parchment-like layer is covered with densely packed shell fragments and plant debris. The upper part of a tube, the so-called "tube cap", usually has a curved shape and sticks from the sediment for several centimeters. These tube caps are used by the species as "food-catching devices" (Fig. 7.12.3.4, Di). The tube caps are large three-dimensional structures that have their own microcommunities of marine invertebrates and plants. They also gather various objects that are floating by with the local water currents. The gut content of omnivorous *Diopatra cuprea* (Bosc, 1802) from Massachusetts comprised both animal and plant materials and was almost identical in species composition to the community of the tube caps (Mangum et al. 1968). *Diopatra ornata* Moore, 1911 from California was also shown to feed on various animal and plant foods gathered on the tube caps with a large portion of foraminifera (Lipps and Ronan 1974).

Ambush predator behavior has been demonstrated in *Longibrachium arariensis* Nishi & Kato, 2009 from the Japanese waters. The worms live in vertical tubes inside the sediment with the tube opening on the surface (Figs. 7.12.3.1C, 7.12.3.4A–C, Lo). When they sense the bait (a small shrimp), they protrude four pairs of extremely modified anterior parapodia with long hook-like falcigers and grasp the prey. Once the prey is caught, the animal retrieves back into the tube (Nishi and Kato 2009).

Australonuphis are the largest onuphids, so-called beachworms, living in sandy beaches in Australia. They actively burrow and move in the sediment and use large amounts of mucus to strengthen their temporary burrows (Figs. 7.12.3.1D, 7.12.3.4A–C, Au). *Australonuphis* are attracted by any kind of animal bait, such as a piece of fish or a squid (Paxton 2000), and have been observed coming in great numbers to large carrion such as a sheep's head or a whale washed up on a beach (Paxton 1979).

Reproduction and development

Onuphidae display a high diversity of reproductive strategies. Many species are gonochoristic, but simultaneous (Lieber 1931, Arias et al. 2013b) or protandric (Arias and Paxton 2015, Arias et al. 2016) hermaphrodites are also known. Gametes usually mature in the coelomic cavity of an adult worm. Oogenesis and spermatogenesis take place in association with blood vessels. However, a single case of an intraovarian oogenesis has been described in the viviparous *Leptoecia vivipara* Orensanz, 1990 (Budaeva

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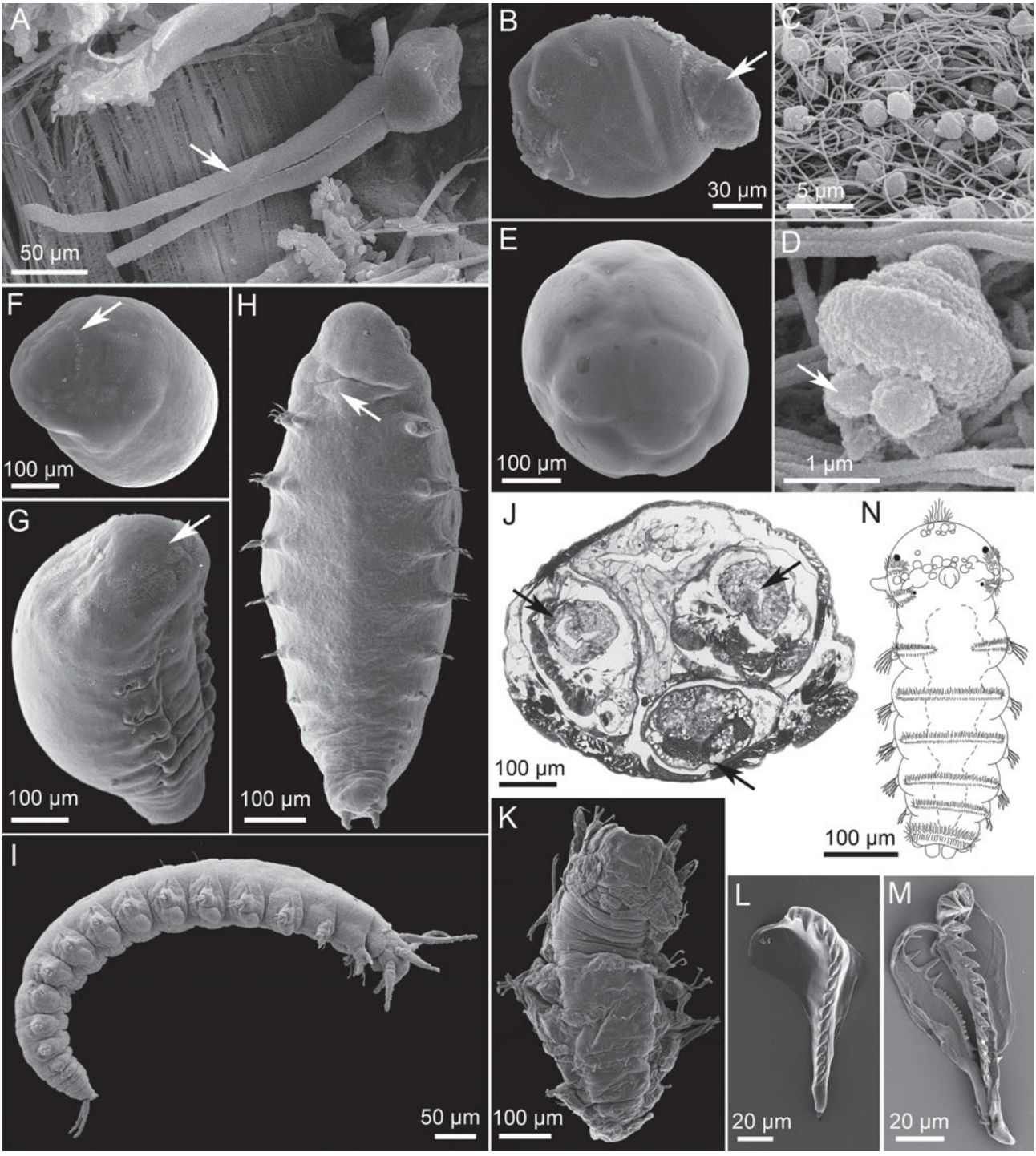


Fig. 7.12.3.5: Reproduction and development in *Mooreonuphis stigmatis* (A, E–I), *Leptoecia vivipara* (B, J–M), *Diopatra neapolitana* (C, D), and *Onuphis elegans* (N). A, Immature oocyte from female coelomic cavity, arrow indicates two strings of attached nurse cells; B, Oocyte from coelomic cavity, arrow indicates a cap of attached nurse cells; C, Spermatozoa; D, Same as C, close-up, arrow indicates mitochondria; E, Early cleavage stage; F, Early-stage juvenile from the parental tube, anterolateral view, arrow indicates reduced patchy ciliation on anterior end; G, 5-Chaetiger juvenile from parental tube, lateroventral view, arrow indicates reduced trochal ciliation; H, 9-Chaetiger juvenile from parental tube, ventral view, arrow indicates the formation of upper and ventral lips surrounding future mouth; I, 16-Chaetiger juvenile from parental tube, lateral view; J, Transverse section through brooding specimen with three developing embryos inside (indicated by arrows); K, 9-Chaetiger juvenile dissected from parental body cavity, dorsal view; L, Left MxII dissected from 7-chaetiger juvenile; M, Larval type of maxillae dissected from 7-chaetiger juvenile (left MxII is shown on L); N, 5-Chaetiger swimming larva, dorsal view. A, © E. Vortsepneva; B, J, K, M, Modified from Budaeva et al. (2014); C, D, Modified from Arias et al. (2016); G, I, Modified from Budaeva and Fauchald (2010); N, Modified from Blake (1975).

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et al. 2014). Oocytes have a number of attached nurse cells arranged either in two strings in Onuphinae (Fig. 7.12.3.5A) or forming a cap-like structure in Hyalinoeciinae (Fig. 7.12.3.5B). The structure of the oocyte surface is also subfamily specific: onuphins have smooth oocytes, whereas hyalinoeciins have a pitted egg surface. In general, the oocytes are quite large, containing a lot of yolk and varying in diameter from 175 µm in *Mooreonuphis jonesi* (Fauchald, 1982) (Fauchald 1982b) to 1400 µm in *Diopatra gigova* Paxton, 1993. Fecundity also varies greatly in different species. Large-bodied intertidal *Australonuphis teres* (Ehlers, 1868) may contain up to 100,000 oocytes in its body cavity (Paxton 1986a), whereas the deep-sea viviparous *Leptoecia vivipara* has only few oocytes and up to 10 developing juveniles inside a single gravid individual (Budaeva et al. 2014).

The shape of spermatozoa can vary even within a single genus (e.g., *Diopatra*) (Conti et al. 2005, Arias et al. 2013b) from having spherical (Fig. 7.12.3.5C, D) to elongated conical heads. Several successful attempts of artificial fertilization in various onuphid species support the presence of the external fertilization mode with both male and female gametes released into the water (Allen 1959, Blake 1975). Following the classification of Jamieson and Rouse (1989), many species of onuphids have typical ect-aquasperm. Spermatophores and sperm-transferring mechanism have been reported in *Kinbergonuphis simoni* (Santos et al. 1981). The mushroom-shaped spermatophores containing sperm are released by males in clumps into the environment and are picked up by the females. The sperm are stored by the females in the dorsal sacks (seminal receptacles) and remain viable up to 1 month (Hsieh and Simon 1990). Another type of sperm storage, dorsal papillae, has been described in *Diopatra neapolitana* Delle Chiaje, 1841. In this species, the papillae are used for storing own sperm in a hermaphroditic species and are also involved in sperm release into the environment (Arias et al. 2016).

Onuphids are known to provide parental care to their young, which has been classified into several types by Paxton (1993). Many known species brood their young inside the parental tubes until quite advanced juvenile stages of 10 to 20 chaetigers (Hartman 1967, Fauchald 1982b, Hsieh and Simon 1987, Fadlaoui et al. 1995, Paxton 2005a, Budaeva and Fauchald 2008, 2010, Paxton and Arias 2014). Several species are known to lay eggs in the sacs or jelly masses attached to their tubes (Paxton 1993). Only few species are reported as free spawners (Allen 1959, Choe 1960, Blake 1975, Arias et al. 2016), and two species are viviparous (Fig. 7.12.3.5K, J) (Hartman 1965, Orensanz 1990, Budaeva et al. 2014).

All onuphids have lecithotrophic development with swimming larvae (Allen 1959, Blake 1975) or directly developing juveniles (Hsieh and Simon 1987, Budaeva and Fauchald 2010). Short-lived pelagic larvae of *Onuphis elegans* (Johnson, 1901) show prominent trochal ciliation with developed apical tuft, prototroch, acrotroch, telotroch, and several rings of nototrochs (Fig. 7.12.3.5N). They are able to swim but settle down after spending just 6 days in the water column and begin to feed (Blake 1975). Juveniles of *Kinbergonuphis simoni* Santos, Day & Rice, 1981 and *Mooreonuphis stigmatis* (Treadwell, 1922) (Fig. 7.12.3.5E–I) developing inside the parental tubes display very reduced ciliation with residuals of the prototroch and the metatroch seen as disjunct ciliated patches on the prostomium. Juveniles of quite advanced stages of about 7 to 15 chaetigers (Fig. 7.12.3.5K) developing inside the adult viviparous worm of *Leptoecia vivipara* Orensanz, 1990 have ciliated bands only in the median segments (Budaeva et al. 2014).

The body of the juveniles and larvae is full of yolk deposits. Independent of the type of development, pelagic or benthic, all onuphids pass through similar stages. Four segments appear first in development with chaetae starting to protrude laterally. Prostomial and pygidial appendages follow the segment development with antennae and palps appearing before the complete development of the frontal lips and the upper and ventral lips surrounding the mouth. Peristomial cirri appear after the prostomial structures are well developed. Parapodial lobes and branchiae are the last external appendages developing in onuphid juveniles and larvae (Budaeva and Fauchald 2010).

The development of Onuphidae is characterized by the progressive replacement of the provisional chaetae by the definitive chaetae from the anterior toward the posterior region of the body (Paxton 1986a, 1996). Three general patterns of chaetal replacement have been suggested by Budaeva and Fauchald (2010). Two of these patterns appear to be subfamily specific, and the third type is characteristic for the genus *Diopatra* and may represent an autapomorphy within Onuphinae. The generalized pattern of chaetal progression in Onuphinae includes the replacement of the provisional anterior falcigers by the definitive falcigers with usually higher number of denticles, the replacement of the transitional compound falcigers by the limbate chaetae in the anteriormost unmodified parapodia, and the replacement of the provisional compound subacicular hooks by the definitive simple subacicular hooks. The pectinate chaetae and large tridentate hooks appear later in development when the adult chaetal pattern is almost achieved. Hyalinoeciinae differ in that the falcigers of the anterior modified parapodia are

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preceded by spinigers, which are subsequently replaced by the definitive falcigers. In addition, no transitional provisional falcigers were found in hyalinoeciins with only provisional subacicular hooks present in all unmodified parapodia (Carrasco 1983, Budaeva et al. 2014). *Diopatra* chaetal progression is characterized by the presence of two types of anterior provisional chaetae: curved chaetae and wing-tipped capillary chaetae. These chaetae appear first in larval development in anterior modified parapodia and are later replaced by the definitive pseudocompound falcigers (Fadlaoui et al. 1995).

Onuphidae have at least three generations of maxillae replacing each other in ontogeny (Paxton and Safarik 2008, Vortsepneva et al. 2017), whereas the mandibles appear to grow continuously throughout the life of a worm. The first type (larval) of maxillae is found in early larvae and juveniles, while they do not feed and live on the yolk deposits. The larval maxillae have an unpaired carrier and lack typical forceps-like MxI. The first pair of maxillae is strongly asymmetrical, with the left plate being long and sharply dentate and the right plate being extremely small with few rounded denticles. MxII are massive and dentate, whereas MxIII are small anterior sclerotized plates (Fig. 7.12.3.5L, M) (Paxton and Safarik 2008, Budaeva et al. 2014). The larval maxillae are being shed and swallowed by the worm before the beginning of feeding (Paxton and Safarik 2008, Vortsepneva et al. 2017). The second type (juvenile) of maxillae comprise paired carriers, with MxI as almost symmetrical falcate forceps-like plates with dentation along the inner proximal edges and paired dentate MxII and MxIV; MxIII are absent. The third generation (adult) of maxillae have a definitive number of elements characteristic to each genus (Fig. 7.12.3.2E). The mechanism of the replacement of the juvenile maxillae by the adult type of maxillae is unknown. Paxton (2005b, 2006) described a similar to insect molting mechanism in adult maxillae of *Diopatra aciculata* Knox & Cameron, 1971. Numerous events of molting in the maxillary apparatuses of the adults of *D. aciculata* were reported by Paxton and Safarik (2008). As a result of molting, the adult maxillae increase in size during the growth of a worm but do not change in shape and number of elements.

Species interactions

Onuphids constitute one of the main food sources for many demersal fishes (Livingston 1987, Serrano et al. 2003). Several cases of large quill worms *Hyalinoecia* digested by a sea star *Proserpinaster neozelanicus* have been reported from the New Zealand slope. The starfishes were densely packed with the *Hyalinoecia* tubes that were almost equal in length to the diameter of a star (Read and Clark 1999).

Onuphids are known to have symbiotic relationships with various organisms, although the nature (benefit-harm) of this symbiosis remains uncertain. Meyer et al. (2016) reported tubes of *H. artifex* hosting epifaunal organisms, including several foraminifera, an athecate hydroid, and a cocculinid limpet. Protozoan symbionts are common on parapodia and branchiae of Onuphidae. Piritrich ciliophora *Epistylis* sp. was found in several *Onuphis* species (Arias and Paxton 2014, 2015a).

Phylogeny and taxonomy

Taxonomic history

The family Onuphidae was erected by Kinberg (1865) under the name "Onuphiaea", but for a long period of time onuphids were treated as a subfamily of Eunicidae with only 8 to 10 genera recognized by most of the authors (McIntosh 1885, Fauvel 1923, Uschakov 1955, Day 1960, 1967). In her catalogue of the polychaetous annelids of the world, Hartman (1959) raised onuphids to the family level, and this has been widely accepted subsequently. The first attempt to revise the family at generic level was performed by Kucheruk (1978), who divided Onuphidae into 14 genera including 3 newly described genera: *Aponuphis*, *Notonuphis* Kucheruk, 1978, and *Neonuphis* Kucheruk, 1978. In his revision, Kucheruk (1978) provided generic diagnoses based on the presence or absence of the frontal lips and peristomial cirri, the shape of anterior parapodia, and the morphology of chaetae. Fauchald (1982a) conducted a study of several onuphid genera based on the examination of type material. This work provided the basis for the future revision of the whole family, accumulating information about morphological variation in many onuphid species. The most comprehensive systematic revision of Onuphidae at generic level has been performed by Paxton (1986a). All known species were assigned to 22 genera (including five newly described genera) based on the revised generic diagnoses. The system proposed by Paxton (1986a) has since been used in onuphid taxonomy with minor subsequent elaborations.

Several authors proposed further changes in the generic composition within Onuphidae. Orensanz (1990) suggested the synonymization of *Neonuphis* with *Leptoecia* based on the examination of extensive material from the Antarctic and Subantarctic waters, which was later supported by Budaeva (2012). Paxton (2005a) described a new monotypic genus *Fauchaldonuphis* from the Mozambique

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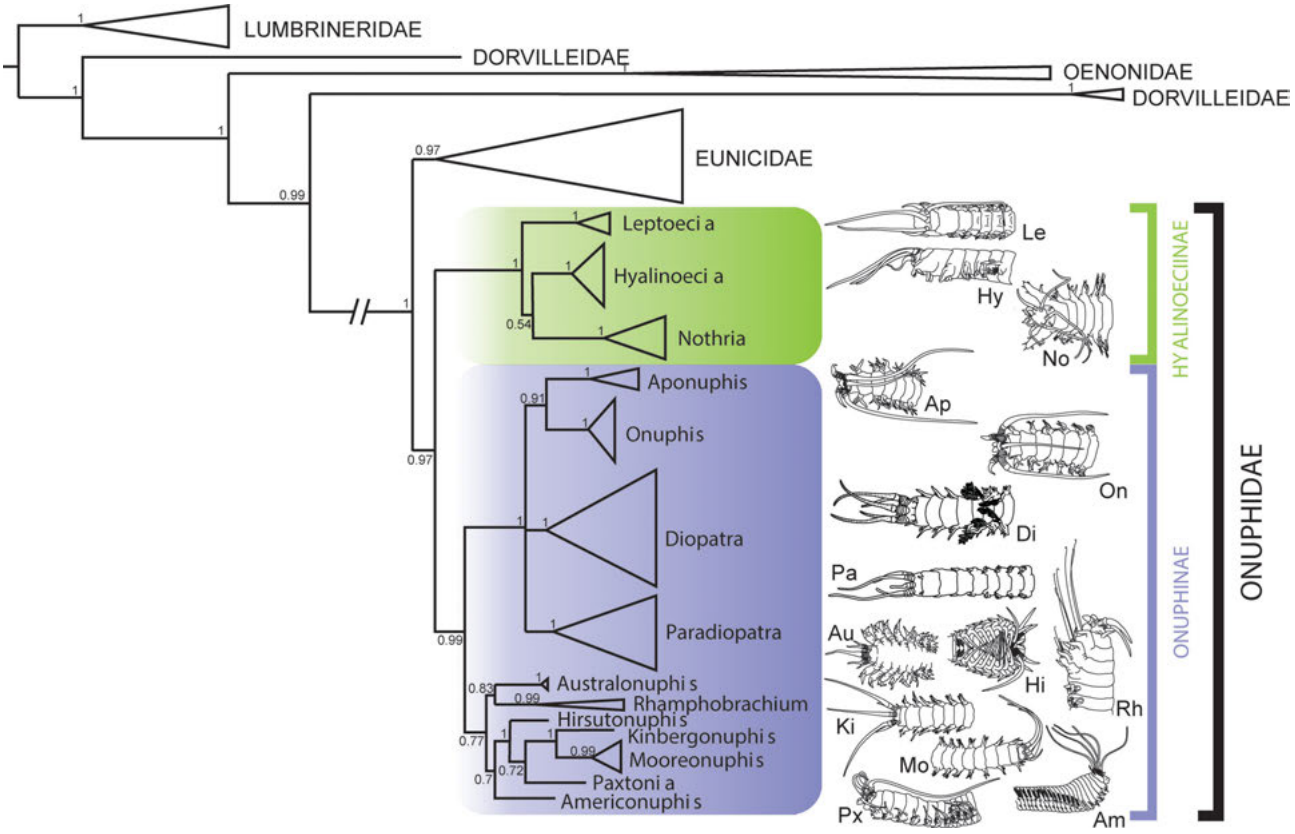


Fig. 7.12.3.6: Phylogeny of Onuphidae. Consensus tree from the Bayesian analysis of the combined 16S and 18S rDNA dataset; numbers on nodes indicate Bayesian posterior probabilities. Am, *Americonuphis*; Ap, *Aponuphis*; Au, *Australonuphis*; Di, *Diopatra*; Hi, *Hirsutonuphis*; Hy, *Hyalinoecia*; Ki, *Kinbergonuphis*; Le, *Leptoecia*; Mo, *Mooreonuphis*; No, *Nothria*; On, *Onuphis*; Pa, *Paradiopatra*; Px, *Paxtonia*; Rh, *Rhamphobrachium*. Modified from Budaeva et al. (2016).

Channel with unique prolonged but not retractable parapodia and spiny anterior falcigers. Budaeva and Fauchald (2011) revised the *Diopatra* generic complex *sensu* Paxton (1986a), suggesting the synonymization of two presumably progenetic genera *Epidiopatra* Augener, 1918 and *Notonuphis* with *Diopatra* and *Paradiopatra*, respectively. They also erected two new monotypic genera *Paxtonia* and *Protodiopatra*, whose type species have been previously assigned to *Paradiopatra* (Paxton 1986a). Several genera have been partially or completely revised: the *Rhamphobrachium* complex of genera (including *Brevibrachium*, *Longibrachium*, and *Rhamphobrachium* Ehlers, 1887) (Paxton 1986b); *Australonuphis* (León-González et al. 2008); *Hirsutonuphis* (Paxton 1996, Estrella-Ruiz et al. 2013); and *Paradiopatra* (Budaeva and Fauchald 2011, Paxton and Budaeva 2013). However, several of the most speciose genera, such as *Diopatra*, *Kinbergonuphis*, *Onuphis*, *Mooreonuphis*, *Anchinothria*, *Hyalinoecia*, and *Nothria*, require further revision. A number of regional taxonomic studies of the East Atlantic *Diopatra* (Rodrigues et al. 2009, Pires et al. 2010, Fauchald et al. 2012, Arias and Paxton 2015a, Arias et al. 2016, Paxton and Arias 2017), *Onuphis* and *Aponuphis* (Arias and Paxton 2014, 2015b, Arias 2016), Australian *Nothria* and *Anchinothria* (Budaeva and Paxton 2013), and *Paradiopatra* (Paxton and Budaeva 2013, Arias and Paxton 2015c) aided the understanding of the local faunal diversity and clarified the status of several widely spread species.

Phylogeny

Onuphidae have been included in general phylogenetic studies of Eunicida (e.g., Struck et al. 2006, Zanol et al. 2010, Tilic et al. 2016) or annelids as a whole (e.g., Rousset et al. 2007, Zrzavý et al. 2009, Struck et al. 2015) based on different molecular markers. Early molecular-based studies showed close relationships between Onuphide and Eunicidae, with the former placed within the latter (Struck et al. 2006, Rousset et al. 2007). However, in all recent studies based on extensive genetic data and wide taxon sampling, Onuphidae appeared as monophyletic and sister to Eunicidae (Zanol et al. 2010, Struck et al. 2015, Tilic et al. 2016). Onuphidae and Eunicidae share a

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number of synapomorphies: both families have eulabidognath maxillae, three antennae, a pair of palps on ceratophores, and subacicular hooks.

Paxton (1986a) proposed a phylogenetic reconstruction of the relationships between the onuphid genera based on 46 morphological and ontogenetic characters. She divided the family into two monophyletic subfamilies: Onuphinae Kinberg, 1865 and Hyalinoeciinae Paxton, 1986, supported by an exclusive synapomorphy, the position of the subacicular hooks in the parapodia. In Onuphinae, the subacicular hooks are in a ventral position in the lower bundle of neurochaetae, whereas Hyalinoeciinae have subacicular hooks in a median position with limbate chaetae located ventrally. Paxton suggested further subdivision of the subfamilies into several complexes of genera (e.g., *Diopatra* complex of genera, *Onuphis* complex of genera, and *Rhamphobrachium* complex of genera).

A phylogenetic analysis of Onuphidae based on the combination of 16S and 18S rDNA genes was performed for 36 species from 14 genera (Fig. 7.12.3.6) (Budaeva et al. 2016). The subdivision of the family into two subfamilies suggested by Paxton (1986a) was supported; however, none of the generic complexes were recovered. Ten of 14 tested genera were monophyletic, and the other 4 genera were either monotypic or represented in the analysis by a single species. Generally, the molecular analysis of onuphid relationships corroborated the traditional view on their systematics but did not support the interrelationships between most of the genera inferred from the morphological data. One of the strongly supported clades comprised *Onuphis*, *Aponuphis*, *Diopatra*, and *Paradiopatra*, the genera that have been previously considered to be the members of two different generic complexes. In contrast, *Mooreonuphis* was found to be sister to *Kinbergonuphis* Fauchald, 1982, confirming the traditional view on their close relationships. Relationships within Hyalinoeciinae were not resolved, and further genetic studies are required to clarify the status of the genera within this subfamily. Similarly, the position of several genera within Onuphinae (e.g., *Australonuphis*, *Americonuphis*, and *Rhamphobrachium*) was poorly supported and awaits further study.

Onuphidae Kinberg, 1865

Type species: *Onuphis eremita* Audouin & Milne Edwards, 1833 (by monotypy)

Diagnosis: Body cylindrical, elongated with iridescent cuticle. Prostomium rounded to triangular with one pair of conspicuous frontal lips attached to prostomium by narrow bases, sometimes reduced, semispherical; one pair of large bulbous upper lips located ventrally; pair of palps and three antennae in the occipital zone of prostomium. Antennae and palps morphologically similar consisting of multiringed ceratophores and elongated ceratostyles. With or without eyes. Nuchal organs present, straight, slightly curved, crescent, or nearly circular. Peristomium (first apodous ring) with or without pair of short dorsal cirri and with large semilunar ventral lip. Parapodia subbiramous; notopodia reduced to dorsal cirri with or without thin internal aciculae; neuropodia well-developed with aciculae and chaetae. One to eight pairs of anterior parapodia modified, with digitiform ventral cirri, specialized parapodial lobes and chaetae. Ventral cirri in posterior parapodia modified to glandular pads. Dorsal cirri digitiform or slender, present in all parapodia, sometimes reduced or absent in posteriormost segments. Branchiae present or absent, if present located at bases of dorsal cirri, filiform, spiral, pectinate, or dichotomously branched. Several kinds of chaetae: limbate chaetae, pectinate chaetae, simple or pseudocompound falcigers, large median hooks, spinigers, and subacicular hooks. Ventral mandibles flat, with elongated shafts and distal cutting plates. Dorsal eulabidognath maxillae with strong forceps-like MxI to MxIII denticulated plates, right Mx III lacking, MxIV curved subsymmetrical denticulated plates, MxV small plates, and MxVI present or absent. Pygidium with one or two pairs of anal cirri and dorsal anus. Oocytes with nurse cells arranged in two strings or clusters. Tubicolous; tubes organic transparent or consisting of parchment-like inner layer with or without foreign particles attached.

Remarks: The terminology describing prostomial appendages in onuphids underwent several changes over time. This was summarized by Paxton (1998), who proposed a new terminology subsequently widely accepted in publications on ohuphids, including the present chapter. The homology of the prostomial and peristomial appendages between different eunicidan families has been traced by Zanol (2010). Nonetheless, the terminologies currently used in Onuphidae and Eunicidae descriptions differ. Frontal lips, upper lips, and ventral lip of Onuphidae are the homologs of dorsal buccal lips, ventral buccal lips, and peristomial ventrolateral lips of Eunicidae, respectively (Zanol et al. 2014, see also chapter Eunicidae, pp. 414, this volume).

Hyalinoeciinae Paxton, 1986

Type genus: *Hyalinoecia* Malmgren, 1866

Diagnosis: Lower limbate chaetae present in all segments. Subacicular hooks in median position in parapodia. Anterior one to three pairs of parapodia modified, enlarged, and strengthened with auricular or trilobed prechaetal

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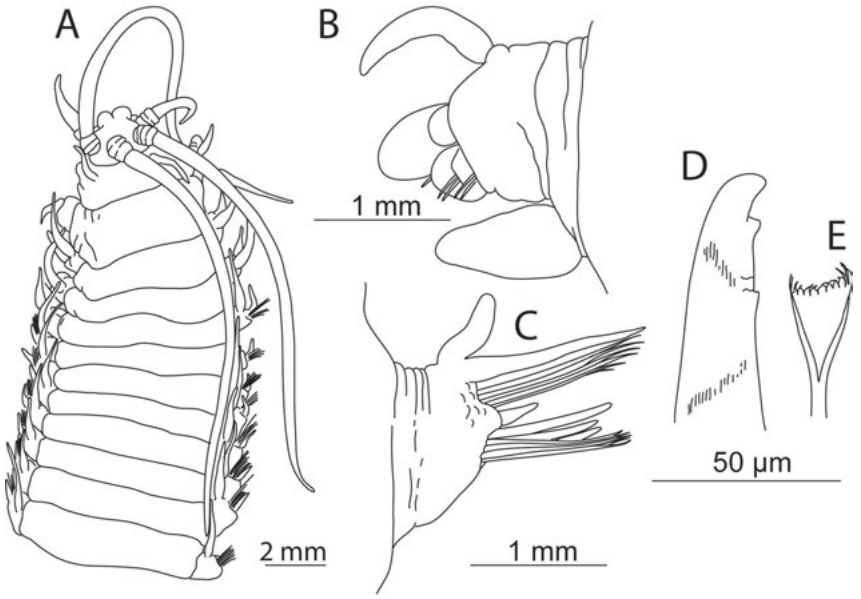


Fig. 7.12.3.7: *Anchinothria pycnobranchiata* (McIntosh, 1885). A, Anterior end, dorsal view; B, Parapodium of chaetiger 1, anterior view; C, Parapodium from midbody region, anterior view; D, Simple falciger from chaetiger 1; E, Pectinate chaeta. Modified from Orensanz (1990).

lobes. Falcigers pseudocompound to simple, with simple or bidentate appendages with short blunt hoods. Nurse cells associated with oocytes in a single cap-like cluster. Oocytes with pitted surface.

***Anchinothria* Paxton, 1986** (Fig. 7.12.3.7)
Type species: *Diopatra pourtalesii* Ehlers, 1887: 74. Gender: feminine.
Diagnosis: Body short, up to 100 segments. Median antenna longer than lateral antennae (Fig. 7.12.3.7A). Ceratophores short, consisting of two to five rings. Nuchal grooves straight. Peristomial cirri present. Anterior two to three pairs of parapodia enlarged, directed anteroventrally with bilobed to trilobed prechaetal lobes (Fig. 7.12.3.7B). Ventral cirri subulate on anterior two to three chaetigers. Branchiae present or absent, single or dichotomously branched with up to 10 filaments (Fig. 7.12.3.7C). Unidentate or bidentate simple or pseudocompound falcigers (Fig. 7.12.3.7D) on first two to four pairs of anterior parapodia, in one species on first seven pairs of parapodia. Pectinate chaetae wide with rolled margins, so-called "scoop-shaped" (Fig. 7.12.3.7E) from chaetigers 2 to 3, in one species from chaetiger 14. Subacicular hooks from chaetigers 4 to 16. MxV present, MxVI absent. Tubes dorsoventrally flattened with parchment-like inner layer covered with mud and often incrusted with scattered large elongated foraminiferans, glass sponge spicules, or echinoid spines attached along longitudinal margins.
Composition: 12 species.
Distribution: Worldwide, except the Arctic. Depth range: 100 to 4464 m (Budaeva and Paxton 2013).

***Hyalinoecia* Malmgren, 1866** (Fig. 7.12.3.8)
Type species: *Nereis tubicola* Müller, 1776: 18. Gender: feminine.
Diagnosis: Small- to large-sized worms up to 20 cm long with up to 200 chaetigers. Prostomium anteriorly rounded with oval or ovoid frontal lips. Antennae with ceratophores with two to five rings and long styles reaching chaetigers 8 to 20 (Fig. 7.12.3.8A). Median antenna longer and thicker than lateral antennae. Nuchal organs straight with narrow to moderately wide middorsal separation. Peristomial cirri absent. Anterior two to three pairs of parapodia modified, moderately prolonged, with large auricular prechaetal and subulate postchaetal lobes (Fig. 7.12.3.8B, C). Ventral cirri subulate on anterior three to four chaetigers. Branchiae from chaetigers 18 to 33, single, strap-like filaments, or absent (Fig. 7.12.3.8D). Pseudocompound falcigers on modified parapodia unidentate to bidentate, simple to pseudocompound, with or without hoods (Fig. 7.12.3.8E, F). Flat pectinate chaetae from chaetiger 2, with up to 20 denticles (Fig. 7.12.3.8H). Paired bidentate hooded subacicular hooks from chaetigers 15 to 30 (Fig. 7.12.3.8G). MxV present, MxVI absent. Tubes round in transverse section, translucent quill-like, completely secreted by worm and lacking external covering of foreign particles. Anterior and posterior ends of tube with two to four internal valves.
Composition: ~20 species.
Distribution: Worldwide, except the Arctic, mostly in slope areas. Depth range: 10 to 2300 m.

***Hyalospinifera* Kucheruk, 1979** (Fig. 7.12.3.9)
Type species: *Hyalospinifera spinosa* Kucheruk, 1979: 1585. Gender: feminine.

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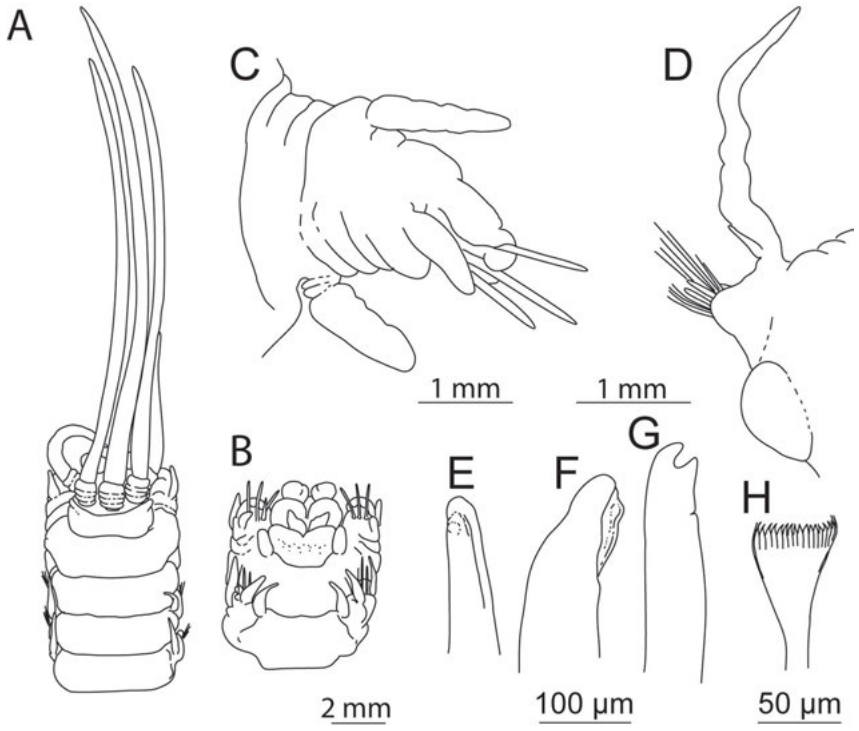


Fig. 7.12.3.8: *Hyalinoecia* sp. A, Anterior end, dorsal view; B, Same as A, ventral view; antennae and palps omitted; C, Parapodium of chaetiger 1, posterior view; D, Posterior parapodium, anterior view; E, F, Tips of anterior simple falcigers from chaetiger 1; G, Subacicular hook; H, Pectinate chaeta. Modified from Orensanz (1990).

Diagnosis: Small-sized worms 20 mm long with 42 chaetigers (incomplete specimen). Prostomium anteriorly rounded with reduced frontal lips (Fig. 7.12.3.9A). Antennae with short ceratophores with three to four indistinct rings and long styles. Nuchal grooves presumably straight. Peristomial cirri absent. Anterior two pairs of parapodia modified. Parapodia 1 prolonged, with auricular prechaetal and short, digitiform postchaetal lobes; parapodia 2 and 3 shorter (Fig. 7.12.3.9B). Ventral cirri subulate on two to three chaetigers. Branchiae from chaetigers 16 to 18, simple filaments throughout body (Fig. 7.12.3.9C). Simple falcigers on first two pairs of modified parapodia with pointed bifurcated tips (Fig. 7.12.3.9E). Flat pectinate chaetae with 18 denticles, from chaetiger 3 (Fig. 7.12.3.9F). Paired bidentate hooded subacicular hooks from chaetigers 18 to 19. Details of jaw apparatus not known. Tubes strongly curved, translucent; egg-shaped in transverse section with thickening on one side; without external covering of foreign particles (Fig. 7.12.3.9D).

Composition: 1 species.

Distribution: Arabian Sea; Bay of Bengal, Sulu Sea. Depth range: 850 to 1300 m (Kucheruk 1979).

***Leptoecia* Chamberlin, 1919** (Fig. 7.12.3.10)

Synonyms: *Parhyalinoecia* Hartmann-Schröder, 1975: 65; *Neonuphis* Kucheruk, 1978: 93.

Type species: *Leptoecia abyssorum* Chamberlin, 1919: 320. Gender: feminine.

Diagnosis: Small-sized worms 10 to 40 mm long with up to ~80 chaetigers. Prostomium rounded, conical or pointed with reduced or absent frontal lips (Fig. 7.12.3.10A–D). Antennae with short one to four ringed ceratophores and long styles. Nuchal organs slightly curved with wide middorsal separation, may be absent in some species. Peristomial cirri absent (Fig. 7.12.3.10A). Anterior one to two pairs of parapodia modified, first pair prolonged with auricular prechaetal lobe and digitiform postchaetal lobe (Fig. 7.12.3.10E). Ventral cirri subulate on first two chaetigers. Branchiae absent (Fig. 7.12.3.10F). Simple or pseudocompound unidentate to bidentate falcigers with short blunt hoods on one to two pairs of anterior parapodia (Fig. 7.12.3.10G). Pectinate chaetae flat with about 10 denticles. Paired bidentate hooded subacicular hooks from chaetigers 12 to 50 (Fig. 7.12.3.10F, H). MxV and MxVI absent. Tubes secreted, quill-like, circular in cross-section or flattened dorsoventrally, with two longitudinal ribs.

Composition: 7 species.

Distribution: Worldwide, except the Arctic, frequently reported circum Antarctic. Depth range: 437 to 6330 m (Budaeva 2012).

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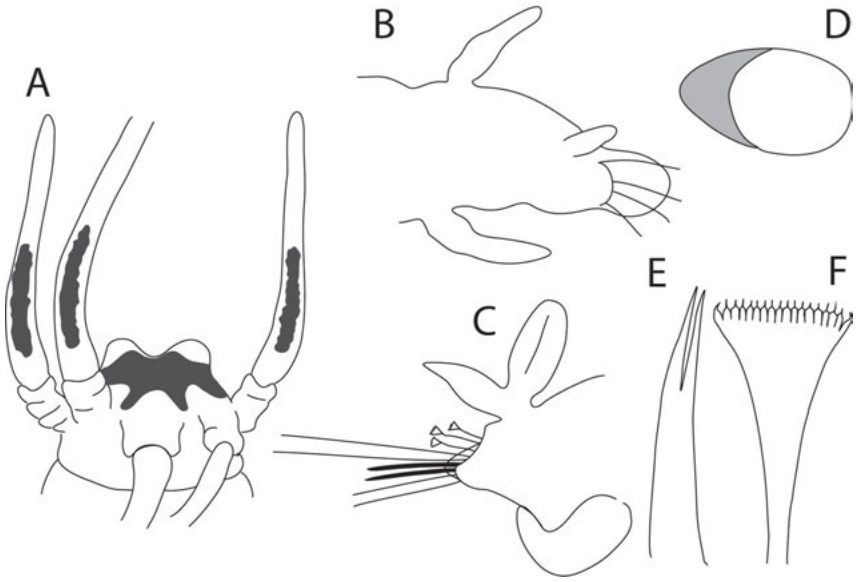


Fig. 7.12.3.9: *Hyalospinifera spinosa* Kucheruk, 1979. A, Anterior end, dorsal view; B, Parapodium of chaetiger 1, posterior view; C, Parapodium of chaetiger 25, anterior view; D, Transverse section through tube; E, Falciger from chaetiger 1; F, Pectinate chaeta from chaetiger 3. Modified from Kucheruk (1979).

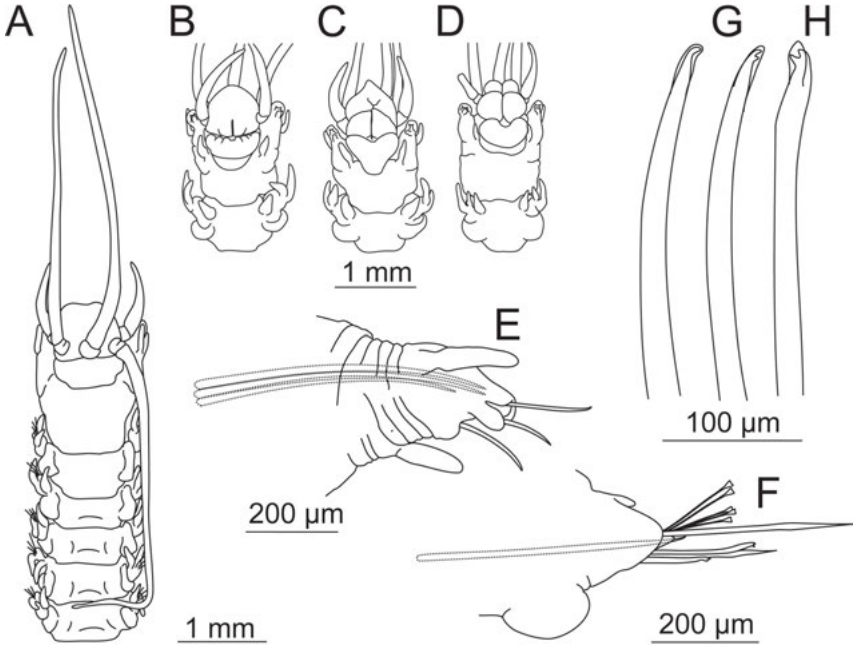


Fig. 7.12.3.10: *Leptoecia midatlantica* Budaeva, 2012. A, Anterior end, dorsal view; B–D, Anterior end, ventral view showing variability in development of frontal lips; E, Parapodium of chaetiger 1, posterior view; F, Parapodium of chaetiger 35, anterior view; G, Simple falcigers from chaetiger 1; H, Subacicular hook from chaetiger 35. Modified from Budaeva (2012).

***Nothria* Malmgren, 1866** (Fig. 7.12.3.11)

Type species: *Onuphis conchylega* Sars, 1835: 61. Gender: feminine.

Diagnosis: Body short, up to 100 segments. Antennae with ceratophores consisting of two to five rings and short to moderately long styles. Median antenna longer than lateral antennae (Fig. 7.12.3.11A). Nuchal organs straight with narrow middorsal separation. Anterior two to three pairs of parapodia enlarged, directed anteroventrally with large auricular prechaetal lobes (Fig. 7.12.3.11B, C). Ventral cirri subulate on first two to three chaetigers (Fig. 7.12.3.11D). Branchiae present or absent, single to up to five filaments. Unidentate, bidentate, or tridentate simple or pseudocompound falcigers on first two to three pairs of anterior parapodia (Fig. 7.12.3.11E). Pectinate chaetae wide with rolled margins, so-called "scoop-shaped" (Fig. 7.12.3.11G), from chaetigers 2 to 3, in one species from chaetiger 9; rarely pectinate chaetae flat (Fig. 7.12.3.11F). Paired

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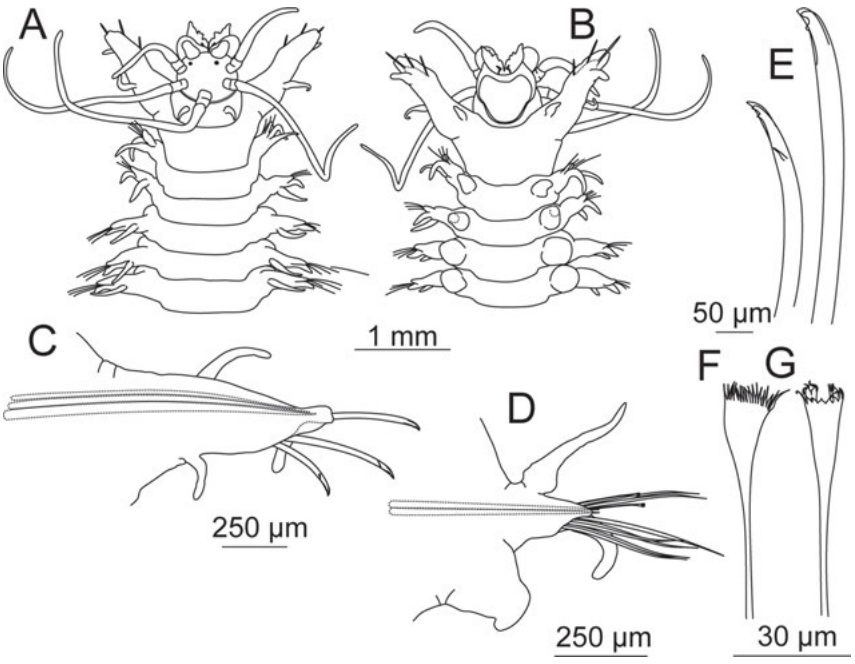


Fig. 7.12.3.11: *Nothria abyssia* Kucheruk, 1978 (A–F) and *Notharia otsuchiensis* Imajima, 1986 (G). A, Anterior end, dorsal view; B, Same as A, ventral view; C, Parapodium of chaetiger 1, anterior view; D, Parapodium of chaetiger 3, anterior view; E, Falcigers from chaetiger 1; F, Flat pectinate chaeta; G, Scoop-shaped pectinate chaeta. Modified from Budaeva and Paxton (2013).

hooded subacicular hooks from chaetigers 7 to 15. MxV present, MxVI absent. Tubes dorsoventrally flattened with thin inner parchment-like layer covered with large shell fragments, small stones, and shells of foraminiferans.
Composition: ~20 species.
Distribution: Worldwide. Depth range: 4 to 5200 m.

Onuphinae Kinberg, 1865

Type genus: *Onuphis* Audouin & Milne Edwards, 1833
Diagnosis: Lower limbate chaetae absent posterior to origin of subacicular hooks. Subacicular hooks in ventral position in parapodia. Anterior two to eight parapodia modified, enlarged and/or elongated in some genera, similar in size to other parapodia in other genera. Prechaetal lobes short, conical to ovoid. Falcigers pseudocompound to simple, appendages simple or bidentate, tridentate, or quadridentate with short blunt or pointed to extremely long pointed hoods. Nurse cells associated with oocytes in two strings. Oocytes with smooth surface.

***Americonuphis* Fauchald, 1973** (Fig. 7.12.3.12)
Type species: *Diopatra magna* Andrews, 1891: 286. Gender: feminine.
Diagnosis: Large-sized worms, up to 100 cm long with more than 300 segments. Prostomium very short weakly incised and anteriorly extended. Median antenna longer than lateral antennae. Ceratophores short, consisting of five to eight rings. Nuchal grooves straight. Peristomial cirri inserted in the middle of expansible peristomium. First three to five pairs of modified parapodia enlarged, directed strongly anteroventrally. Ventral cirri of chaetiger 5 almost touching in ventral midline (Fig. 7.12.3.12A, B). Branchiae pectinate from chaetiger 6 (Fig. 7.12.3.12C). Anterior falcigers pseudocompound with short hoods (Fig. 7.12.3.12D). Pectinate chaetae broad with numerous teeth. Subacicular hooks from chaetigers 16 to 18. MxV and MxVI present. Tubes with inner parchment-like layer and outer layer of mud with foreign particles.
Composition: 2 species.
Distribution: Western Atlantic from North Carolina (Andrews 1891), Gulf of Mexico, Caribbean Sea (Fauchald 1980) to Venezuela (Andrade and Liñero 1993); Eastern Pacific, Gulf of Panama (Fauchald 1973). Intertidal to shallow subtidal (Fauchald 1973).

***Aponuphis* Kucheruk, 1978** (Fig. 7.12.3.13)
Type species: *Hyalinoecia bilineata* Baird, 1870: 358. Gender: feminine.
Diagnosis: Small-sized worms with up to 250 chaetigers, less than 1.5 mm wide. Prostomium anteriorly extended. Antennae long reaching up to chaetiger 22. Median antenna shorter than lateral antennae. Ceratophores with up to 20 rings; palpophores longer than palpostyles (Fig. 7.12.3.13A). Nuchal organs straight. Peristomial cirri absent (Fig. 7.12.3.13A). Anterior three to six (rarely seven to eight) pairs of parapodia modified but not enlarged (Fig. 7.12.3.13B). Ventral cirri subulate on four to seven chaetigers. Branchiae, rarely absent, usually present from chaetiger 4, rarely one to seven; single filaments. Pseudocompound falcigers on modified parapodia bidentate to tridentate, rarely quadridentate (Fig. 7.12.3.13C). Pectinate chaetae with about 12 denticles. Subacicular hooks

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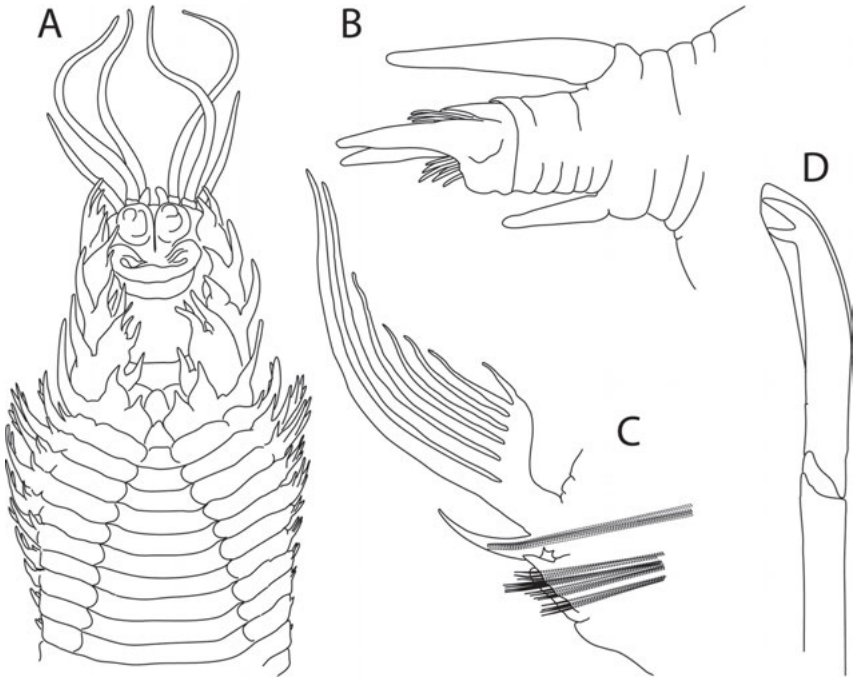


Fig. 7.12.3.12: *Americonuphis reesei* Fauchald, 1973. A, Anterior end, ventral view; B, Parapodium from chaetiger 1, posterior view; C, Parapodium with branchia, posterior view; D, Pseudocompound falciger from chaetiger 1. Modified from Fauchald (1973).

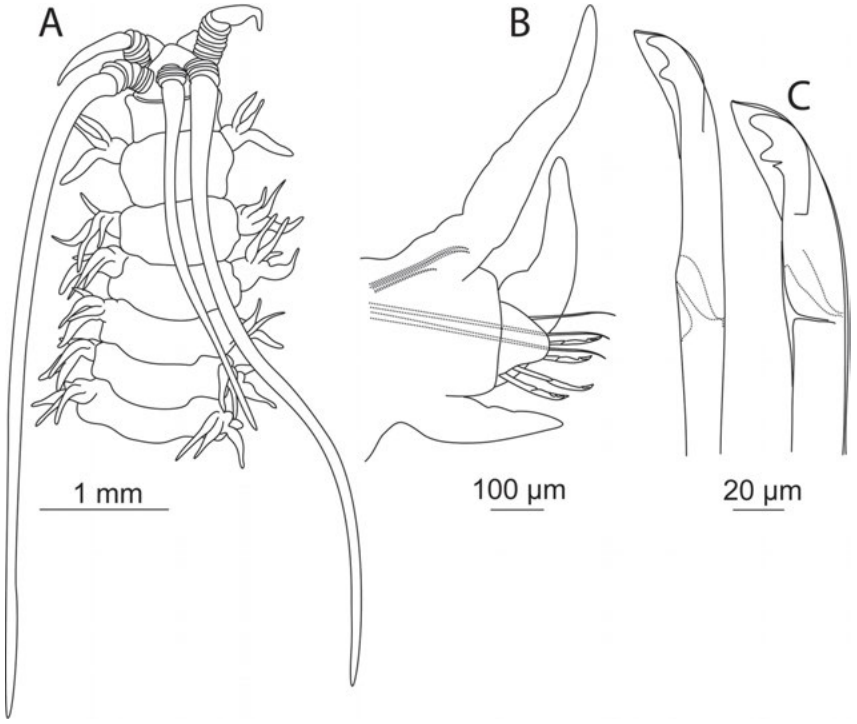


Fig. 7.12.3.13: *Aponuphis* sp. (A) and *Aponuphis bilineata* (Baird, 1870) (B, C). A, Anterior end, dorsal view; B, Parapodium of chaetiger 1, anterior view; C, Pseudocompound falcigers from chaetiger 1. A, Modified from Budaeva et al. (2016); B, C, Modified from Paxton (1986a).

from chaetigers 9 to 15. MxV present, MxVI absent. Tubes thin, consisting of inner mucous and outer layer of sand or shell fragments.

Composition: 10 species; *Aponuphis bilineata* (Baird, 1870) and *Aponuphis brementi* (Fauvel, 1916) possibly represent species complexes with at least three genetic species in each complex (Borisova et al. 2018).

Distribution: Northeastern Atlantic, Reykjanes Ridge (Detinova 1985); Eastern Atlantic, North Sea, Mediterranean Sea, Iberian Peninsula, Bay of Biscay, from off Morocco to off Angola (Arias and Paxton 2015b, Borisova et al. 2018).

***Australonuphis* Paxton, 1979** (Fig. 7.12.3.14)

Americonuphis Orensanz, 1974: 100

Type species: *Americonuphis casamiquelorum* Orensanz, 1974: 100. Gender: feminine.

Diagnosis: Large-sized worms up to 300 cm long and 2.5 cm wide with about 1000 chaetigers. Prostomium short and

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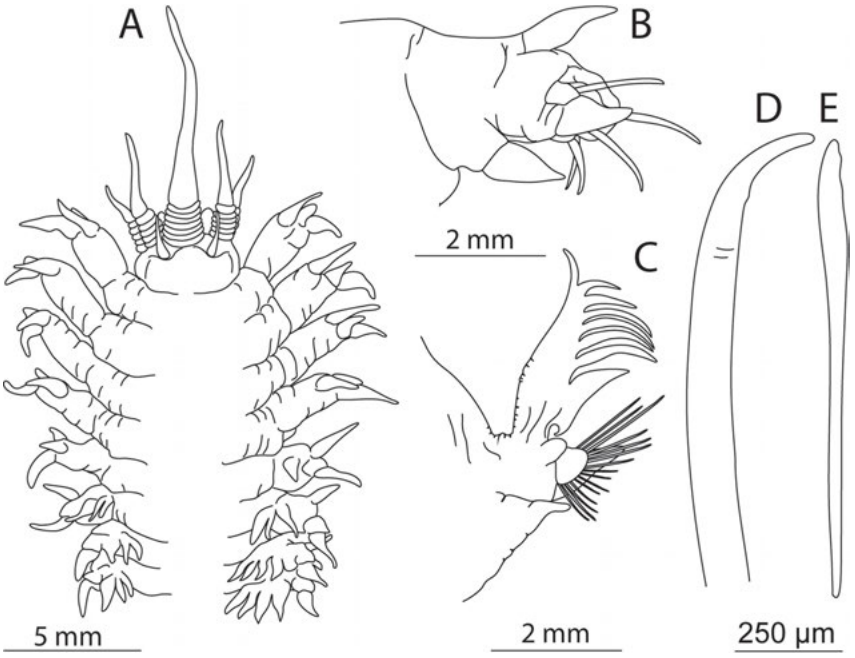


Fig. 7.12.3.14: *Australonuphis violacea* Rozbaczylo & Castilla, 1981. A, Anterior end, dorsal view; B, Parapodium of chaetiger 1, posterior view; C, Parapodium of chaetiger 17, anterior view; D, Pseudocompound falciger from chaetiger 3; E, Subacicular hook from chaetiger 100. Modified from Rozbaczylo and Castilla (1981).

rounded almost covered dorsally by wide bases of antennae. Antennae short, up to chaetigers 2 to 6. Median antenna longer than lateral antennae. Ceratophores with 7 to 14 rings; ceratostyles equal in length to ceratophores (Fig. 7.12.3.14A). Nuchal organs widely separated, curved toward the base of median antenna. Peristomial cirri present. Anterior fold of peristomium reduced, middorsal part of peristomium extending along nuchal organs toward median antenna. Anterior five to eight pairs of parapodia modified, enlarged and moderately prolonged (Fig. 7.12.3.14B). Dorsal cirri with basal swelling developing into digital process posteriorly (Fig. 7.12.3.14C). Ventral cirri subulate on anterior 8 to 25 chaetigers. Branchiae pectinate with up to eight filaments from chaetiger 6 (Fig. 7.12.3.14C). Pseudocompound falcigers on anterior five to seven parapodia, unidentate to weakly bidentate, without hoods (Fig. 7.12.3.14D). Pectinate chaetae with numerous small teeth. Subacicular hooks distally entire, without hoods, from chaetigers 44 to 75 (Fig. 14E). MxV present, MxVI absent. Live in borrows with mucous inner lining.

Composition: 7 species.

Distribution: Australian and American coastal waters: western Mexico, Salvador, Ecuador, Chile, Brazil, and Argentina (León-González et al. 2008). Depth range: intertidal to 14 m (Paxton 1986a).

***Brevibrachium* Paxton, 1986** (Fig. 7.12.3.15)

Type species: *Rhamphobrachium capense* Day, 1960: 355. Gender: neuter.

Diagnosis: Small-sized worms up to 42 mm long with about 100 chaetigers. Prostomium rounded. Antennae short with ceratophores consisting of two to four rings and very short styles (Fig. 7.12.3.15A, B). Median antenna shorter or equal to lateral antennae. Nuchal organs widely separated and curved laterally. Peristomial cirri present. Anterior three to five pairs of parapodia modified, moderately prolonged (Fig. 7.12.3.15C). Ventral cirri subulate on first three to five chaetigers. Branchiae from chaetigers 2 to 40, single or pectinate with up to five filaments. Modified parapodia with more than three smooth distally recurved or unidentate to tridentate falcigers (Fig. 7.12.3.15D). Falcigers smooth or with two rows of immoveable spines. Chaetal sacs extending to chaetigers 4 to 8. Pectinate chaetae oblique with up to 25 small denticles. Subacicular hooks from chaetigers 8 to 10 (Fig. 7.12.3.15E). MxV present, MxVI absent. Tubes with mucous or parchment-like inner layer covered by sand, mud, or foreign particles, one species makes borrows in limestone (Smith and Jensz 1968).

Composition: 4 species.

Distribution: Southern Hemisphere: South Africa, Australia, New Zealand, Brazil. Depth range: intertidal to 137 m (Paxton 1986a, b, Lana 1991).

***Diopatra* Audouin & Milne Edwards, 1883** (Fig. 7.12.3.16)

Epidiopatra Augener, 1918: 355

Type species: *Diopatra amboinensis* Audouin & Milne Edwards, 1833: 229. Gender: feminine.

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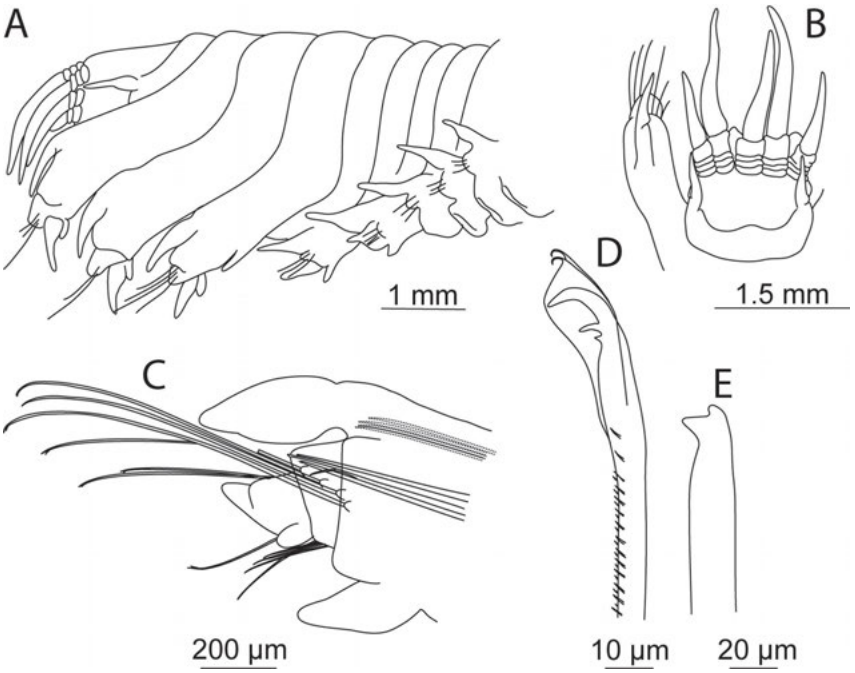


Fig. 7.12.3.15: *Brevibrachium hanneloreae* Lana, 1991 (A, B) and *Brevibrachium capense* (Day, 1960) (C–E). A, Anterior end, lateral view; B, Anterior end, dorsal view; C, Parapodium of chaetiger 1, anterior view; D, Modified falciger from chaetiger 1; E, Subacicular hook from chaetiger 60. A, B, Modified from Lana (1991); C–E, Modified from Paxton (1986a).

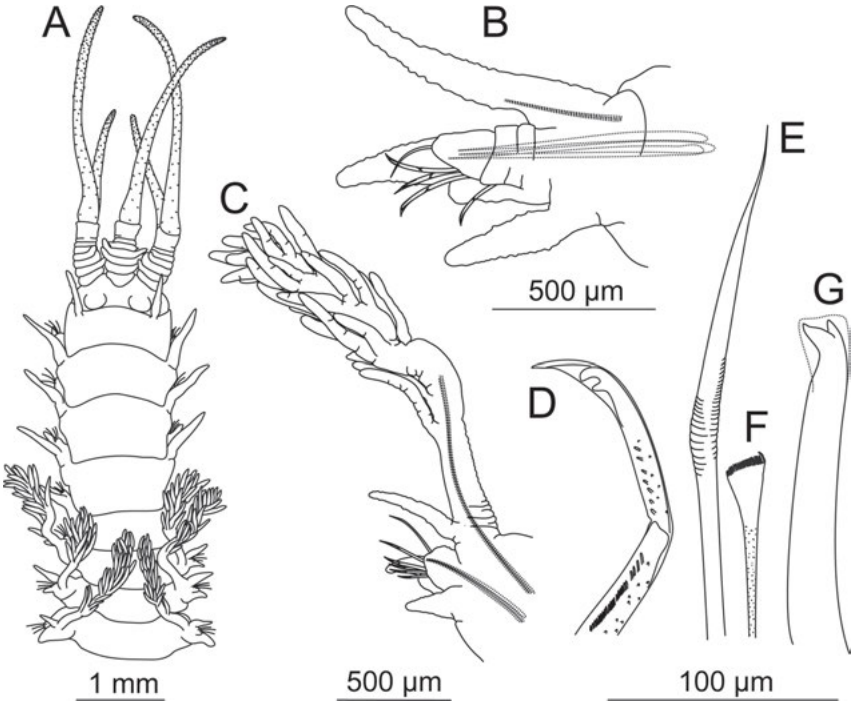


Fig. 7.12.3.16: *Diopatra tuberculantennata* Budaeva & Fauchald, 2008. A, Anterior end, dorsal view; B, Parapodium of chaetiger 1, anterior view; C, Parapodium of chaetiger 5, anterior view; D, Pseudocompound falciger from chaetiger 2; E, Serrated limbate chaeta from chaetiger 12; F, Pectinate chaeta from chaetiger 12; G, Subacicular hook from chaetiger 25. Modified from Budaeva and Fauchald (2008).

Diagnosis: Medium- to large-sized worms up to 30 cm long with 250 chaetigers. Prostomium anteriorly rounded to pointed with ovoid to subulate frontal lips. Antennae moderately long with median antenna shorter or equal to lateral antennae (Fig. 7.12.3.16A). Styles of palps and antennae covered with sensory papillae in some species forming longitudinal rows (Fig. 7.12.3.16A). Ceratophores with 3 to 30 rings, may bear lateral projections. Nuchal organs from straight to crescentic and almost circular. Peristomial cirri present or absent. Anterior four to six pairs of parapodia modified but not enlarged, directed lateroventrally (Fig. 7.12.3.16B). Ventral cirri subulate on anterior four to six chaetigers. Some species with additional ventral lobes on chaetigers 5 to about 25. Branchiae spiral, with up to

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20 whorls of filaments, present from chaetigers 4 to 5, only to median chaetigers (Fig. 7.12.3.16C). Pseudocompound falcigers unidendate to tridentate with short to long pointed hoods and, in some species, with two rows of small spines on shafts (Fig. 7.12.3.16D). Limbate chaetae serrated (Fig. 7.12.3.16E). Pectinate chaetae with 3 to 30 denticles (Fig. 7.12.3.16F). Subacicular hooks from chaetigers 8 to 30 (Fig. 7.12.3.16G). MxV present, MxVI absent. Tubes cylindrical, covered with mud or shell fragments, in some species with distal recurved part incrusted with debris (fragments of shells, algae, aquatic plants, small stones, etc.)

Composition: ~60 species.

Distribution: Worldwide, except the Arctic. Depth range: from intertidal to 2525 m (Budaeva and Fauchald 2011).

***Fauchaldonuphis* Paxton, 2005** (Fig. 7.12.3.17)

Type species: *Diopatra parad*oxa Quatrefages, 1866. Gender: feminine.

Diagnosis: Medium-sized worms up to 117 mm long with about 180 chaetigers. Prostomium short, with two oval frontal lips. Antennae with ceratophores with four to five rings and short styles, reaching chaetiger 1 (Fig. 7.12.3.17A). Nuchal organs curved laterally, without obvious middorsal separation. Peristomial cirri present. Anterior five chaetigers elongated. Anterior five pairs of parapodia modified, moderately to greatly prolonged (parapodia 3 and 4 longest) (Fig. 7.12.3.17A). Ventral cirri subulate on six anterior chaetigers. Branchiae from chaetigers 15 to 20; pectinate filaments, covering most of the body (Fig. 7.12.3.17B). Modified parapodia with capillary chaetae and simple to weakly pseudocompound bidentate falcigers with long pointed hoods, shafts of both types of chaetae distally spinous (Fig. 7.12.3.17C). Chaetal sacs limited to respective enlarged chaetigers. Pectinate and limbate chaetae from chaetiger 6. Bidentate hooded subacicular hooks from chaetigers 15 to 17. MxV present, MxVI absent. Tubes with tough inner secreted layer and outer layer of mud.

Composition: 1 species.

Distribution: Indian Ocean; Gulf of Mastatan, Mozambique Channel and Andaman Sea near Phuket, Thailand. Depth range: 20 to 72 m (Paxton 2005a).

***Hartmanonuphis* Paxton, 1986** (Fig. 7.12.3.18)

Type species: *Onuphis pectinata* Knox & Hicks, 1973: 289. Gender: feminine.

Diagnosis: Large-sized worms up to 50 cm long with ~800 chaetigers. Prostomium with anterior median incision, almost covered dorsally with the bases of antennae. Antennae short with ceratophores consisting of six to eight rings and styles reaching chaetigers 3 to 5 (Fig. 7.12.3.18A). Median antenna shorter than lateral antennae. Nuchal organs with wide middorsal separation, curved toward the base of median antenna. Anterior fold of peristomium reduced, middorsal part of peristomium extending along nuchal organs toward the median antenna (Fig. 7.12.3.18B). Peristomial cirri present. Anterior six pairs of parapodia modified, moderately prolonged (Fig. 7.12.3.18C). Ventral cirri subulate on anterior six chaetigers with long transition zone of ventral glandular pads with reduced cirri (until chaetigers 14–16). Branchiae pectinate from chaetiger 1 (Fig. 7.12.3.18A, C, D). Pseudocompound falcigers on anterior modified parapodia bidentate (Fig. 7.12.3.18E). Pectinate chaetae oblique with about 25 denticles (Fig. 7.12.3.18F). Bidentate hooded subacicular hooks

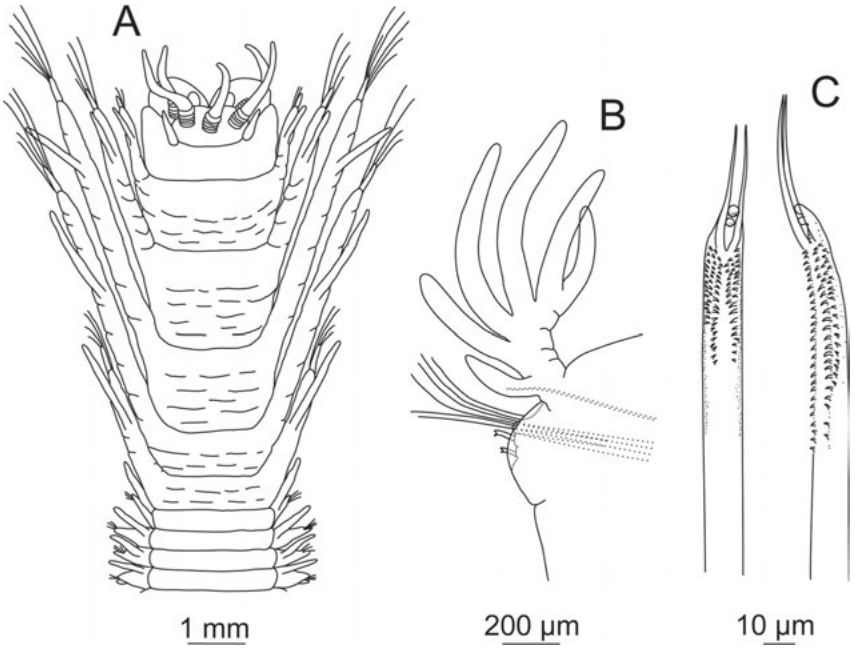


Fig. 7.12.3.17: *Fauchaldonuphis paradoxa* (Quatrefages, 1866). A, Anterior end, dorsal view; B, Parapodium of chaetiger 69, posterior view; C, Simple falciger from chaetiger 3, frontal and lateral views. Modified from Paxton (2005a).

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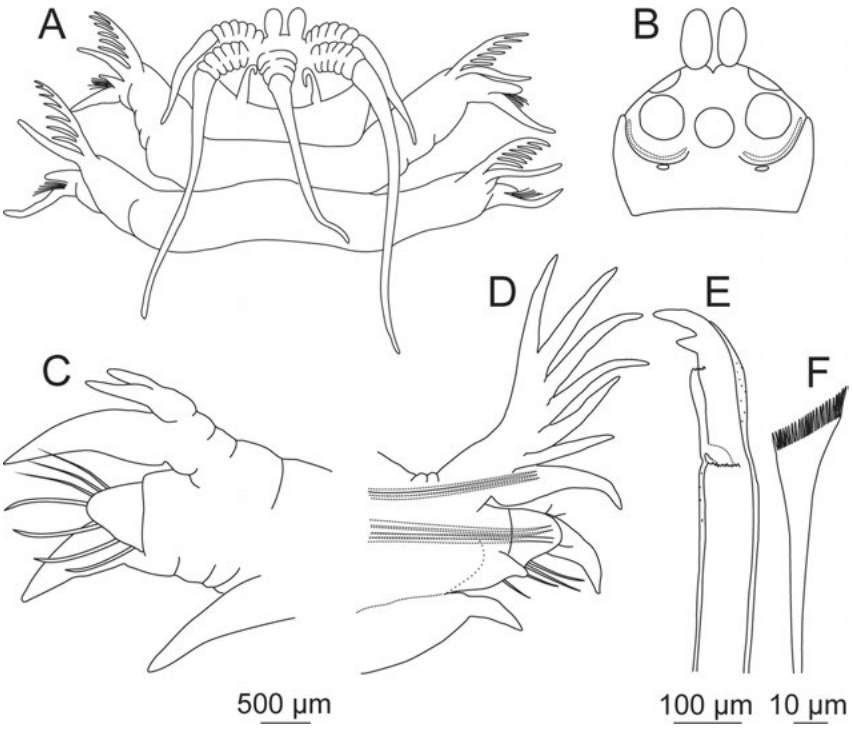


Fig. 7.12.3.18: *Hartmanonuphis pectinata* (Knox & Hicks, 1973). A, Anterior end, dorsal view; B, Scheme of prostomium and peristomium, dorsal view, antennae and palps omitted; C, Parapodium of chaetiger 1, anterior view; D, Parapodium of chaetiger 12, anterior view; E, Pseudocompound falciger from chaetiger 2; F, Pectinate chaeta from chaetiger 200. A, Modified from Knox and Hicks (1973); B–F, Modified from Paxton (1986a).

from chaetigers 29 to 31. MxV present, MxVI absent. Live in burrows with mucous inner lining.
Composition: 1 species.
Distribution: South Pacific Ocean: New Zealand. Depth range: intertidal to 85 m (Paxton 1986a).

***Heptaceras* Ehlers, 1868** (Fig. 7.12.3.19)
Type species: *Diopatra phyllocirra* Schmarda, 1861: 133. Gender: neuter.
Diagnosis: Medium-sized worms up to 26 cm long with ~500 chaetigers. Prostomium with frontal extension with frontal lips attached to it distally (Fig. 7.12.3.19A). Bases of ceratophores cover most of prostomium dorsally. Ceratophores of antennae and palps very long consisting of 20 to 74 rings, with relatively short styles reaching chaetigers 3 to 11 (Fig. 7.12.3.19B). Median antenna shorter than lateral antennae. Peristomium with deep middorsal notch. Nuchal organs follow edge of peristomium including notch, separated in the middle by ridge connecting peristomium with median antenna (Fig. 7.12.3.19B). Peristomial cirri present, inserted on each side of notch. Anterior three pairs of parapodia modified, slightly prolonged (Fig. 7.12.3.19C). Ventral cirri subulate on first five chaetigers. Dorsal cirri with small basal swelling (Fig. 7.12.3.19D). Branchiae from chaetiger 1, pectinate with up to seven filaments (Fig. 7.12.3.19D). Modified parapodia with bidentate to tridentate pseudocompound falcigers and short hoods (Fig. 7.12.3.19E). Pectinate chaetae with about 15 denticles (Fig. 7.12.3.19F). Paired bidentate hooded subacicular hooks from chaetigers 9 to 10. MxV present, MxVI absent. Live in borrows with mucous inner lining.
Composition: 4 species.
Distribution: Indo-Pacific: South Africa, Arabia, Sri Lanka, India, Taiwan Strait (Paxton 1986a); Andaman Sea, near Phuket, Thailand (Nateewathana 1988). Depth range: intertidal to 22 m (Paxton 1986a).

***Hirsutonuphis* Paxton, 1986** (Fig. 7.12.3.20)
Type species: *Onuphis mariahirsuta* Paxton, 1979: 277. Gender: feminine.
Diagnosis: Small- to large-sized worms up to 56 cm long with 1040 chaetigers. Prostomium with anterior median incision. Antennae with ceratophores with 10 to 16 rings and styles (reaching to chaetigers 4–19) (Fig. 7.12.3.20A). Median antenna shorter than lateral antennae. Nuchal grooves widely separated in midline, curved toward the base of median antenna. Middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna (Fig. 7.12.3.20B). Peristomial cirri present. Anterior five to eight pairs of parapodia modified and prolonged (Fig. 7.12.3.20C). Dorsal cirri long to very long with basal swellings (Fig. 7.12.3.20A, D). Ventral cirri subulate on first six to eight chaetigers. Branchiae from chaetigers 6 to 9, pectinate (Fig. 7.12.3.20D). Pseudocompound falcigers on modified parapodia bidentate to tridentate, with short hoods (Fig. 7.12.3.20E). Pectinate chaetae slightly oblique with 10 to

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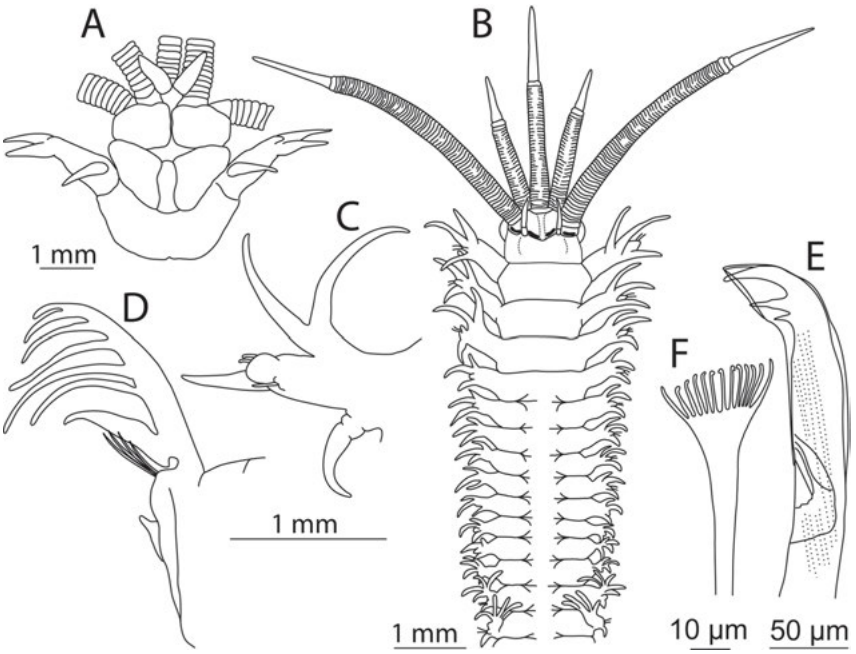


Fig. 7.12.3.19: *Heptaceras hyllebergi* Nateewathana, 1988. A, Prostomium, peristomium, and chaetiger 1, ventral view; B, Anterior end, dorsal view; C, Parapodium of chaetiger 1, anterior view; D, Parapodium of chaetiger 40, anterior view; E, Pseudocompound falciger from chaetiger 1; F, Pectinate chaeta from chaetiger 225. Modified from Nateewathana (1988).

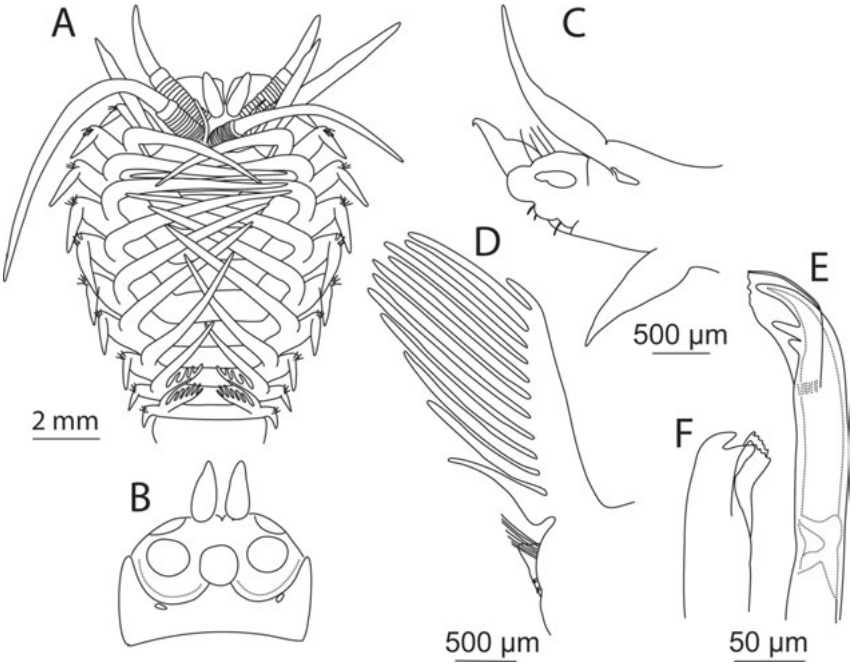


Fig. 7.12.3.20: *Hirsutonuphis gygis* (Paxton, 1979) (A) and *Hirsutonuphis mariahirsuta* (Paxton, 1979) (B–F). A, Anterior end, dorsal view; B, Scheme of prostomium, dorsal view, antennae and palps omitted; C, Parapodium of chaetiger 1, anterior view; D, Parapodium of chaetiger 60, anterior view; E, Pseudocompound falciger from chaetiger 1; F, Subacicular hook from chaetiger 60. A, C–F, Modified from Paxton (1979); B, Modified from Paxton (1986a).

15 denticles. Paired bidentate hooded subacicular hooks from chaetigers 11 to 35 (Fig. 7.12.3.20F). MxV present, MxVI absent. Tubes thin, temporary with inner mucous layer covered by sand particles.

Composition: 9 species.

Distribution: Pacific Ocean: Guatemala, Mexico, Australia (Paxton 1986a, 1996, Estrella-Ruiz et al. 2013); Atlantic Ocean: Caribbean (Fauchald 1980). Depth range: intertidal to 95 m (Paxton 1996).

***Kinbergonuphis* Fauchald, 1982** (Fig. 7.12.3.21).

Type species: *Onuphis tenuis* Hansen, 1882: 10. Gender: feminine.

Diagnosis: Small- to medium-sized worms with most species less than 10 cm long. Prostomium distally incised or extended with oval or ovoid frontal lips. Antennae with short to moderately long ceratophores with 3 to 10 rings and long to moderately long style reaching chaetigers 5 to 25 (Fig. 7.12.3.21A). Median antenna shorter or equal to

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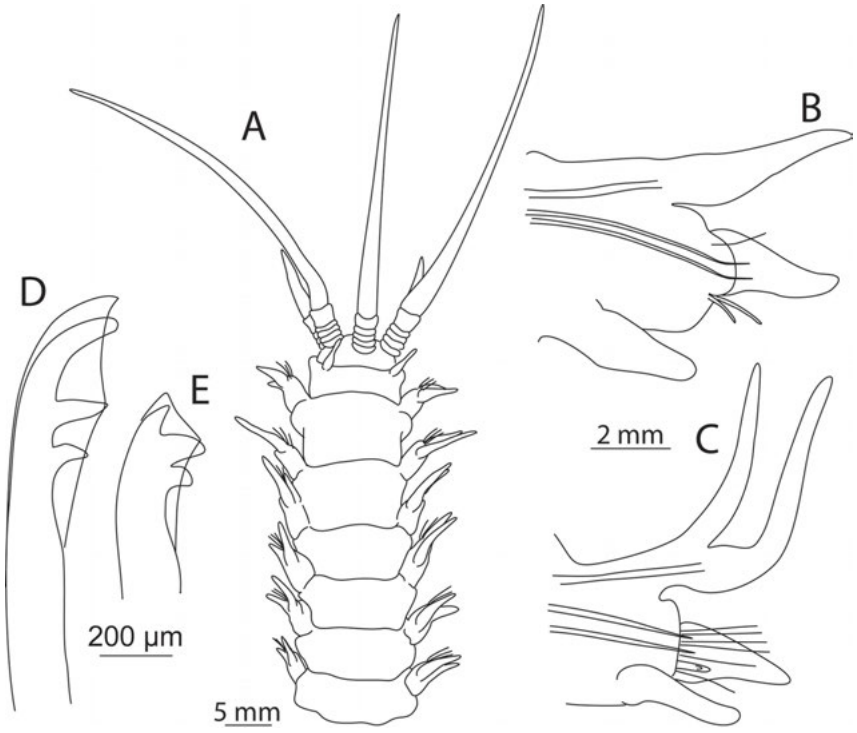


Fig. 7.12.3.21: *Kinbergonuphis pulchra* (Fauchald, 1980). A, Anterior end, dorsal view; B, Parapodium from chaetiger 2, anterior view; C, Parapodium of chaetiger 7, anterior view; D, Pseudocompound falciger from chaetiger 1; E, Large median tridentate hook from chaetiger 6. A, Modified from Budaeva et al. (2016); B–E, Modified from Fauchald (1980).

lateral antennae. Palpal styles longer than palpophores. Nuchal organs straight with narrow middorsal separation. Anterior three to seven pairs of parapodia slightly modified, not enlarged (Fig. 7.12.3.21B). Ventral cirri subulate on first two to seven chaetigers. Branchiae usually present, from chaetiger 6, rarely before or after, single or pectinate with up to seven filaments (Fig. 7.12.3.21C). Pseudocompound falcigers on anterior parapodia unidentate to tridentate with short hoods (Fig. 7.12.3.21D). Large median hooks present in transitional parapodia in some species (Fig. 7.12.3.21E). Pectinate chaetae oblique with up to 10 denticles. Bidentate hooded subacicular hooks from chaetigers 12 to 32, two to three per parapodium. MxV present, MxVI absent. Tubes thin with inner mucous or parchment-like layer with outer layer of mud or sand grains.
Composition: ~40 species.
Distribution: Worldwide, with the majority of species distributed along the American coasts. Depth range: intertidal to 1000 m (Fauchald 1982a).

***Longibrachium* Paxton, 1986** (Fig. 7.12.3.22)
Type species: *Rhamphobrachium atlanticum* Day, 1973: 55. Gender: neuter.
Diagnosis: Small- to medium-sized worms exceeding 16 cm long with about 200 chaetigers. Prostomium rounded with globular frontal lips. Antennae with ceratophores consisting of five to eight rings and moderately long styles reaching chaetigers 6 to 15 (Fig. 7.12.3.22A). Median antenna longer or equal to lateral antennae. Nuchal organs curved laterally with small to large middorsal separation. Peristomial cirri present. Anterior four pairs of parapodia modified, moderately to greatly prolonged with reduced prechaetal and postchaetal lobes (Fig. 7.12.3.22A, B). Dorsal cirri with basal swelling or process. Ventral cirri subulate on anterior five to six chaetigers. Branchiae pectinate with up to seven filaments, from chaetigers 6 to 8 (Fig. 7.12.3.22C). More than three distally recurved simple falcigers with two rows of immoveable spines on each modified parapodium (Fig. 7.12.3.22D). Chaetal sacs extending to chaetigers 20 to 60. Limbate chaetae from chaetiger 5. Pseudocompound and compound limbate chaetae may be present. Pectinate chaetae from chaetiger 5, with 12 to 20 denticles. Paired bidentate subacicular hooks with or without hoods from chaetigers 15 to 31 (Fig. 7.12.3.22E). MxV present, MxVI present or absent. Tubes with parchment-like inner layer covered with sediment.
Composition: 5 species.
Distribution: North Atlantic: North Carolina and Florida, Meteor and Plato Seamounts; North Pacific: Japan, Gulf of Tonkin; Australia. Depth range: 5 to 695 m (Nishi and Kato 2009).

***Mooreonuphis* Fauchald, 1982** (Fig. 7.12.3.23)
Type species: *Onuphis nebulosa* Moore, 1911: 269. Gender: feminine.

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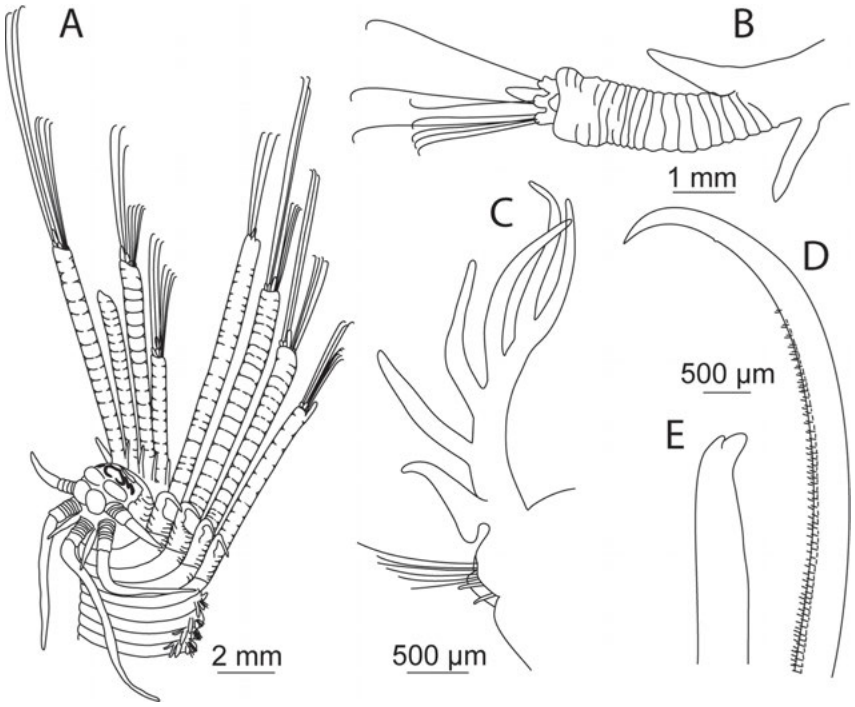


Fig. 7.12.3.22: *Longibrachium longipes* Paxton, 1986. A, Anterior end, anterolateral view; B, Parapodium of chaetiger 3, anterior view; C, Parapodium of chaetiger 45, anterior view; D, Modified recurved falciger from chaetiger 2; subacicular hook from chaetiger 44. Modified from Paxton (1986b).

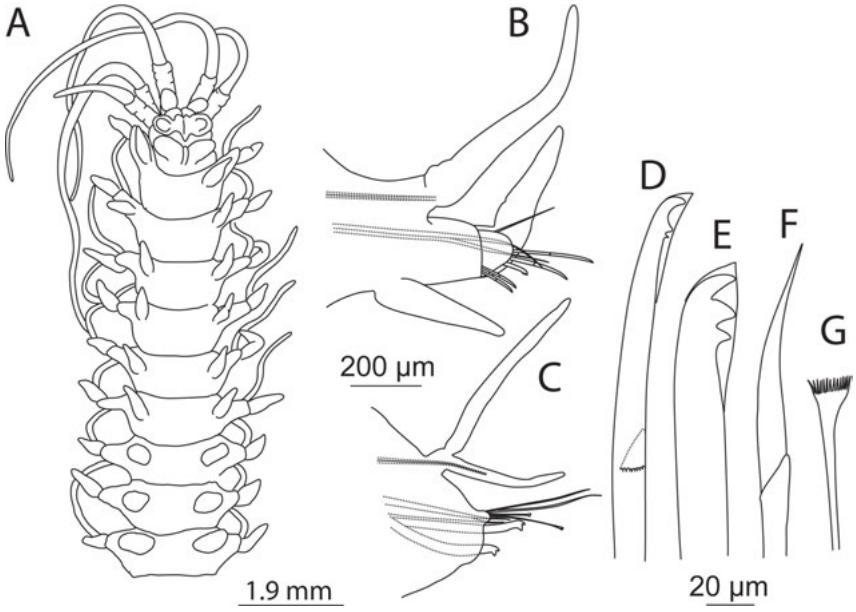


Fig. 7.12.3.23: *Mooreonuphis vespa* Arias et al., 2013. A, Anterior end, ventral view; B, Parapodium of chaetiger 1, anterior view; C, Parapodium of chaetiger 76, posterior view; D, Pseudocompound falciger from chaetiger 1; E, Simple, large median hook from chaetiger 3; F, Spiniger from chaetiger 6; G, Pectinate chaeta from chaetiger 76. Modified from Arias et al. (2013).

Diagnosis: Small- to medium-sized worms up to 10 cm long. Prostomium anteriorly weakly incised or extended with oval frontal lips. Antennae moderately long with ceratophores with three to five rings and long styles reaching chaetigers 3 to 13 (Fig. 7.12.3.23A). Median antenna shorter or equal to lateral antennae. Palpal styles longer than palpophores. Nuchal organs straight with narrow middorsal separation. Peristomial cirri present. Anterior three to eight pairs of parapodia modified but not enlarged (Fig. 7.12.3.23B). Ventral cirri subulate on anterior 3 to 10 chaetigers. Branchiae usually as single filaments, rarely pectinate (Fig. 7.12.3.23C). Pseudocompound falcigers on modified parapodia usually tridentate, rarely bidentate and tridentate, with short hoods (Fig. 7.12.3.23D). Large simple tridentate median hooks may be present in transitional parapodia (Fig. 7.12.3.23E). Ventral compound limbate chaetae (=spinigers) from chaetiger 4 or later (Fig. 7.12.3.23F) until replaced by bidentate hooded subacicular hooks from chaetigers 13 to 29. Pectinate chaetae with up to 10 denticles (Fig. 7.12.3.23G). Tubes cylindrical, with thin

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mucous or tough parchment-like inner layer covered with sand or mud.

Composition: 23 species.

Distribution: Intertidal to shallow shelf areas of both the Pacific and Atlantic coasts of Americas (Fauchald 1982a), two species are known from the Eastern Atlantic (Arias et al. 2013a, Arias 2016).

***Onuphis* Audouin & Milne Edwards, 1833** (Fig. 7.12.3.24)

Type species: *Onuphis eremita* Audouin & Milne Edwards, 1833: 226. Gender: feminine.

Diagnosis: Small- to medium-sized worms up to 30 cm long with about 200 chaetigers. Prostomium often anteriorly extended; with ovoid or oval frontal lips. Antennae and palps with ceratophores with 10 to 25 rings and short to moderately long styles reaching chaetigers 5 to 25. Median antenna shorter than lateral antennae. Palpostyles shorter than palpophores (Fig. 7.12.3.24A). Nuchal organs straight with narrow to wide middorsal separation. Peristomial cirri present. Anterior two to five pairs of parapodia modified but not enlarged (Fig. 7.12.3.24B). Ventral cirri subulate on anterior four to six chaetigers. Branchiae rarely absent, usually present from chaetiger 1, rarely from chaetigers 3 to 6; single or pectinate with up to 12 filaments. Pseudocompound falcigers on modified parapodia usually tridentate (rarely only bidentate, sometimes bidentate to multidentate) with short pointed hoods (Fig. 7.12.3.24C). Pectinate chaetae flat (Fig. 7.12.3.24D). Paired bidentate hooded subacicular hooks from chaetigers 10 to 12 (Fig. 7.12.3.24E). MxV present, MxVI absent. Tubes cylindrical, with thin mucous or tough parchment-like inner layer covered with sediment particles.

Composition: ~50 species.

Distribution: Worldwide, except the Arctic, from intertidal to mostly shelf areas, but occur in all depths (Paxton 1986a, Arias and Paxton 2015b).

***Paradiopatra* Ehlers, 1887**

Synonyms: *Diopatra* (*Paradiopatra*) Ehlers, 1887: 73; *Notonuphis* Kucheruk, 1978: 93; *Sarsonuphis* Fauchald, 1982: 64 (Fig. 7.12.3.25)

Type species: *Diopatra* (*Paradiopatra*) *fragosa* Ehlers, 1887: 75. Gender: feminine.

Diagnosis: Small- to medium-sized worms up to 17 cm long with about 250 chaetigers. Prostomium anteriorly rounded with ovoid frontal lips. Antennae with ceratophores consisting of 3 to 10 rings and short to moderately long styles reaching chaetigers 3 to 13. Median antenna shorter or rarely equal to lateral antennae (Fig. 7.12.3.25A, B). Ceratophores of antennae may bear lateral projections. Nuchal organs slightly curved with wide middorsal separation. Peristomial cirri present or absent. Anterior two to four pairs of parapodia modified, but not enlarged, projecting anteroventrally (Fig. 7.12.3.25B, C). Ventral cirri subulate on first two to four chaetigers. Postchaetal lobes limited to about 10 anterior chaetigers. Branchiae simple or pectinate (up to 14 filaments), present only through median chaetigers or absent. Pseudocompound falcigers on modified parapodia unidentate to tridentate with moderately long to very long pointed hoods (Fig. 7.12.3.25E). Pectinate chaetae oblique with 11 to 29 small denticles (Fig. 7.12.3.25F). Paired bidentate hooded subacicular hooks from chaetigers 8 to 17 (Fig. 7.12.3.25D, G). MxV present, MxVI absent. Tubes long, round in cross-section, with thick inner parchment-like layer and outer layer of mud.

Composition: 33 species.

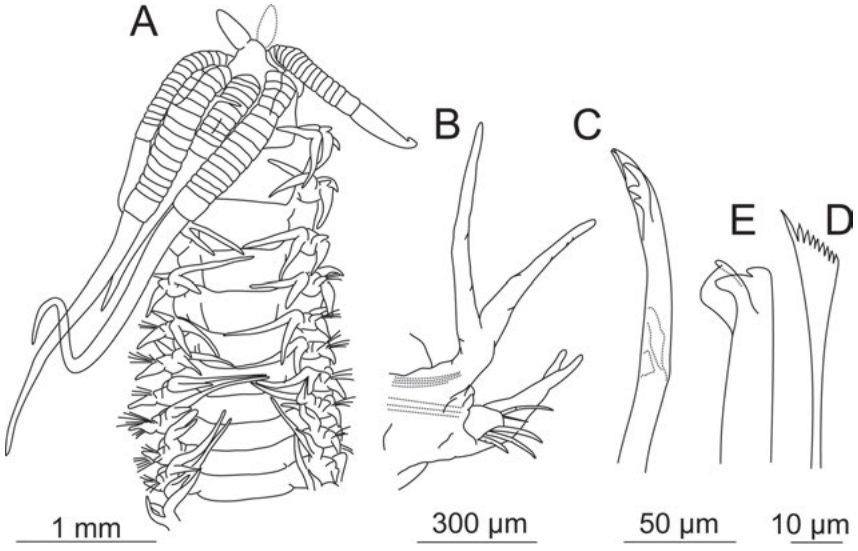


Fig. 7.12.3.24: *Onuphis iriei* Maekawa & Hayashi, 1999. A, Anterior end, dorsal view; B, Parapodium from chaetiger 3, anterior view; C, Pseudocompound falciger from chaetiger 2; D, Subacicular hook from chaetiger 17; E, Pectinate chaeta from chaetiger 1. Modified from Maekawa and Hayashi (1999).

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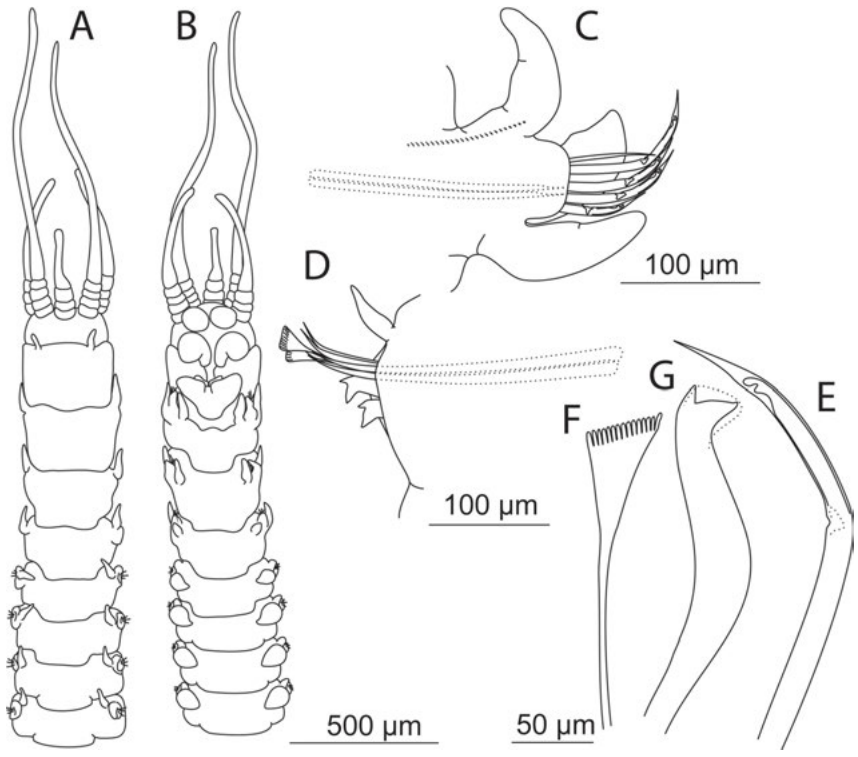


Fig. 7.12.3.25: *Paradiopatra fragosa* (Ehlers, 1887). A, Anterior end, dorsal view; B, Same as A, ventral view; C, Parapodium of chaetiger 1, anterior view; D, Parapodium of chaetiger 31, anterior view; E, Pseudocompound falciger from chaetiger 1; F, Pectinate chaeta from chaetiger 15; G, Subacicular hook from chaetiger 31. Modified from Budaeva and Fauchald (2011).

Distribution: Worldwide. Depth range: 13 to 6335 m (Budaeva and Fauchald 2011).

***Paxtonia* Budaeva & Fauchald, 2011** (Fig. 7.12.3.26)
Type species: *Onuphis amoureuxi* Intes & Le Loeuff, 1975: 313. Gender: feminine.
Diagnosis: Small- to medium-sized worms up to ~14 cm long with 230 chaetigers. Prostomium wide and rounded with ovoid frontal lips. Antennae with ceratophores consisting of five to eight rings and long styles reaching chaetigers 12 to 22. Median antenna longer than lateral antennae (Fig. 7.12.3.26A, B). Peristomial cirri present. Anterior seven to eight pairs of parapodia modified but not enlarged (Fig. 7.12.3.26A, C). Parapodia of approximately chaetigers 6 to 25 with large pockets, limited frontally by a fold of tissue. Ventral cirri subulate on first seven to eight chaetigers. Branchiae pectinate, with up to four filaments, from chaetigers 9 to 10 (Fig. 7.12.3.26D). Pseudocompound falcigers on modified parapodia one to three bidentate with moderately long and pointed hoods (Fig. 7.12.3.26E); replaced by falcate pointed pseudocompound chaetae from chaetiger 4 (Fig. 7.12.3.26F). Pectinate chaetae oblique with 12 to 20 denticles (Fig. 7.12.3.26H). Paired bidentate hooded subacicular hooks from chaetigers 17 to 26 (Fig. 7.12.3.26G). MxV and MxVI present. Tubes unknown.
Composition: 1 species.
Distribution: Western Africa, Gulf of Guinea. Depth range: 80 to 170 m (Budaeva and Fauchald 2011).

***Protodiopatra* Budaeva & Fauchald, 2011** (Fig. 7.12.3.27)
Type species: *Nothria willemoesii* McIntosh, 1885: 322. Gender: feminine.
Diagnosis: Small- to medium sized worms more than 21 cm long with up to about 300 chaetigers. Prostomium rounded with ovoid frontal lips. Antennae with ceratophores consisting of four to six rings and long styles reaching chaetigers 13 to 39 (Fig. 7.12.3.27A, B). Median antenna longer than lateral antennae. Nuchal organs slightly curved with wide middorsal separation. Peristomial cirri present. Anterior four pairs of parapodia modified but not enlarged, shifted ventrally (Fig. 7.12.3.27C). Ventral cirri subulate to conical on first three to four chaetigers. Branchiae pectinate with up to nine filaments, from chaetigers 11 to 18 (Fig. 7.12.3.27D). Pseudocompound falcigers on modified parapodia bidentate with moderately long pointed hoods (Fig. 7.12.3.27E). Pectinate chaetae slightly oblique, with 22 to 34 denticles (Fig. 7.12.3.27G). Paired bidentate hooded subacicular hooks from chaetigers 15 to 21 (Fig. 7.12.3.27F). MxV present, MxVI absent. Tube cylindrical, with inner parchment-like layer and external coating of mud and fine sand particles, distally curved, with very long and thin spines coated with

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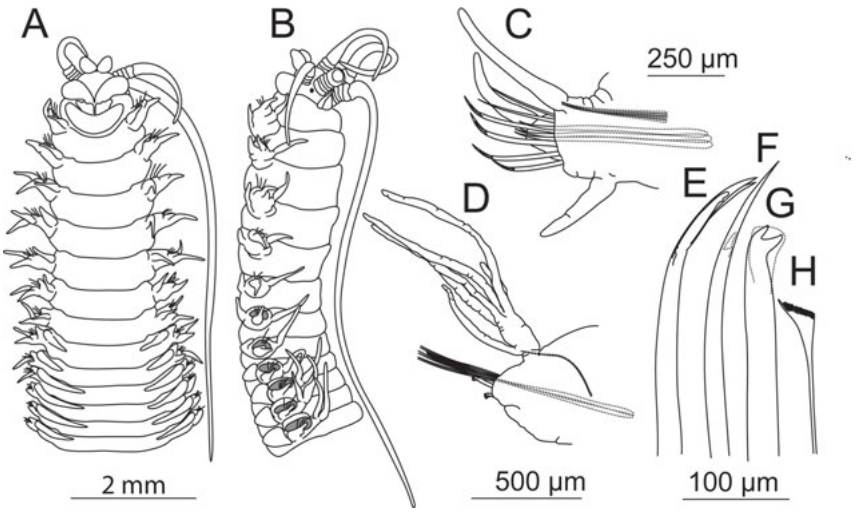


Fig. 7.12.3.26: *Paxtonia amoureuxi* (Intes & Le Loeuff, 1975). A, Anterior end, ventral view; B, Same as A, lateral view; C, Parapodium of chaetiger 1, anterior view; D, Posterior parapodium, anterior view; E, Pseudocompound falciger from chaetiger 1; F, Pointed pseudocompound chaeta from chaetiger 4; G, Subacicular hook from chaetiger 29; H, Pectinate chaeta from chaetiger 44. Modified from Budaeva and Fauchald (2011).

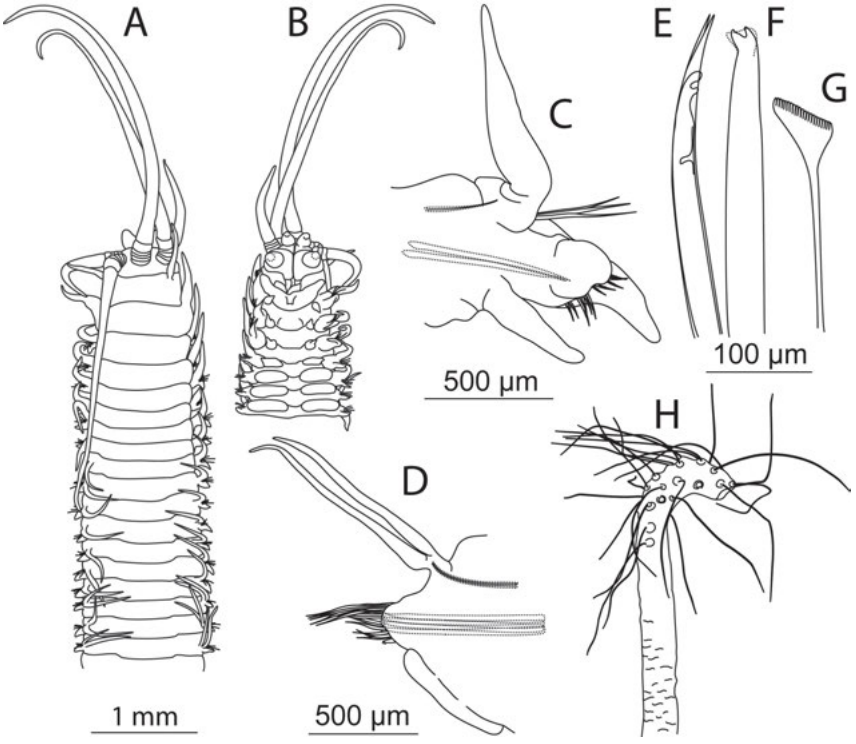


Fig. 7.12.3.27: *Protodiopatra willemoesii* (McIntosh, 1885). A, Anterior end, dorsal view; B, Same as A, ventral view; C, Parapodium of chaetiger 2, anterior view; D, Parapodium of chaetiger 16, anterior view; E, Pseudocompound falciger from chaetiger 4; F, Subacicular hook from chaetiger 43; G, Pectinate chaeta from chaetiger 116; H, Tube, anterior end. Modified from Budaeva and Fauchald (2011).

mud (Fig. 7.12.3.27H). The largest reported tube 400 mm long and 10 mm wide (Imajima 1999).

Composition: 1 species.

Distribution: South China Sea (Gulf of Tonkin), Japan, Philippines, New Guinea; Northern Australia. Depth range: 31 to 280 m (Budaeva and Fauchald 2011).

***Rhamphobrachium* Ehlers, 1887** (Fig. 7.12.3.28)

Type species: *Rhamphobrachium agassizii* Ehlers, 1887: 70. Gender: neuter.

Diagnosis: Small- to large-sized worms 1.6 to 19 cm long with 50 to 200 chaetigers. Prostomium anteriorly rounded with globular frontal lips. Antennae with ceratophores of two to five rings and short styles reaching chaetigers 2 to 5 (Fig. 7.12.3.28A). Nuchal organs curved laterally with narrow or wide middorsal separation. Peristomial cirri present or absent. Anterior two or three pairs of parapodia modified, moderately prolonged with reduced prechaetal and postchaetal lobes (Fig. 7.12.3.28B). Ventral cirri subulate on first two to four chaetigers (Fig. 7.12.3.28C). Branchiae

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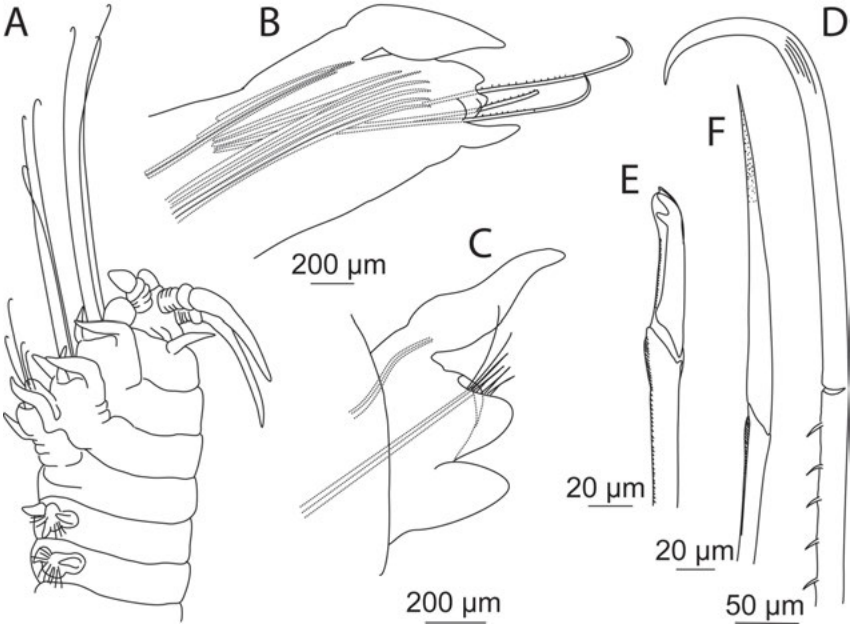


Fig. 7.12.3.28: *Rhamphobrachium brevibrachiatum* (Ehlers, 1875). A, Anterior end, lateral view; B, Parapodium of chaetiger 2, posterior view; C, Parapodium of chaetiger 4, posterior view; D, Modified recurved falciger from chaetiger 2; E, Compound falciger from chaetiger 4; F, Spiniger from chaetiger 4. A, Modified from Imajima (1999); B–F, Modified from Paxton (1986b).

single or pectinate, from chaetigers 6 to 17, or absent. Anterior falcigers highly modified, simple or pseudocompound with unidentate or bidentate recurved tips and two rows of moveable spines on shafts (Fig. 7.12.3.28D). Compound bidentate falcigers may be present in some median parapodia (Fig. 7.12.3.28E). Chaetal sacs extending to chaetigers 20 to 60. Pectinate chaetae flat, slightly oblique, with 10 to 20 denticles. Limbate chaetae simple or pseudocompound to compound (=spinigers) (Fig. 7.12.3.28F). Bidentate hooded subacicular hooks from chaetigers 5 to 16, up to 10 hooks per parapodium. MxV present, MxVI present or absent. Tubes cylindrical with thick inner parchment-like layer covered with sediment particles or thin mucous with incrustation of large pieces of shells and sediment.

Composition: 15 species.

Distribution: Worldwide, except the Arctic. Depth range: 6 to 2165 m (Paxton and Budaeva 2015).

References

Allen, M.J. (1959): Embryological development of the polychaetous annelid, *Diopatra cuprea* (Bosc). *Biological Bulletin* 116: 339–361.

Andrade, J. & Liñero, I. (1993): Aspectos etologicos de *Americonuphis magna* (Andrews), (Polychaeta, Onuphidae). *Boletín del Instituto Oceanográfico de Venezuela, Universidad de Oriente* 32: 11–16.

Andrews, E.A. (1891): Reproductive organs of *Diopatra*. *Journal of Morphology* 5: 113–124.

Arias, A. (2016): *Onuphis* and *Mooreonuphis* (Annelida: Onuphidae) from West Africa with the description of three new species and the reinstatement of *O. landanaensis* Augener, 1918. *Zootaxa* 4168: 481–511.

Arias, A. & Paxton, H. (2014): Hidden diversity within the polychaete *Onuphis eremita sensu lato* (Annelida: Onuphidae) — Redescription of *O. eremita* Audouin & Milne-Edwards, 1833 and reinstatement of *Onuphis pancerii* Claparède, 1868. *Zootaxa* 3861: 145–169.

Arias, A. & Paxton, H. (2015a): The cryptogenic bait worm *Diopatra biscayensis* Fauchald et al., 2012 (Annelida: Onuphidae) — Revisiting its history, biology and ecology. *Estuarine, Coastal and Shelf Science* 163: 22–36.

Arias, A. & Paxton, H. (2015b): *Onuphis* and *Aponuphis* (Annelida: Onuphidae) from southwestern Europe, with the description of a new species. *Zootaxa* 3949: 345–369.

Arias, A. & Paxton, H. (2015c): *Paradiopatra* Ehlers, 1887 (Annelida: Onuphidae) from southwestern Europe with the description of a new species and new ultramorphological data for the genus. *Zootaxa* 4040: 149–168.

Arias, A., Paxton, H. & Anadón, N. (2013a): *Mooreonuphis vespa*, a new brooding species of Onuphidae (Annelida) from northern Spain (Bay of Biscay). *Zootaxa* 3741: 583–592.

Arias, A., Richter, A., Anadón, N. & Paxton, H. (2013b): Evidence of simultaneous hermaphroditism in the brooding *Diopatra marocensis* (Annelida: Onuphidae) from northern Spain. *Journal of the Marine Biological Association of the United Kingdom* 93: 1533–1542.

Arias, A., Paxton, H. & Budaeva, N. (2016): Redescription and biology of *Diopatra neapolitana* (Annelida: Onuphidae), a protandric hermaphrodite with external spermaducal papillae. *Estuarine, Coastal and Shelf Science* 174: 1–17.

Audouin, J.V. & Milne Edwards, H. (1833): Classification des annelides, et description de celles qui habitent les cotes de la France. *Annales des Sciences Naturelles (Paris)* 29: 195–269.

Augener, H. (1918): Polychaeta. In: Michaelsen, W. (ed.), *Beiträge zur Kenntnis der Meeresfauna West-Afrikas* Vol. 2. Friedrichsen & Co., Hamburg: 67–625.

Bailey-Brock, J. (1984): Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg, 1865 (Onuphidae) in Hawaii: community structure, and sediment stabilizing properties. *Zoological Journal of the Linnean Society, London* 80: 191–199.

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Baird, W. (1870): Remarks on several genera of annelids belonging to the group Eunicea with a notice of such species as are contained in the collection of the British Museum and a description of some others hitherto undescribed. *Journal of the Linnean Society of London* 10: 341–361.

Blake, J.A. (1975): The larval development of Polychaeta from the northern California coast. II. *Nothria elegans* (Family Onuphidae). *Ophelia* 13: 43–61.

Bosc, L. A. G. (1802): *Histoire naturelle des vers contenant leur description et leurs moeurs, avec figures dessinées d'après nature*. Tome Premiere. De l'imprimerie de Guilleminet; a Paris, chez Deterville. 1–324., P. 142–143.

Borisova, P., Schepetov, D. & Budaeva, N. (2018): *Aponuphis* Kucheruk, 1978 (Annelida: Onuphidae) from western African waters. *Invertebrate Zoology* 15: 19–41.

Budaeva, N. (2012): *Leptoecia midatlantica*, a new species of the deep-sea quill-worms (Polychaeta: Onuphidae: Hyalinoeciinae) from the Mid-Atlantic Ridge. *Zootaxa* 3176: 45–60.

Budaeva, N. & Fauchald, K. (2008): *Diopatra tuberculantennata*, a new species of Onuphidae (Polychaeta) from Belize with a key to onuphids from the Caribbean Sea. *Zootaxa* 1795: 29–45.

Budaeva, N. & Fauchald, K. (2010): Larval development of *Mooreonuphis stigmatis* (Treadwell 1922) (Polychaeta: Onuphidae) from the north-east Pacific. *Marine Biology Research* 6: 6–24.

Budaeva, N. & Fauchald, K. (2011): Phylogeny of the *Diopatra* generic complex with a revision of *Paradiopatra* Ehlres, 1887 (Polychaeta: Onuphidae). *Zoological Journal of the Linnean Society, London* 163: 319–436.

Budaeva, N. & Paxton, H. (2013): *Nothria* and *Anchinothria* (Annelida: Onuphidae) from eastern Australian waters, with a discussion of ontogenetic variation of diagnostic characters. *Journal of the Marine Biological Association of the United Kingdom* 93: 1481–1502.

Budaeva, N., Pyataeva, S. & Meißner, K. (2014): Development of the deep-sea viviparous quill worm *Leptoecia vivipara* (Hyalinoeciinae, Onuphidae, Annelida). *Invertebrate Biology* 133: 242–260.

Budaeva, N., Schepetov, D., Zanol, J., Neretina, T. & Willassen, E. (2016): When molecules support morphology: phylogenetic reconstruction of the family Onuphidae (Eunicida, Annelida) based on 16S rDNA and 18S rDNA. *Molecular Phylogenetics and Evolution* 94: 791–801.

Carrasco, F.D. (1983): Description of adults and larvae of a new deep water species of *Hyalinoecia* (Polychaeta, Onuphidae) from the southeastern Pacific Ocean. *Journal of Natural History* 17: 87–93.

Chamberlin, R.V. (1919): The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48: 1–514.

Choe, S. (1960): On the life history of the polychaete worm *Diopatra neapolitana* Delle Chiaje. *Bulletin of the Japanese Society for Scientific Fisheries* 26: 430–437.

Conti, G., Loffredo, F. & Lantini, M.S. (2005): Fine structure of the spermatozoon of *Diopatra neapolitana* (Polychaeta, Onuphidae). *Zoomorphology* 124: 155–160.

Day, J.H. (1960): The Polychaet [sic] fauna of South Africa. Part 5. Errant species dredged off Cape coasts. *Annals of the South African Museum* 45: 261–373.

Day, J.H. (1967): A monograph on the Polychaeta of southern Africa. Part I. Errantia. *British Museum (Natural History) Publications* 656: 1–458.

Day, J.H. (1973): New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service Circular* 375: 1–140.

Dayton, P.K. & Hessler, R.R. (1972): Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Research* 19: 199–208.

Delle Chiaje, S. (1841–1844): *Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822–1830*. Batteli & Co., Naples. Parts 1–8.

Detinova, N.N. (1985): Polychaetous worms from the Reykjanes Ridge (the North Atlantic). Bottom fauna from mid-ocean rises in the North Atlantic. *Trudy Instituta Okeanologii, Akademia Nauk SSSR* 120: 96–136. [in Russian]

Ehlers, E. (1868): *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt.* Engelmann, Leipzig: 269–748 (pp. 1–268 of this work were published in 1864).

Ehlers, E. (1887): Reports on the results of dredging, under the direction of L.F. Pourtales, during the years 1868-1870, and of Alexander Agassiz, in the Gulf of Mexico (1877-78), and in the Caribbean Sea (1878-79), in the U.S. Coast Survey Steamer "Blake", Lieut.-Corn. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 31. Report on the annelids. *Memoirs of the Museum of Comparative Zoology at Harvard College* 15: 1–335.

Estrella-Ruiz, A., Hernández-Alcántara, P. & Solís-Weiss, V. (2013): Description of a new species of *Hirsutonuphis* (Annelida: Onuphidae) from the Mexican Pacific, with notes on the world distribution of the genus. *Journal of the Marine Biological Association of the United Kingdom* 93: 1777–1783.

Fadlaoui, S., Lechapt, J.-P. & Retiere, C. (1995): Larval development of the onuphid *Diopatra marocensis* (Annelida: Polychaeta) from the Atlantic coast of Morocco. *Journal of the Marine Biological Association of the United Kingdom* 75: 957–966.

Fauchald, K. (1973): Polychaetes from Central American sandy beaches. *Bulletin of the Southern California Academy of Sciences* 72: 19–31.

Fauchald, K. (1980): Onuphidae (Polychaeta) from Belize, Central America, with notes on related taxa. *Proceedings of the Biological Society of Washington* 93: 797–829.

Fauchald, K. (1982a): Revision of *Onuphis*, *Nothria*, and *Paradiopatra* (Polychaeta: Onuphidae) based upon type material. *Smithsonian Contributions to Zoology* 356: 1–109.

Fauchald, K. (1982b): Description of *Mooreonuphis jonesi*, a new species of onuphid polychaete from shallow water in Bermuda, with comments on variability and population ecology. *Proceedings of the Biological Society of Washington* 95: 807–825.

Fauchald, K. & Jumars, P.A. (1979): The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology, Annual Review* 17: 193–284.

Fauchald, K., Berke, S.K. & Woodin, S.A. (2012): *Diopatra* (Onuphidae: Polychaeta) from intertidal sediments in southwestern Europe. *Zootaxa* 3395: 47–58.

Fauvel, P. (1916): Deux Polychètes nouvelles (*Disoma watsoni* n.sp. et *Hyalinoecia brementi* n.sp.). *Bulletin de l'Institute Océanographique* 316: 1–10.

Fauvel, P. (1923): *Polychètes Errantes*. Faune de France 5: 1–488.

Gaston, G.R. (1987): Benthic polychaeta of the Middle Atlantic Bight: Feeding and distribution. *Marine Ecology Progress Series* 36: 251–262.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Hansen, G.A. (1882): Recherches sur les annélides, recueillies par M. le professeur Édouard van Beneden pendant son voyage au Brésil et à la Plata. *Mémoires couronnes et memoires des savants étranges publies par l'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique (Bruxelles)* 44: 1–29.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Occasional Papers* 23: 1–628.

Hartman, O. (1965): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Occasional Papers* 28: 1–378.

Hartman, O. (1967): Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. *Allan Hancock Monographs in Marine Biology* 2: 1–387.

Hartmann-Schröder, G. (1975): Polychaeten der Iberischen Tiefsee, gesammelt auf der 3. Reise der METEOR im Jahre 1966. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 72: 47–73.

Hsieh, H.-L. & Simon, J.L. (1987): Larval development of *Kinbergonuphis simoni*, with a summary of development patterns in the family Onuphidae (Polychaeta). *Bulletin of the Biological Society of Washington* 7: 194–210.

Hsieh, H.-L. & Simon, J.L. (1990): The sperm transfer system in *Kinbergonuphis simoni* (Polychaeta: Onuphidae). *Biological Bulletin* 178: 85–93.

Imajima, M. (1999): Onuphidae (Annelida, Polychaeta) from Japan, excluding the genus Onuphis. *National Science Museum monographs* 16: 1–115.

Intes, A. & Le Loeuff, P. (1975): Les annélides polychètes de Côte d'Ivoire. I.-Polychètes errantes-compte rendu systématique. *Cahiers de la Office de la Recherche Scientifique et Technique des outre mer (Oceanographie)* 13: 267–321.

Jamieson, B.G. & Rouse, G.W. (1989): The spermatozoa of the Polychaeta (Annelida): an ultrastructural review. *Biological Reviews* 64: 93–157.

Johnson, H. P. (1901): The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History* 29(18): 381–437.

Jirkov, I.A. (2001): *Polychaeta of the Arctic Ocean*. Yanus-K, Moscow. [in Russian]

Kinberg, J.G.H. (1865): Annulata nova. *Öfversigt af Kongl. Vetenskaps-akademiens förhandlingar, Stockholm* 21: 559–574.

Knox, G. A. & Cameron, D. B. (1971): Port Phillip Bay Survey 1957–1963, Victoria, Australia. Part 2(4) Polychaeta. *Memoirs of the National Museum of Victoria* 32: 21–42.

Knox, G.A. & Hicks, K. (1973): The polychaetes of New Zealand. Part 5. Onuphidae. *Journal of the Royal Society of New Zealand* 3: 281–294.

Kucheruk, N.V. (1977): On the specific composition and distribution of the deep-sea genus *Paraonuphis* (sic) (Polychaeta, Eunicidae). *Trudy Instituta Okeanologii, Akademia Nauk SSSR* 108: 44–51. [in Russian]

Kucheruk, N.V. (1978): Deep-water Onuphidae (Polychaeta) from the collections of the 16th Cruise of the R/V *Dmitry Mendeleev* (to the generic classification of the family Onuphidae). *Trudy Instituta Okeanologii, Akademia Nauk SSSR* 113: 88–106. [in Russian]

Kucheruk, N.V. (1979): A new genus and species of polychaetes (Onuphidae). *Zoologicheskii Zhurnal* 58: 1585–1587. [in Russian]

Lana, P.C. (1991): Onuphidae (Annelida: Polychaeta) from southeastern Brazil. *Bulletin of Marine Science* 48: 280–295.

León-González, J.A., Cornejo-Rodriguez, M.H. & Degraer, S. (2008): A new species of *Australonuphis* (Polychaeta: Onuphidae) from the eastern Pacific. *Journal of the Marine Biological Association of the United Kingdom* 88: 739–742.

Lieber, A. (1931): Zur Oogenese einiger Diopatraarten. *Zeitschrift für wissenschaftliche Zoologie* 138: 580–649.

Lipps, J.H. & Ronan, T.E. (1974): Predation of foraminifera by the polychaete worm, *Diopatra*. *Journal of Foraminiferal Research* 4: 139–143.

Livingston, M.E. (1987): Food resource use among five flatfish species (Pleuronectiformes) in Wellington Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 21: 281–293.

Maekawa, N. & Hayashi, I. (1999): Taxonomic study on the genus *Onuphis* (Polychaeta, Onuphidae) from Japan and adjacent seas, with descriptions of six new species. *Bulletin of the National Science Museum, Tokyo* 25: 163–214.

Malmgren, A.J. (1866): *Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita*. Frenckelliana, Helsingfors.

Mangum, C.P., Santos, S.L. & Rhodes, Jr., W.R. (1968): Distribution and feeding in the onuphid polychaete, *Diopatra cuprea* (Bosc). *Marine Biology* 2: 33–40.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1872–76* 12: 1–554.

Meyer, K.S., Wagner, J.K.S., Ball, B., Turner, P.J., Young, C.M. & Van Dover, C.L. (2016): *Hyalinoecia artifex*: Field notes on a charismatic and abundant epifaunal polychaete on the US Atlantic continental margin. *Invertebrate Biology* 135: 211–224.

Moore, J.P. (1911): The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of southern California in 1904: Ill. Euphrosynidae to Goniadidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 63: 234–318.

Müller, O.F. (1776): *Zoologica Danicae prodromus seu animalium Daniae et Norvegiae indigenarum characters, nomine et synonyma imprimis popularium*. Havniae, pp. xxxii + 274.

Nateewathana, A. (1988): *Heptaceras hyllebergi* sp.n. (Polychaeta: Onuphidae) from Kata Beach, west coast of Phuket Island, Andaman Sea, Thailand, with notes on the habitat. *Phuket Marine Biological Center, Research Bulletin* 48: 1–9.

Nishi, E. & Kato, T. (2009): *Longibrachium arariensis*, a new species of Onuphidae (Annelida: Polychaeta) from the shallow water of Izu Peninsula, central Japan, with notes on its feeding behavior. *Zootaxa* 2081: 46–56.

Orensanz, J.M. (1974): Los anelidos poliquetos de la provincial biogeografica Argentina. V. Onuphidae. *Physis (Buenos Aires)* A33: 75–122.

Orensanz, J.M. (1990): The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the Southern Indian Ocean. *Antarctic Research Series* 52: 1–183.

Palubitzki, T. von & Purschke, G. (2020): Ultrastructure of pigmented eyes in Onuphidae and Eunicidae (Annelida: Errantia: Eunicida) and its importance in understanding the evolution of eyes in Annelida. *Zoomorphology* 139: 1–19.

Paterson, G.L.J., Glover, A.G., Frojan, C.B., Whitaker, A., Budaeva, N., Chimonides, J. & Doner, S. (2009): A census of abyssal polychaetes. *Deep-Sea Research II* 56: 1739–1746.

Paxton, H. (1979): Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Onuphidae). *Australian Journal of Marine and Freshwater Research* 30: 265–294.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Paxton, H. (1986a): Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). *Records of the Australian Museum* 38: 1–74.

Paxton, H. (1986b): Revision of the *Rhamphobrachium* complex (Polychaeta: Onuphidae). *Records of the Australian Museum* 38: 75–104.

Paxton, H. (1993): *Diopatra* Audouin and Milne Edwards (Polychaeta, Onuphidae) from Australia, with a discussion of developmental patterns in the genus. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 10: 115–154.

Paxton, H. (1996): *Hirsutonuphis* (Polychaeta: Onuphidae) from Australia, with a discussion of chaetal progression in juveniles. *Invertebrate Taxonomy* 10: 77–96.

Paxton, H. (1998): The *Diopatra chiliensis* confusion — Redescription of *D. chiliensis* (Polychaeta, Onuphidae) and implicated species. *Zoologica Scripta* 27: 31–48.

Paxton, H. (2000): Eunicida. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.). *Polychaetes and Allies: The Southern Synthesis. Vol. 4A: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula.* Csiro Publishing, Canberra: 89–106.

Paxton, H. (2005a): Molting polychaete jaws — Ecdysozoans are not the only molting animals. *Evolution and Development* 7: 337–340.

Paxton, H. (2005b): *Fauchaldonuphis*, a new genus for the enigmatic polychaete *Diopatra paradoxa* Quatrefages, 1866. *Marine Ecology* 26: 209–215.

Paxton, H. (2006): Replacement of adult maxillary jaws in Eunicida (Polychaeta). *Scientia Marina* 70S3: 331–336.

Paxton, H. & Arias, A. (2014): Brooding deep-water onuphid polychaetes (Annelida) from the Bay of Biscay. *Marine Biology Research* 10: 892–905.

Paxton, H. & Arias, A. (2017): Unveiling a surprising diversity of the genus *Diopatra* Audouin & Milne Edwards, 1833 (Annelida: Onuphidae) in the Macaronesian region (eastern North Atlantic) with the description of four new species. *Zootaxa* 4300: 505–535.

Paxton, H. & Bailey-Brock, J.H. (1986): *Diopatra dexiognatha*, a new species of Onuphidae (Polychaeta) from Oahu, Hawaiian Islands. *Pacific Science* 40: 1–6.

Paxton, H. & Budaeva, N. (2013): *Paradiopatra* (Annelida: Onuphidae) from eastern Australian waters, with the description of six new species. *Zootaxa* 3686: 140–164.

Paxton, H. & Budaeva, N. (2015): *Minibrachium*, a new subgenus of *Rhamphobrachium* (Annelida: Onuphidae) from Australia with the description of three new species. *Zootaxa* 4019: 621–634.

Paxton, H. & Safarik, M. (2008): Jaw growth and replacement in *Diopatra aciculata* (Annelida: Onuphidae). *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 24: 15–21.

Pires, A., Paxton, H., Quintino, V. & Rodrigues, A.M. (2010): *Diopatra* (Annelida: Onuphidae) diversity in European waters with the description of *Diopatra micrura*, new species. *Zootaxa* 2395: 17–33.

Quatrefages, A. de (1866): *Histoire naturelle des Annelés marins et d'eau douce: Annélides et Géphyriens. Tome premier.* Librairie Encyclopédique de Roret, Paris.

Rodrigues, A.M., Pires, A., Mendo, A. & Quintino, V. (2009): *Diopatra neapolitana* and *Diopatra marocensis* from the Portuguese coast: Morphological and genetic comparison. *Estuarine, Coastal and Shelf Science* 85: 609–617.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.

Rozbaczylo, N. & Castilla, J.C. (1981): *Australonuphis violacea*, a new polychaete (Onuphidae) from the southwest Pacific Ocean. *Proceedings of the Biological Society of Washington* 94: 761–770.

Santos, S.L., Day, R. & Rice, S.A. (1981): *Onuphis simoni*, a new species of polychaete (Polychaeta: Onuphidae) from South Florida. *Proceedings of the Biological Society of Washington* 94: 663–668.

Sars, M. (1835): *Beskrivelser og iagttagelser over nogle maerkelige eller nye i havet ved den Bergenske kyst levende dyr af Polypernes, Acalophernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen.* Bergen.

Schmarda, L.K. (1861): *Neue Turbellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857.* Zweite Halfte. Wilhelm Engelmann, Leipzig.

Serrano, A., Velasco, F. & Olaso, I. (2003): Polychaete annelids in the diet of demersal fish from the southern shelf of the Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* 83: 619–623.

Smith, B.J. & Jensz, R.L. (1968): Unusual mode of reproduction in a new species of polychaete. *Nature* 218: 777.

Struck, T.H., Purschke, G. & Halanych, K.M. (2006): Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach. *Systematic Biology* 55: 1–20.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Tilic, E., Bartolomaeus, T. & Rouse, G.W. (2016): Chaetal type diversity increases during evolution of Eunicida (Annelida). *Organisms Diversity and Evolution* 16: 105–119.

Treadwell, A. L. (1922): Polychaetous annelids collected at Friday Harbor, State of Washington, in February and March, 1920. *Carnegie Institute of Washington Publication* 312: 171–181.

Uschakov, P.V. (1955): *Polychaeta of the Far Eastern Seas of the USSR.* Keys of the Fauna of the USSR 56: 1–1445. [in Russian. Translated 1965 by Israel Program for Scientific Translations, Jerusalem]

Verrill, A.E. (1881): Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part 2. Mollusca, with notes on Annelida, Echinodermata, etc. collected by the United States Fish Commission. *Smithsonian Miscellaneous Collections* 22: 356–405.

Vortsepneva, A., Tzetlin, A. & Budaeva, N. (2017): Morphogenesis and fine structure of the developing jaws of *Mooreonuphis stigmatis* (Onuphidae, Annelida). *Zoologischer Anzeiger* 267: 49–62.

Wigley, R.L. & Emery, K.O. (1967): Benthic animals, particularly *Hyalinoecia* (Annelida) and *Ophiomusium* (Echinodermata), in sea-bottom photographs from the continental slope. In: Hersey, J.B. (ed.), *Deep-Sea Photography.* John Hopkins Press, Baltimore: 235–250.

Zanol, J. (2010): Homology of prostomial and pharyngeal structures in Eunicida (Annelida) based on innervation and morphological similarities. *Journal of Morphology* 271: 1023–1043.

Zanol, J., Halanych, K., Struck, T. & Fauchald, K. (2010): Phylogeny of the bristle worm family Eunicidae (Eunicida, Annelida) and the phylogenetic utility of noncongruent 16S, COI and 18S in combined analyses. *Molecular Phylogenetics and Evolution* 55: 660–676.

Zanol, J., Halanych, K.M. & Fauchald, K. (2014): Reconciling taxonomy and phylogeny in the bristleworm family Eunicidae (polychaete, Annelida). *Zoologica Scripta* 43: 79–100.

Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): Total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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Joana Zanol and Nataliya Budaeva

7.12.4 Eunicidae

Introduction

Eunicidae is one of the oldest annelid families. However, before 1818, all species (*Eunice aphroditois* (Pallas, 1788), *Eunice norvegica* (Linnaeus, 1767), *Leodice pennata* (Müller, 1776)) as well as its type genus *Eunice* Cuvier, 1817 were described under the family Nereididae (see also Read 2019). The concept of the family Eunicidae was first proposed by Lamarck (1818) under the name Eunicae. It was more inclusive than the current definition of the family, including eunicid genera *Leodice* (considered synonym of *Eunice*) and *Lysidice* and, also, oenonid genera *Aglaura* and *Oenone*. Berthold (1827) was the first to write Eunicidae in its currently accepted valid form; thus, he is considered the family author (Fauchald 1992a). The names Eunicidae, Eunicae, Eunicea, and Leodicidae have been used interchangeably to refer to the same taxon (e.g., Lamarck 1818, Savigny 1820, Kinberg 1865, Grube 1878, McIntosh 1910, Izuka 1912, Treadwell 1921). The name Eunicea has also been used to designate subgroups within Eunicidae (e.g., Kinberg 1865, McIntosh 1910).

The more inclusive definition of Eunicidae, including genera from the different families of the order Eunicida, was used until mid-1900s (e.g., Savigny 1820, Audouin and Milne Edwards 1834, Quatrefages 1866, Ehlers 1868, Claparède 1868, Grube 1878, Gravier 1900, McIntosh 1910, Izuka 1912, Day 1967). Informal groupings, subfamilies, and tribes were suggested based on the presence or absence of branchiae (Audouin and Milne Edwards 1834, Quatrefages 1866), shape of maxillae (Ehlers 1868, Grube 1878, Claparède 1868), presence of notopodial and ventral cirri (Gravier 1900), and prostomial features and cirri (Treadwell 1921). With the exception of subgroups based on the presence or absence of branchiae, most of the other proposed subgroups agreed in dividing Eunicidae in three or four groups, which would represent current Eunicidae + Onuphidae, Dorvilleidae, and Lumbrineridae + Oenonidae (or Lumbrineridae and Oenonidae).

The current definition of the family Eunicidae and genera composition started to be delineated by Kinberg (1865), who recognized 10 families within Eunicea based on the characteristics of the prostomium, prostomial appendages, peristomium, and peristomial cirri and the number of maxillae. Kinberg (1865) distinguished Eunicidae and Onuphidae as different families, limited Eunicidae to include genera *Eunice*, *Euriphyle*, *Nauphanta*, *Nausicaa*, and *Nicidion*, but included *Amphiro* and *Lysidice* in a different family named Lycidicea. Hartman (1944) developed on Kinberg's (1865) proposition and established the current composition of Eunicidae. It has been a stable taxon ever since despite the variation in the list of valid genera and the diagnosis based on plesiomorphies and homoplasious features, such as wide bilobed (at least ventrally) prostomium, the presence of one to five prostomial appendages, double-ringed peristomium, and eulabidognath jaws (Fauchald 1970, 1977, Orensanz 1990, Zanol et al. 2014).

Morphology

External morphology

The family Eunicidae shows the greatest length variation among polychaetes, sexually mature forms vary from about 6 mm (e.g., *Fauchaldius cyrtauloni* Carrera-Parra & Salazar-Vallejo, 1998) to up to 6 m (e.g., *Eunice* cf. *aphroditois*) (see Fauchald 1992a). The body is slender with a variable number of chaetigers, from just a few to hundreds (Fig. 7.12.4.1). The number of chaetigers is not fixed within a given species. Growth happens by the posterior addition of new chaetigers, but at least in one *Eunice* species growth in large specimens happens mainly due to an increase in length and width of the chaetigers (Parapar et al. 1993). Most segmented and slender forms in relation to length are in the genus *Palola*, which may reach 565 chaetigers being 200 mm long and just 3 mm wide (Fauchald 1992b). Features, such as branchiae, notopodial cirri, parapodial lobes, chaetae, and ventral cirri, vary in structured ways along the body, but no body regions are clearly distinguishable. The variable numbers of chaetigers among specimens make it a challenge to compare chaetigers from different individuals. Thus, comparisons are usually based on the relative placement of chaetigers along the body. It is currently a common practice to sample at least one anterior, one median, and one posterior chaetiger. However, more thorough sampling of parapodia allows the observation of, for example, inconspicuous pectinate chaetae in *Marphysa* and tridentate compound falciger chaetae in *Leodice*. Thus, the following scheme of sampling of parapodia was suggested by Zanol et al. (2014, 2016) to observe features of different parts of the body: one parapodium from anteriormost 10% (P1), one parapodium each from 1/8 (P2), from 3/8 (P3), from 5/8 (P4), and from 7/8 (P5), and one parapodium from the posteriormost 10% (P6) of the body (counts based on the number of chaetigers).

The long slender bodies and the ability of eunicids to autotomize make the collection of complete specimens a challenge. Thus, information on posterior features and distribution of branchiae is missing for many species.

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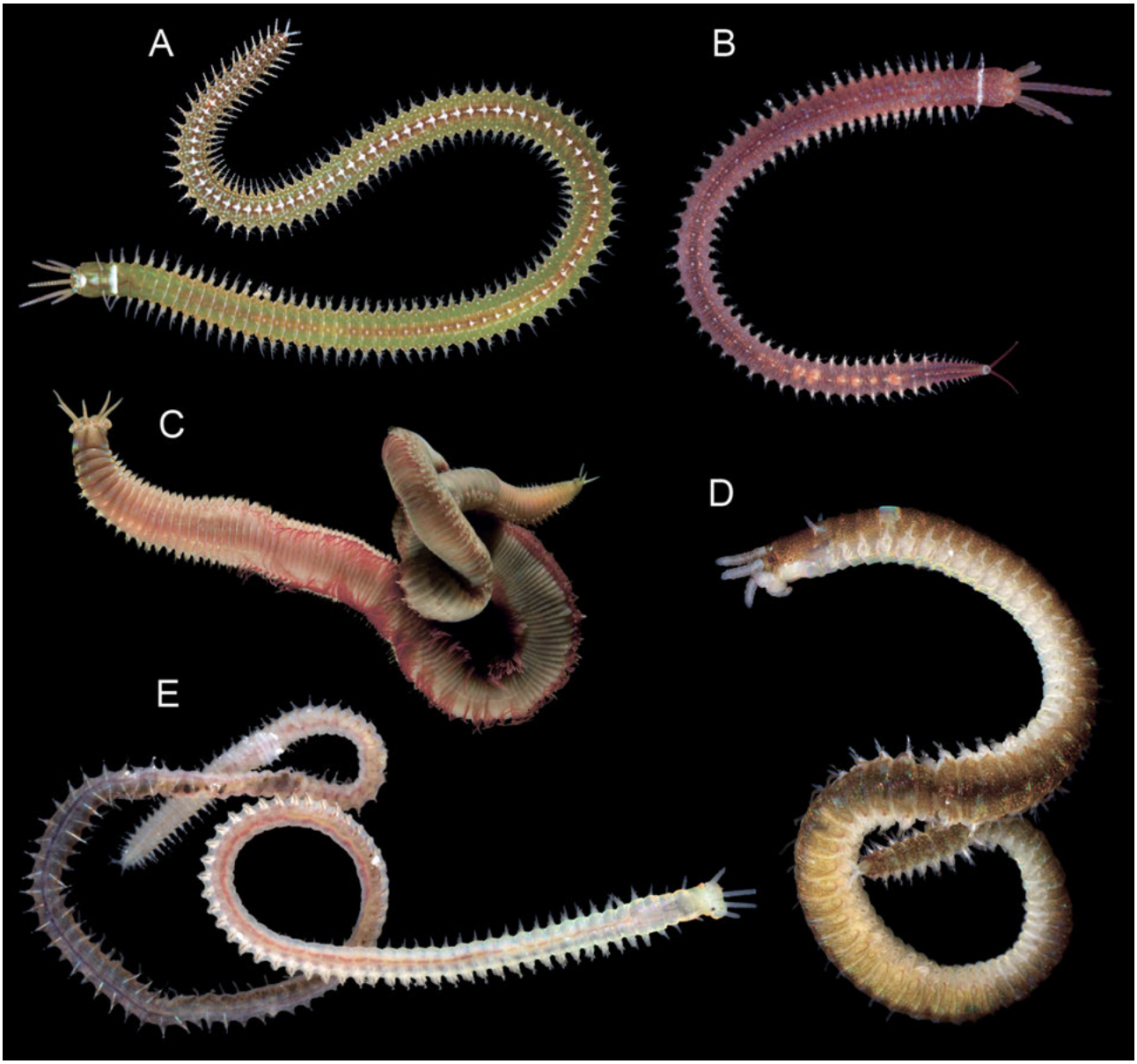


Fig. 7.12.4.1: Body shape and coloration of live eunicids. A, B, *Leodice* sp., dorsal view; C, *Marphysa* sp., dorsal view; D, *Nicidion* sp., lateral view; E, *Palola* sp., dorsal view. A, B, D, E, © A. Semenov; C, © L. Altoff.

Three body shapes have been recognized (Fauchald 1992a):

(1) The maximum width is at the posterior end of the pharyngeal bulb. The body tapers evenly and gradually toward the posterior end.
(2) The maximum width is at around chaetiger 10. It is retained until the end of the body, which tapers abruptly at the posterior end of the last 20 chaetigers.
(3) The maximum width is at the posterior third of the body (based on chaetiger counts). The body is usually flattened at this region. This shape is common in species of *Marphysa*, but it is also observed in species of *Eunice*.

The anteriormost end of the body is round in cross-section because of the pharyngeal muscles. The shape of cross-sections may vary along the body; a round cross-section with the dorsal side more convex than ventral is the most common body shape (Fauchald 1992a, Zanol et al. 2014). Some species of *Eunice*, *Euniphysa*, and, mainly, *Marphysa* have flattened body regions. *Marphysa* species have, most commonly, dorsally flattened cross-sections in the median and posterior regions of the body. Most species of *Palola* have a dorsally convex and a ventrally flattened anterior region (Fauchald 1992b). Dorsal and ventral longitudinal muscles are better developed in the anterior and median regions than in the posterior region.

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Color

The color of live individuals varies between species and thus may be taxonomically informative (Treadwell 1921, Fauchald 1992a), although the color pattern and intraspecific variation remain unknown for most species. Most common body colors are brown, red, magenta, purple, white, and green (Fig. 7.12.4.1). Solid red hues are common due to blood visible through the body wall. The prostomium often has lighter shades around the antennophores, palpophores, and anterior margin. One to three white chaetigers at the anterior end are present in many species (Fig. 7.12.4.2B–D). In white *Lysidice* species, the anterior ends may have a few chaetigers of distinct color (e.g., *Lysidice caribensis* Carrera-Parra, Fauchald & Gambi, 2011). Photos of *Eunice* posted online display colors not registered in the scientific literature, such as yellow with purple patterns and green with black leopard-like patterns (links in Salazar-Vallejo et al. 2011). *Leodice* species commonly have red bands around regular articulations of prostomial appendages and peristomial and notopodial cirri (Fig. 7.12.4.2C). In *Eunice*, these same appendages and cirri may have white rings. In *Nicidion*, a common color pattern is the presence of conspicuous to inconspicuous white dots (Fig. 7.12.4.2B) (Zanol et al. 2014). Live color pattern has not been described for species of *Aciculomarphysa*, *Fauchaldius*, and *Euniphysa*. Most preserved specimens lose their coloration. They are mostly beige, brown, white, or yellowish. Iridescence is common in most species. Some *Eunice* and *Marphysa* species have crisscross patterns on the cuticle, which appear to increase the intensity of iridescence.

Prostomium

Traditionally, the prostomium is described based on dorsal view. Prostomia lacking the anterior incision are described as undivided, entire, or rounded. They are present in some species of *Lysidice* and *Marphysa* (Fig. 7.12.4.3C–F). Prostomia with the anterior incision are the most common in the family, being described as bilobed (Figs. 7.12.4.2A, C, D, 7.12.4.3A, B). Bilobed prostomia are anteriorly rounded (Fig. 7.12.4.4A, B), round multilobed (Fig. 7.12.4.3H), steep truncate, or expanded truncate (Zanol et al. 2014). Truncate prostomia are longest along the median incision and evenly shorter toward the lateral edges (Fig. 7.12.4.4C). In steep truncate, the lateral edges of the prostomium are on a plane more ventral than median incision (Fig. 7.12.4.2C). In expanded truncate, both edges, lateral and along the median incision, are on the same plane (Fig. 7.12.4.1C).

Dorsal buccal lips (*sensu* Orrhage 1995) are present as a swollen region anterior to prostomial appendages (Fig. 7.12.4.3E, G, H) (Pruvot and Racovitza 1895, Von Haffner 1959, Zanol et al. 2014). They have been referred to as palps (Pruvot 1885), frontal palps (Paxton 1986, Orensanz 1990), or frontal lips (Paxton 1998). Dorsal buccal lips are clearly seen under scanning electron microscopy (SEM) and may be almost unnoticeable under light microscopy (Fig. 7.12.4.3E, G, H). The degree of swelling increases with the size of specimens (Zanol et al. 2014). It is absent (*Lysidice* species with only median antenna) to inconspicuous (*Lysidice* species with three antennae) in small specimens. In large specimens, it may be so conspicuous that gives a four-lobed appearance to the prostomium (Fig. 7.12.4.3H) (Treadwell 1921), which has been considered an important diagnostic feature at the generic level (Kinberg 1865, Ehlers 1868). The shape of the prostomia also varies dorsally. They are flat, inflated, with thickened lateral edges (dimpled *sensu* Fauchald 1992a) (Fig. 7.12.4.4D–F), or flat with anterior edge on a plane more dorsal than the rest of the prostomium. These shapes are determined on frontal and lateral views of the prostomium.

The ventral region of the prostomium bears fused ventral buccal lips (Fig. 7.12.4.3G–I) homologous to those of onuphids (Orrhage 1995, Zanol 2010, Zanol et al. 2014). Ventral buccal lips have been described as cushion-like palps (Day 1967), labial palps (Paxton 1986), upper lips (Paxton 1998), or just palps (Fauchald 1992a). In most eunicids, with the exception of some *Lysidice* species bearing only a median antenna, the prostomium bears a ventromedial groove, which medially separates the ventral buccal lips. The groove may extend to the anterior end as the anterior incision of varying depth, making the prostomium appear bilobed in a dorsal view.

The relative length, width, and depth (dorsoventral dimension) of the prostomium in relation to the peristomium are variable (Fauchald 1992a) (Fig. 7.12.4.3A–F). It is relatively constant within species and even within certain genera. Most species of *Palola* have a prostomium expanded anterolaterally, making it wider than the peristomium (Fig. 7.12.4.17A) (Zanol et al. 2014).

Up to five prostomial appendages of sensory function are placed on the posterior half of the prostomium, one median antenna, two lateral antennae, and a pair of palps (*sensu* Orrhage 1995). The terms “tentacles” (e.g., Crossland 1903, Treadwell 1921, Åkesson 1967) and “antennae” (e.g., Gravier 1900, Hartman 1944, Day 1967, Fauchald 1992a, Orensanz 1990) have also been used to describe all five prostomial appendages. Species of all genera, with the exception of *Lysidice*, have all five prostomial appendages (Figs. 7.12.4.2A–C, E, 7.12.4.3A–D). *Lysidice* includes

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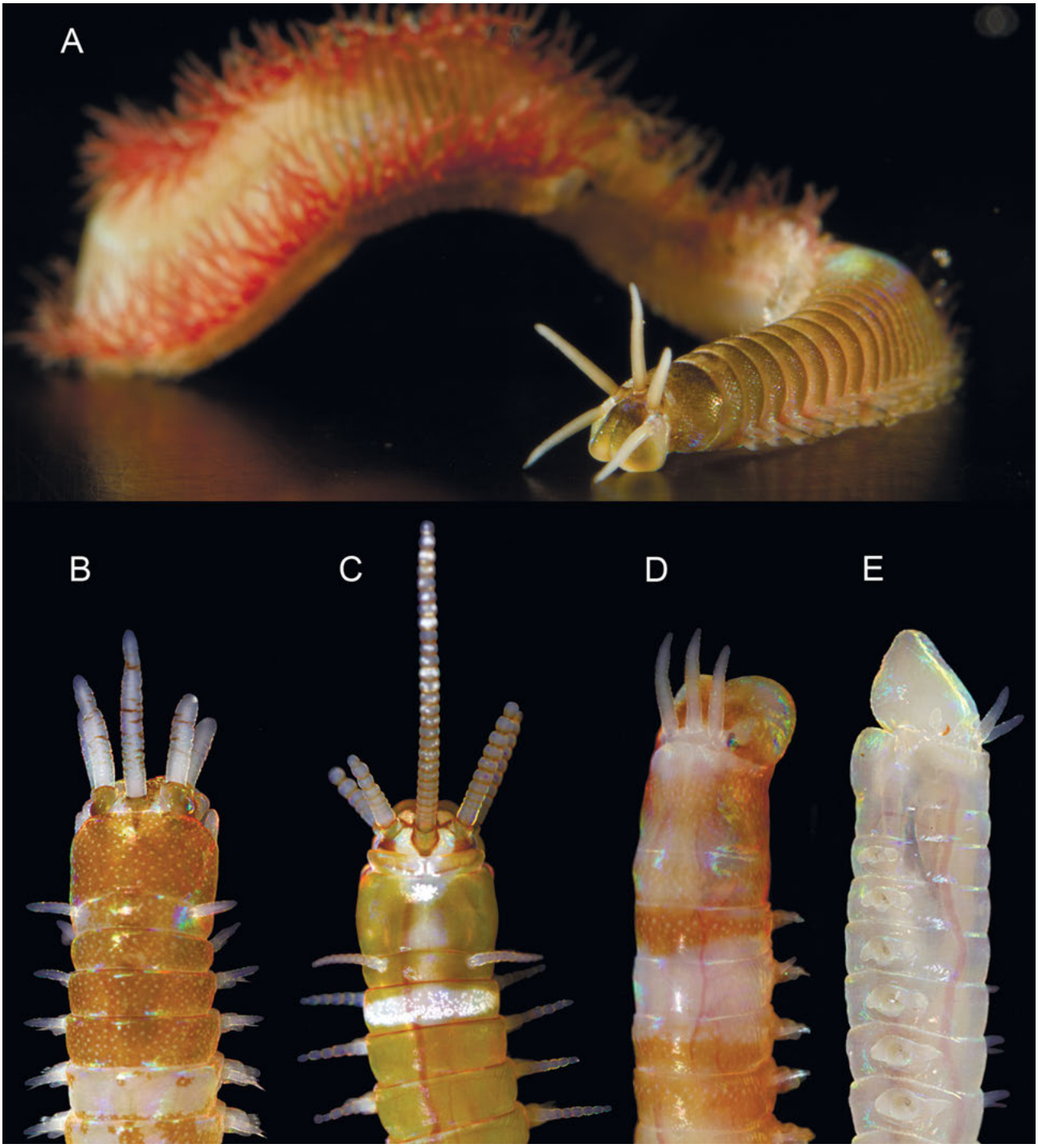


Fig. 7.12.4.2: Anterior body regions of live eunicids. A, *Marphysa* sp., frontal view; B, *Nicidion* sp., dorsal view; C, *Leodice* sp., dorsal view; D, *Lysidice* sp., dorsolateral view; E, *Marphysa* bifurcata, lateral view. A, © L. Altoff; B–E, © A. Semenov.

species with three (median and lateral antennae) (Figs. 7.12.4.2D, 7.12.4.3E) or one (Fig. 7.12.4.3F) (median antenna) prostomial appendages.

Prostomial appendages are usually arranged in a semicircle, where palps are the most anterolateral appendages and the median antennae are the posteriormost appendages (Figs. 7.12.4.3A–D, 7.12.4.4A–C). They may also be arranged in a straight line (all are equally posterior), antennae in a straight line and palps more anterior (Figs. 7.12.4.3B, 7.12.4.4C), and in a horseshoe-like pattern (palps most anterior appendage placed directly anterior to lateral antennae and median antenna

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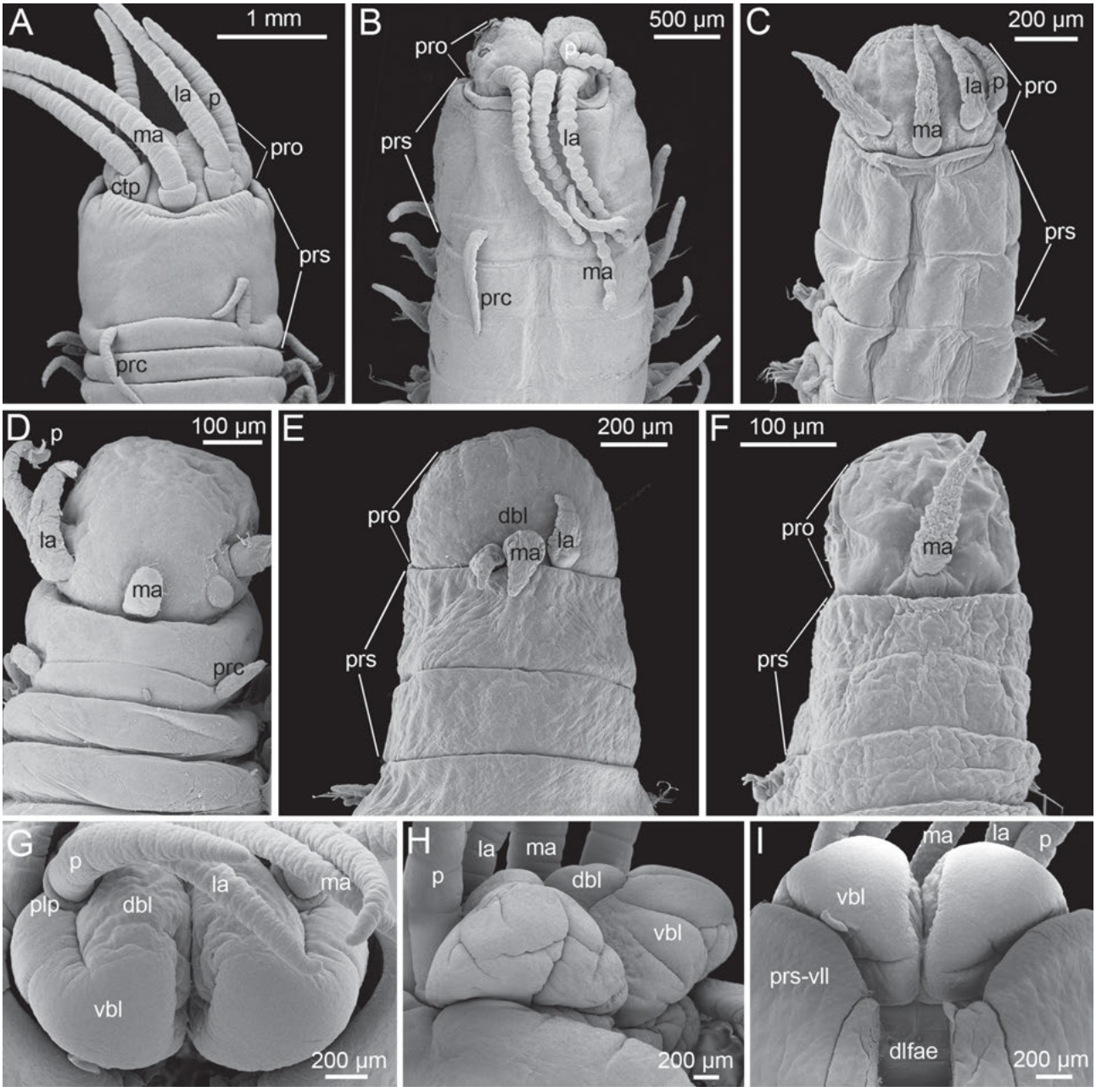


Fig. 7.12.4.3: Morphology of anterior body regions, A–F, Dorsal view of anterior end; G, Frontal view of prostomium; H, latero-ventral view of prostomium; I, Ventral view of prostomium and peristomium; *Nicidion mikeli*, prostomial appendages with irregular annulation; B, *Leodice antennata*, prostomial appendages with moniliform articulation; C, *Paucibranchia fallax*, peristomium lacking cirri; D, *Fauchaldius cyrtauloni*; E, *Lysidice ninetta*, dorsal buccal lip inconspicuous and fused to dorsal side of prostomium, prostomium dorsally entire and inflated; F, *Lysidice unicornis*, prostomium with only median antenna present; G, *Eunice filamentosa*, frontal view of prostomium, dorsal buccal lip inconspicuous and fused to dorsal side of prostomium, prostomium dimpled; H, *Eunice violaceomaculata*, ventrolateral view of prostomium, dorsal buccal lip fused to dorsal side of prostomium, prostomium round multilobed; I, *Eunice filamentosa*, ventral view of prostomium and anterior end of peristomium cut to show dorsolateral fold anterior extension. ctp, ceratophore; dbl, dorsal buccal lip; dlfae, dorsolateral fold anterior extension; la, lateral antenna; ma, median antenna; p, palp; plp, palpophore; prc, peristomial cirrus; pro, prostomium; prs, peristomium; prs-vll, peristomial ventrolateral lips; vbl, ventral buccal lip. B, E, F–I, Modified from Zanol et al. (2014).

most posterior appendage) (Fig. 7.12.4.3D). In any of these arrangements, the prostomial appendages may be evenly spaced (Fig. 7.12.4.4C), and the median antennae or the palps may be separated by a wider gap from the remaining appendages (Fig. 7.12.4.4A, B). In moving live specimens, the palps usually touch the bottom anterior to the individual, whereas the antennae are stretched upward (Fig. 7.12.4.2A).

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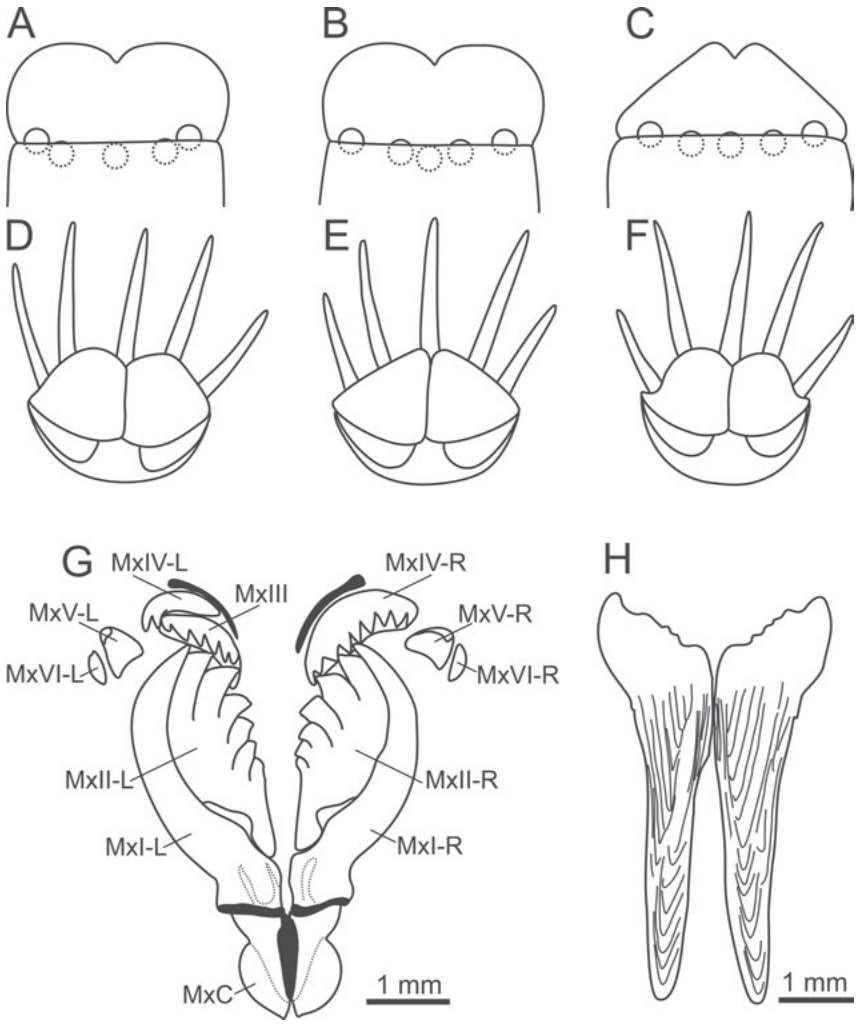


Fig. 7.12.4.4: Schematic drawings of prostomium (A–F) and jaw apparatus (G, H). A–B, G, Dorsal view; D–F, Frontal view; H, Ventral view, circles represent the arrangement of prostomial appendages (antennae and palps); A, Bilobed prostomium anteriorly rounded, median antennae isolated by a gap from the other antennae and palps; B, Bilobed prostomium anteriorly rounded, palps isolated by a gap from the antennae; C, Bilobed prostomium anteriorly truncate, antennae and palps evenly spaced; D, Prostomium dorsally inflated; E, Prostomium dorsally flat; F, Prostomium dorsally dimpled; G, Maxillae of *Eunice denticulata*; H, Mandibles of *Eunice dubitata*. MxC, maxillary carriers; MxI–VI, maxillary plates; L, left row of maxillary plates; R, right row of maxillary plates. A–G, Modified from Zanol et al. (2007); H, Modified from Winsnes (1989).

Antennae and palps have distal and proximal joints named ceratostyles and ceratophores, respectively, whereas all five prostomial appendages were thought to be antennae (Fauchald 1977). To make the difference between antennae and palps clear, distal joints are named antennal style and palpostyle and proximal joints antennophore and palpophore (Zanol et al. 2017). The length of antennal styles and palpostyles usually increases from palps to median antenna (Figs. 7.12.4.2B, C, 7.12.4.3B). Shorter antennal styles than palpostyles may be due to regeneration. In most species, at least the median antenna is longer than the prostomium. However, all prostomial appendages may be shorter than the prostomium (Figs. 7.12.4.2E, 7.12.4.3E), for example, in *Marphysa bifurcata* Kott, 1951, all appendages are shorter than half of the prostomium (Kott 1951). It is common to describe how far along the dorsal side of the specimen antennal styles and palpostyles reach when folded back (Crossland 1903, Fauchald 1992a).

In general, antennal styles and palpostyles have a similar width. In *Euniphysa*, styles are more slender in relation to the prostomium width than in the other genera (Fig. 7.12.4.11A) (Lu and Fauchald 2000). Different shapes of styles are digitiform, tapering, clavate, or medially inflated (fusiform). Some species have a constriction at the base of the styles (narrow peduncle *sensu* Glasby and Hutchings 2010). Styles are smooth or articulated. Articulated styles have at least some distinct perpendicular grooves around the whole circumference (complete grooves). Styles with only complete grooves are conspicuously regularly articulated. In these, articles are cylindrical or moniliform (Figs. 7.12.4.2C, 7.12.4.3B). Irregularly articulated styles, generally described as wrinkled, have complete and incomplete grooves. Incomplete grooves do not surround the styles completely, having an appearance of a wrinkle even in live specimens (Figs. 7.12.4.2B, 7.12.4.3A). It is not possible to clearly determine the number of articles in irregularly articulated styles. Only *Leodice* species have conspicuous and regular articulated styles (Zanol et al. 2014).

Antennophores and palpophores are mostly short and ring-like (Fig. 7.12.4.3C, D). In fewer species, they are cylindrical and confluent with prostomium (Fig. 7.12.4.3A).

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Anterior peristomial fold often covers the bases of prostomial appendages.

Nuchal organs and eyes

The dorsoposterior end of the prostomium also bears a pair of nuchal organs in shape of ciliate bands usually covered by the anterior peristomial fold (Jourdan 1887, Heider 1925, Von Haffner 1962, Åkesson 1967, Zanol et al. 2010).

The presence of eyes varies among species. Larval eyes are paired small pigment cups present at the anterior end of the prostomium of juveniles (Åkesson 1967), which appear not to remain in the adults (von Palubitzki and Purschke 2020). Two pairs of cerebral adult eyes are present. The anterior pair is minute, placed anterior to the prostomial appendages, and appears to be miniaturized adult eyes (von Palubitzki and Purschke 2020). These are rarely observed and reported. The posterior pair are the best-known adult eyes. It appears early in juveniles, in which it is still possible to observe an anterior pair of minute eye considered to be larval eyes (Aiyar 1931). Adult eyes of the posterior pair are red to purple-black and placed on the posterior edge of prostomium, close to the antennophores of the lateral antennae or the palpophores. Adult eyes are cup-shaped multicellular everse ocelli, which may be slit-shaped, kidney-shaped, and, most commonly, round to ovoid in external view (Figs. 7.12.4.2B–E, 7.12.4.10A, 7.12.4.13A, 7.12.4.14A, 7.12.4.16A, 7.12.4.17A). In fixed specimens, eyes may fade out (Fauchald 1992a); thus, the presence or absence of eyes is often an inconsistent taxonomic feature. Adult eyes described for species of *Eunice*, *Leodice*, *Marphysa*, *Paucibranchia*, and, maybe, *Lysidice unicornis* (Grube, 1840) have an internal lens-like structure (also named refractive body, crystalline lens, or vitreous body) (Graber 1880, Jourdan 1887, Andrews 1892, Tampi 1949, Suschenko and Purschke 2009, von Palubitzki and Purschke 2020). The posterior eyes of *Marphysa gravelyi* Southern, 1921 have a feeble lens-like structure (Tampi 1949).

Segmental ocelli are also present in some species (Purschke 2005). These are especially developed in epitokous forms of the genus *Palola* and of the species *Eunice fucata* Ehlers, 1887, which have unpaired ventral eyes close to the ventral nerve cord (Von Haffner 1961, Hauenschild et al. 1968, Eakin and Hermans 1988) and chaetigers sensitive to light despite the lack of visible ocelli (Clark and Hess 1940), respectively.

Peristomium

The peristomium is double ringed and has a presegmental origin during ontogenesis (Åkesson 1967). The first ring is usually longer than the second ring (Figs. 7.12.4.2B–E, 7.12.4.3A–F). The separation between peristomial rings is prominent all around or only on dorsal and ventral sides. The peristomium bears ventrolateral lips as conspicuous structures or just as elevated surface. A pair of peristomial cirri attached to the second peristomial ring is present in adult forms of all species of *Eunice*, *Euniphysa*, *Fauchaldius*, *Leodice*, and *Palola* and in most species of *Nicidion* (Figs. 7.12.4.2B, C, 7.12.4.3A, B, D). Peristomial cirri have also been named nuchal cirri (e.g., Treadwell 1921) and tentacular cirri (e.g., Hartman 1944, Day 1967, Giangrande 1989, Orensanz 1990, Hartmann-Schröder and Zibrowius 1998). These cirri vary in length from barely reaching the posterior end of the first ring to reaching beyond the peristomial anterior end. They may be irregularly or regularly articulated. Some species with regularly articulated prostomial appendages also show regularly articulated peristomial cirri. The shape of the cirri varies among digitiform, ovate (button-shaped), slender, tapering, and club-shaped (clavate). The relative length, articulation, and shape of peristomial cirri are used in species-level taxonomy.

Digestive system and jaws

The digestive system is composed of a ventral muscularized pharynx following the buccal opening and running through the peristomium and few anterior chaetigers, a muscular esophagus connecting at the dorsoanterior end of the muscularized pharynx, a cylindrical digestive tube with folds, and a pygidial dorsal anus (Ehlers 1868). The ventral muscularized pharynx (ventral muscle bulb *sensu* Purschke 1988, ventral pharyngeal organ *sensu* Tzetlin and Purschke 2005, and pharyngeal bulb *sensu* Purschke 1988, Fauchald 1992a, Zanol et al. 2007) is composed of muscle masses mostly associated with four pairs of folds and with jaws (dorsal maxillae and ventral mandible) (Wolf 1980). The four pairs of folds from dorsal to ventral are dorsolateral, maxillary, pharyngeal, and mandible folds, respectively (Zanol 2010). Dorsolateral folds fuse just posterior to the prostomium in a structure named anterior extension of the dorsolateral fold, which is one of the synapomorphies of Eunicidae (Fig. 7.12.4.3I). Maxillary and mandibular folds support maxillae and mandible plates, respectively. On the ventral side of the muscularized pharynx, the placement of transverse and central ventral muscles, F1 + F2 (Figs. 7.12.4.13B, 7.12.4.14B, 7.12.4.17B) (*sensu* Desière 1967) or VM3 + VM4 (*sensu* Wolf 1980), respectively, in relation to the mandible shafts (mandible carriers *sensu* Zanol et al. 2007) varies with the shape of the mandibles (flat, curved X-shaped, and curved scoop-shaped; 7.12.4.11F, 7.12.4.13D, 7.12.4.14D, E, 7.12.4.17D, E) (Zanol et al. 2007).

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Jaws (maxillae and mandibles) are composed of scleroproteins and mineralized with calcium carbonate in the form of aragonite at least in the maxillae (Colbath 1986). Maxillae are eulabidognath (*sensu* Paxton 2009) with four or five paired plates, one unpaired plate, a pair of dorsal carriers (Fig. 7.12.4.4G), and an unpaired ventral carrier. Maxillae plates are numbered from I to VI (MxI–MxVI), starting from the dorsalmost. The dorsal carriers are sclerotized, short, and connected anteriorly with MxI. Their shape is seldom described, but the relative length in relation to MxI varies among species and genera. The ventral carrier is not sclerotized, extends posteriorly from the maxillary fold, and is deeply embedded in muscles (Paxton 2009). It is only visible after a complete removal of the muscles. Its variation within the family is unknown.

MxI are the largest plates. They are curved, falcate, and, usually, lack median teeth. MxI bear median teeth only in a few species of *Euniphysa* and juvenile jaws (Paxton and Eriksson 2012). The plates are closest at the base (posterior end), which bears a locking system composed of ridges and furrows (Paxton 2009, closing system sensu Molina-Acevedo and Carrera-Parra 2015). The left side has a furrow on each side of the ridge and the right side has a ridge on each side of the furrow.

The basal inner edge of MxI (*sensu* Molina-Acevedo 2018) are usually parallel to each other. They start diverging at the falcal arch (*sensu* Molina-Acevedo 2018) and become forceps-shaped toward the anterior (Fig. 7.12.4.15). Recently, the ratio between the length of the longest ridge of the locking system and that of MxI and the shape of the falcate section and base of MxI have been used as taxonomic features (Molina-Acevedo and Carrera-Parra 2015, 2017). The shape of MxI falcal arch, basal inner edge, and basal outer edge appear to be informative at the generic level as suggested by Molina-Acevedo and Carrera-Parra (2017) at least for some genera (Fig. 7.12.4.15). The presence or absence of a curve at MxI basal outer edge appears to be variable at least within *Eunice* and *Marphysa*; for additional discussion, see remarks on the genera below. MxI falcal arch may be extended or not. Extended falcal arch is rectangular or rounded (*sensu* Molina-Acevedo and Carrera-Parra 2015, Molina-Acevedo 2018). The falcal arch is extended in an abruptly tapering MxI (Fig. 7.12.4.15) and missing in smoothly tapering falcate section of MxI (Fig. 7.12.4.13C). In some *Palola* species, the falcal arch is so extended that it resembles a denticle (Fig. 7.12.4.17C). The basal inner edge of MxI may have a curvature that fits the base of MxII (Fig. 7.12.4.15C) (Molina-Acevedo and Carrera-Parra 2017).

MxII are large plates almost as long as MxI and are placed ventral to the latter. They have smooth outer edges and dentate inner edges (Fig. 7.12.4.4G). The ventral side is shorter due to the opening to the pulp cavity where muscles are inserted. Teeth may be distributed over most of the inner edge (Fig. 7.12.4.4G) or only on a distal portion, and the number of teeth varies from 3 to 15 and is not linked to the size of the specimen (Fauchald 1992a). In most genera, teeth are wide, triangular, and curved posteriorly (Figs. 7.12.4.4G, 7.12.4.13C). In some species of *Euniphysa*, most anterior teeth of MxII are fang-shaped (Fig. 7.12.4.11E). The most common taxonomic features described for MxII are the number and the distribution of teeth on the plate. Molina-Acevedo and Carrera-Parra (2015, 2017) described also the ratio between the legth of the pulp cavity and the total length of MxII, but its taxonomic information is not clear. In contrast, a dorsal projection at the posteriormost end of the base of MxII is a diagnostic feature of the genus *Treadwellphysa* (see Molina-Acevedo and Carrera-Parra 2017).

MxIII is an unpaired plate on the left side in most species. Exceptions are a few species of *Eunice* and the genus *Fauchaldius*, which have paired MxIII (Fauchald 1992a, Molina-Acevedo and Carrera-Parra 2017). Some specimens of species that normally have left MxIII only may have right MxIII also, which is probably a defect. In many *Palola* species, MxIII is reduced to a ridge and completely ventral to MxII (Fig. 7.12.4.17C). In all other genera, it is dentate. Teeth are short and wide in most species and fang-shaped in *Euniphysa* species (Fig. 7.12.4.11E). The number of teeth varies from 1 to 9 and it is not related to the placement of MxIII or the size of the specimen. In *Leodice* species with tridentate or bidentate light subacicular hooks, MxIII is flat with inner edge curved toward the dorsal side and mostly ventral to MxII (Fig. 7.12.4.13C), similar to those of the family Onuphidae. In the remaining *Leodice* species and other eunicid genera, MxIII is arched, part of the distal arc, mostly anterior to MxII and adjacent to MxIV (Figs. 7.12.4.4G, 7.12.4.14C), and the shape and relative length of teeth vary among species. The number of teeth, shape, and placement of MxIII are taxonomically informative.

MxIV are paired plates part of the distal arc. The left plate is usually smaller and with fewer teeth than the right one (Figs. 7.12.4.4G, 7.12.4.14C). In specimens or species with paired MxIII, right MxIV is identical to the left one. As for MxIII, the number of teeth, shape, and placement of MxIV are taxonomically informative. In some species, mainly of the genus *Eunice*, the sum of teeth of left MxIII and MxIV is similar to the number of teeth in right MxIV. *Euniphysa* species have fang-shaped MxIV (Fig. 7.12.4.11E). In *Palola*, both MxIV have the attachment base narrower than the length of the plate (Fig. 7.12.4.17C). In most species, left MxIV is arched dorsoventrally and teeth may be distributed along the dorsal quarter only, along the dorsal half only, along the dorsal half and part of the ventral half or along

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the whole length of the plate. Species of *Eunice* with teeth restricted to the dorsal quarter of left MxIV may represent a distinct monophyletic genus (Zanol et al. 2014). Few *Leodice* species have left MxIV arched anteroposteriorly. Right MxIV is arched anteroposteriorly and more uniform in most genera.

MxV are paired small plates, mostly similar on both sides, placed lateral to MxIV on the distal arc (Fig. 7.12.4.4G). In most species, MxV are plate-like with a small tooth; in a few cases, several teeth are present (Fauchald 1992a). The exception is *Euniphysa*, which have fang-shaped MxV (Fig. 7.12.4.11E). In most species, MxV is the most external plate of the maxillae. However, in some species of genera *Eunice*, *Euniphysa*, *Leodice*, and *Palola*, MxVI is present as paired lateral plates to MxV (Fig. 7.12.4.4G). These are the smallest plates and usually edentate.

Attachment lamellae (*sensu* Wolf 1980) are flat sclerotized parts adjacent to maxillae plates. In Eunicidae, they are mainly associated with MxIII and IV but poorly described and illustrated in the literature of the family. Attachment lamellae have also been described as callosities (Heider 1925, Desière 1967) and paragnath plates (Orensanz 1990). The presence and absence of these lamellae have been included in descriptions of *Euniphysa* (accessory plates *sensu* Lu and Fauchald 2000). The shape, degree of sclerotization, and relative length of these lamellae in relation to the associated plate have been included in descriptions of *Marphysa*, *Nicidion*, *Paucibranchia*, and *Treadwellphysa* by Molina-Acevedo and Carrera-Parra (2015, 2017) and Molina-Acevedo (2018, 2019). These authors also described the sclerotized parts among MxI-MxII, left MxII-MxIII, and right MxII-MxIV, which they named ligaments. Ligaments between MxI and MxII appear to be uniform among species as dark and retangular. Ligaments between left MxII-MxIII and right MxII-MxIV appear to vary in the degree of sclerotization.

Hypotheses about the pairing of maxillae plates and their evolution are controversial. To explain the unpaired plate, right MxIV has been suggested as the result of the fusion of left MxIII and IV (Hartman 1944). The most external ridge of the locking system of right MxI has been hypothesized as homologous to the basal plate (Kielan-Jaworowska 1966) and to the right MxI itself (Paxton 2009) of the maxillae of other Eunicida. The latter hypothesis extends also to the homology of plates traditionally named right MxI and MxII, which would be, respectively, homologous to MxII and III of other Eunicida. Thus, MxIII thought to be unpaired would be paired and MxI-IV would have asymmetrical shape. Such hypothesis is based on larval and juvenile maxillae (Paxton 2009, Paxton and Eriksson 2012).

Mandibles are a ventral pair of plates not medially fused. They are composed of calcified cutting plates and elongated shafts, where muscles attach (Fig. 7.12.4.4H). The cutting plates are often fragile, breaking easily or being lost by decalcification due to fixatives such as formaldehyde. Mandibles may have (1) strongly curved and calcified cutting plates, forming an open scoop and parallel shafts (scoop-shaped mandibles), occurs in the genus *Palola* (Fig. 7.12.4.17D, E); (2) curved and poorly calcified cutting plates and diverging shafts (X-shaped mandible), occurs in *Lysidice* (Fig. 7.12.4.14D, E); and (3) flat and calcified cutting plates and parallel to diverging shafts (flat mandibles), occurs in all remaining genera (Figs. 7.12.4.11F, 7.12.4.13D). Their exact shape varies within these three main types of mandible, but the taxonomic significance of this variation remains unclear. Some variation appears to be due to wear down.

Branchiae

Branchiae are present in all known species of *Eunice*, *Euniphysa*, *Leodice*, *Marphysa*, *Paucibranchia*, and *Treadwellphysa* but are absent in *Aciculomarphysa*, *Fauchaldius*, and *Lysidice* and may be present or absent in species of *Nicidion* and *Palola*. At least in *Nicidion*, the presence or absence of branchiae may vary intraspecifically (e.g., Nogueira et al. 2001). Branchiae have single or multiple filaments (2 to >40) (Fig. 7.12.4.5B, C). In the latter case, filaments are linearly distributed on a main stem (or shaft *sensu* Fauchald 1992a, Zanol et al. 2014). The base of branchial stems or the filament itself, in the case of single filament branchiae, are usually connected to the dorsal side of the base of the notopodial cirri and, in few cases, to the dorsal side of the body close to notopodial cirri (Fauchald 1992a). In rare cases, the complete branchial stems, not only the bases, are attached to the dorsal body wall (e.g., *M. bifurcata* and *Marphysa sessilobranchiata* Hartmann-Schröder, 1984) (see Zanol et al. 2017). Branchiae have different appearance (palmate or pectinate) according to the length of the stems. In palmate branchiae, the stem is so short that filaments appear to branch around a central origin. In pectinate branchiae, filaments clearly branch linearly from the stem, which may be shorter or longer than branchial filaments. The relative length of branchiae to that of notopodial cirri varies among species.

Branchial distribution and number of filaments vary along the body. Six patterns of variation have been recognized (Miura 1986, Fauchald 1992a, b, Zanol et al. 2016): (1) branchiae present from anterior to posterior chaetigers, maximum number of filaments at anterior chaetigers,

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occurs in *Eunice*; (2) branchiae restricted to anterior region (30–40% of all chaetigers), maximum number of filaments at the middle of the distribution, occurs in *Eunice*, *Leodice*, and *Paucibranchia*; (3) branchiae present from anterior to posterior chaetigers, maximum number of filaments at anterior and posterior chaetigers, minimum number at median chaetigers, occurs in *Eunice* and *Leodice*; (4) branchiae restricted to posterior chaetigers, usually with single filaments, occurs in *Nicidion*; (5) branchiae present from anterior to posterior chaetigers, maximum number of filaments at posterior chaetigers, occurs in *Marphysa*; and (6) branchiae present from chaetiger 50, midbody or about chaetiger 100, may be missing in chaetigers at the middle of the distribution, single filaments, occurs in *Palola*.

Branchiae present from anterior to posterior chaetigers usually are present in more than 65% of chaetigers, whereas branchiae restricted to anterior or posterior chaetigers are present in 55% of the chaetigers at most. Branchiae never start before chaetiger 3. The start of the branchiae at chaetiger 3 appears to be constant, without intraspecific variation (e.g., Parapar et al. 1993). More posterior origin of the branchiae is commonly not fixed to a certain chaetiger, varying intraspecifically within a narrow interval (Miura 1986, Fauchald 1992a). Branchiae in *Euniphysa* species start at around chaetiger 9, 17, or 25. It is species specific and appears not to be dependent on the body width (Lu and Fauchald 2000). In all patterns of branchial distribution, the number of filaments in the first branchiae, maximum number of filaments, and last chaetiger with branchiae appear to be dependent on body size (Miura 1986, Parapar et al. 1993). However, the relative position of the last branchiate chaetiger in relation to the total number of chaetigers is relatively conserved at the species level (Miura 1986). Branchial features, such as the beginning and end of the distribution, shape, and maximum number of filaments, are always present in species descriptions. Other informative features are the relative length of filaments to stem and of branchiae to notopodial cirri.

Parapodia

Parapodia appear uniramous, but they are subbiramous with notopodia reduced to notopodial cirri (Fig. 7.12.4.5A–F). The presence of notopodial cirri led Fauchald (1992a) to describe parapodia as biramous, a classification not followed by most authors due to the reduced form of the notopodia. Notopodial cirri vary in shape from button-shaped, tapering, digitiform, medially inflated (fusiform), thumb-shaped, and filiform (Fig. 7.12.4.5A–F). They may be smooth, irregularly or regularly articulated. Regularly articulated notopodial cirri are present in some of the species with regularly articulated prostomial appendages. The shape and length of notopodial cirri may vary along the body. In *Nicidion*, notopodial cirri commonly become short and button-shaped at the posterior region of the body. A cirrophore, usually ring-shaped, may be present at the base of the notopodial cirri. Aciculae are the only chaetae that may be present in notopodial cirri. In *Lysidice*, notoaciculae appear to be absent in notopodial cirri of the first quarter of the body, the only region of the body where notopodial aciculae were consistently observed in other genera (Zanol et al. 2014). Notoaciculae are slender, varying from clear to black in color. Clear notoaciculae may be difficult to observe, especially in small specimens, and they are poorly reported in the literature. They are usually only visible in parapodia mounted on slides and observed under a compound microscope.

Flat, slightly elevated, or bulging (pendant lobe *sensu* Lu and Fauchald 2000) ciliated structures are present at the ventral side of the proximal end of notopodial cirri (Fig. 7.12.4.5D). They were first described in eunicids as dorsal cirrus organ (Hayashi and Yamane 1994, Hayashi's organ *sensu* Zanol et al. 2014) and latter have been hypothesized as homologous to lateral organs of other polychaetes (*sensu* Purschke 2005, Purschke and Hausen 2007). Thus, lateral organs should be the preferred name to make the hypothesis of homology evident. The shape of lateral organs varies along the body. They are least developed on most anterior and posterior chaetigers. In *Euniphysa*, lateral organs are always bulging where best developed (Lu and Fauchald 2000). In other genera, they vary from flat to bulging where best developed. This feature taxonomic information is not clear, as it is not commonly present in the descriptions.

Neuropodia are fully developed with prechaetal, postchaetal, and chaetal lobes. Prechaetal and postchaetal lobes are continuous structures that wrap around the chaetal lobe (Fauchald 1992a). They are very different in morphology and vary independently, thus are described as different structures. Prechaetal lobes are usually shorter than chaetal lobes but may be as long (Fig. 7.12.4.5B–F). Zanol et al. (2014) defined shorter prechaetal lobes as those that are lower than the base of anteriormost chaeate in the chaetal lobe and prechaetal lobes as long as the chaetal lobes as those that are higher than the base of anteriormost chaeate in the chaetal lobe but lower than the base of aciculae.

Postchaetal lobes vary in length in relation to chaetal lobes among species and along the body. They may be

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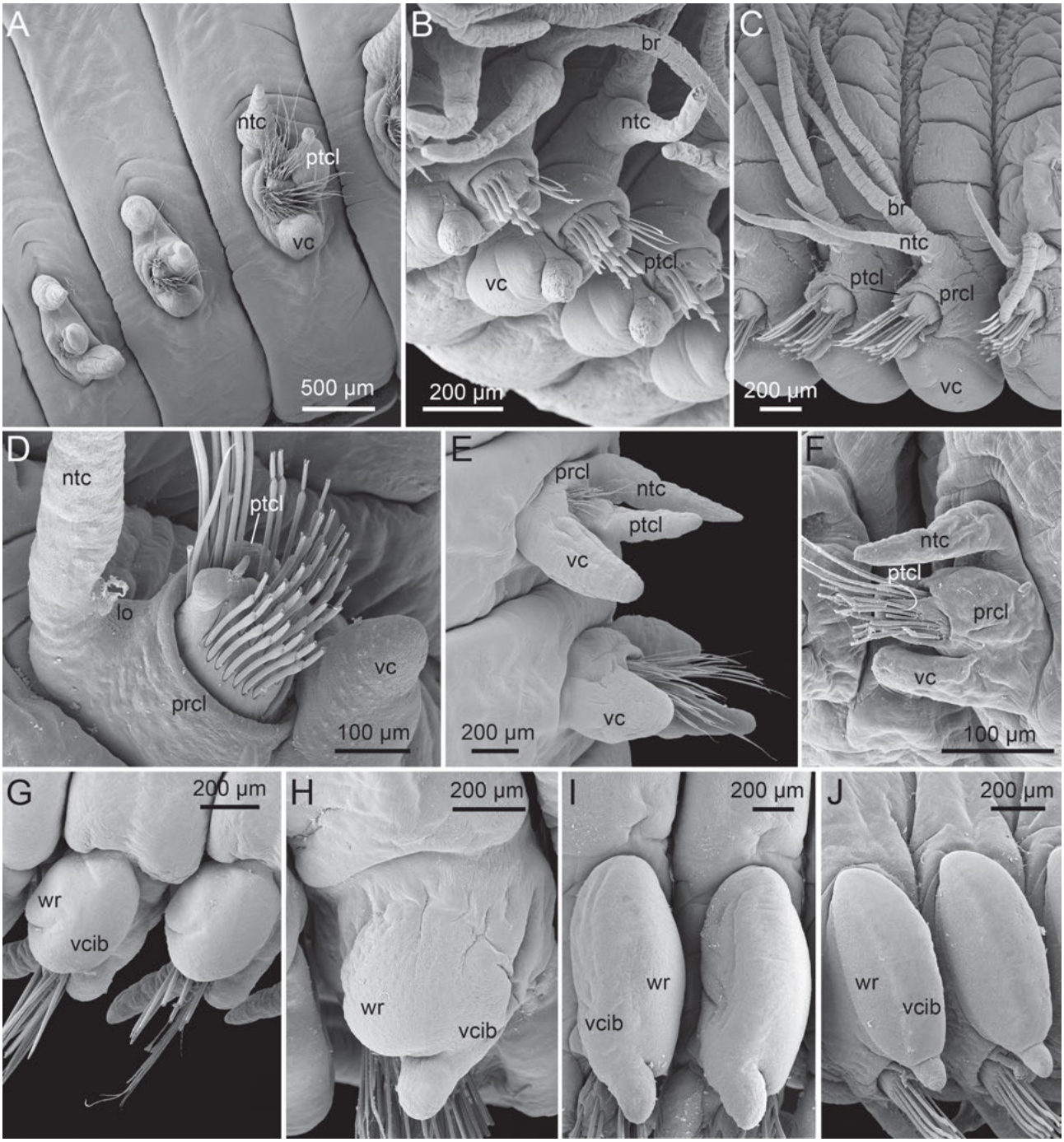


Fig. 7.12.4.5: Morphology of parapodia, SEM micrographs. A, *Marphysa sanguinea*, lateral view of anterior parapodia with conical dorsal and thumb-shaped ventral cirri; B, *Leodice antennata*, ventrolateral view of parapodia with branchiae and inflated ventral cirri; C, *Eunice filamentosa*, lateral view of parapodia with elongated dorsal cirri and branchiae; D, *E. filamentosa*, anterior parapodium with lateral organ; E, *M. sanguinea*, anterior parapodia with different shape of ventral cirri and tapering postchaetal lobes; F, *Lysidice ninetta*, parapodium with thumb-shaped ventral cirrus; G, *Eunice fucata*, inflated ventral cirri without a tip; H, *M. sanguinea*, rounded inflated ventral cirri with tips as continuation of the base; I, *Eunice violaceomaculata*, elongated inflated ventral cirri with tips as continuation of the base; J, *E. filamentosa*, elongated inflated ventral cirri with tips separated from the base. br, branchia; lo, lateral organ; ntc, notopodial cirrus; prcl, prechaetal lobe; ptcl, postchaetal lobe; vc, ventral cirrus; vcib, ventral cirrus inflated base; wr, wrinkled region.

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shorter, as long as, or longer than chaetal lobes (Fig. 7.12.4.5A–F). Longer postchaetal lobes are restricted to most anterior parapodia (Fig. 7.12.4.5A, E). These are most common in *Marphysa* and *Paucibranchia* and have also been reported in most of the other genera, with the exception of *Aciculomarphysa*, *Fauchaldius*, and *Leodice*. Longer postchaetal lobes may be tapering, round, digitiform, fusiform, or truncate. Truncate longer postchaetal lobes decrease in length continuously from the dorsal to the ventral side, with dorsal side being the longest. These shapes are taxonomically informative at the species level at least in *Marphysa* and *Paucibranchia* (Glasby and Hutchings 2010, Zanol et al. 2016, Molina-Acevedo 2018).

The shape of distal end of neuropodial chaetal lobe varies among species and along the body, being rounded, truncate, pointed, or bilobed (Fig. 7.12.4.5B–D, F). Some species bear a fleshy knob at the dorsal margin of the chaetal lobe (Fig. 7.12.4.5D). In most of these species, the fleshy knob is continuous with the remaining of the chaetal lobe. In *Euniphysa*, a fleshy knob ovoid and distinctly separated from the chaetal lobe by a groove (Fig. 7.12.4.11G) is one of the diagnostic characters of the genus (Lu and Fauchald 2000).

Ventral cirri are placed on the ventral side of the parapodia. In anteriormost chaetigers, they are shorter than the chaetal lobes, fusiform, tapering, digitiform, or thumb-shaped (Fig. 7.12.4.5A, E, F). Before chaetiger 10, the bases of the ventral cirri start to swell, forming the inflated base, which is a glandular structure (Hilbig 1986). The distribution, size, and shape of ventral cirri and inflated bases are used in species identification. After the first appearance, inflated bases may be restricted to a region of the body or present in all chaetigers thereafter. The shapes of the inflated bases are round or transverse welts (ridge *sensu* Zanol et al. 2014) (Fig. 7.12.4.5G–J). Ventral cirri with inflated bases most commonly have a tip, which continuously or abruptly tapers from the inflated base (Fig. 7.12.4.5H–J), but some completely lack tips (Fig. 7.12.4.5G). The tip may be button-shaped, tapering, or digitiform. In species with inflated ventral cirri as transverse welts, posterior ventral cirri usually maintain a small round inflated base and a digitiform tip longer than chaetal lobe (bowling pin *sensu* Zanol et al. 2014). In many *Nicidion* species, posterior ventral cirri are minute (button-shaped or inconspicuous knobs). Ventral cirrus inflated base is partially or completely wrinkled under SEM (a lighter whitish area under optical microscopy) (Zanol et al. 2014). The shape of the wrinkled region varies among species, and it may be restricted to an anterior shield-like area or to the whole anterior half (Fig. 7.12.4.5G–J).

Close to the ventral cirri lies the nephridiopore. Every chaetiger, with the exception of most anterior and posterior, has a pair of metanephridia that function as excretory and genital ducts (Goodrich 1945, Krishnamoorthi and Krishnaswamy 1966, Bartolomaeus and Quast 2005). In *M. gravelyi*, the ratio between the excretory surface of metanephridia and the length of the specimen is larger than in other species in the same estuary, suggesting that metanephridia have a role in osmoregulation and thus in the ability of the species to tolerate a wide range of salinities (Krishnamoorthi and Krishnaswamy 1966).

Chaetae

The complete set of chaetae, present in most species, includes limbate chaetae (Fig. 7.12.4.6A) and pectinate chaetae (Fig. 7.12.4.6B–H) in the supra-acicular bundle, aciculae, compound chaetae (Fig. 7.12.4.6I–M) in the subacicular bundle, and a subacicular hook ventral to all other chaetae. Pseudocompound spiniger chaetae (spinigers) (Fig. 7.12.4.6N), when present, are restricted to *Euniphysa* species. Pseudocompound falciger chaetae (falcigers) have been reported for two *Leodice* species described from Peru (*Leodice afuerensis* (Hartman, 1944) and *Leodice pelamidis* (Quatrefages, 1866)). Pectinate chaetae and subacicular hooks are absent in *Palola*. Compound chaetae are absent in some *Marphysa* species, in *Aciculomarphysa*, which also lacks pectinate chaetae, and in *Fauchaldius*, which lacks all chaetae, except subacicular hooks. The distribution of chaetae in most anterior parapodia in preacicular (anterior) and postacicular (posterior) fascicles is a unique feature present in one species of *Euniphysa* (*E. aculeata* Wesenberg-Lund, 1949) (Fig. 7.12.4.6N) (Lu and Fauchald 2000). The term acicular chaetae has been used to refer to subacicular hooks (Kott 1951), or, in some cases, the authors were not able to distinguish aciculae and subacicular hooks (Hartmann-Schröder and Zibrowius 1998).

The characteristics of chaetae are considered species diagnostic features, but the number and shape of chaetae may vary along the body. Limbate, pectinate, and compound chaetae have been described as serrated under light microscopy. Under SEM, it becomes clear that serrations are chaetal peripheral spinules that terminate at different heights (Fig. 7.12.4.6G, I, J). The density of spinules may vary along the body and among species.

Limbate chaetae do not always have flattened margins as the name suggests. They vary from thin capillary-like chaetae (Fig. 7.12.4.6A) to chaetae with asymmetrical broader margin tapering distally. They are usually the

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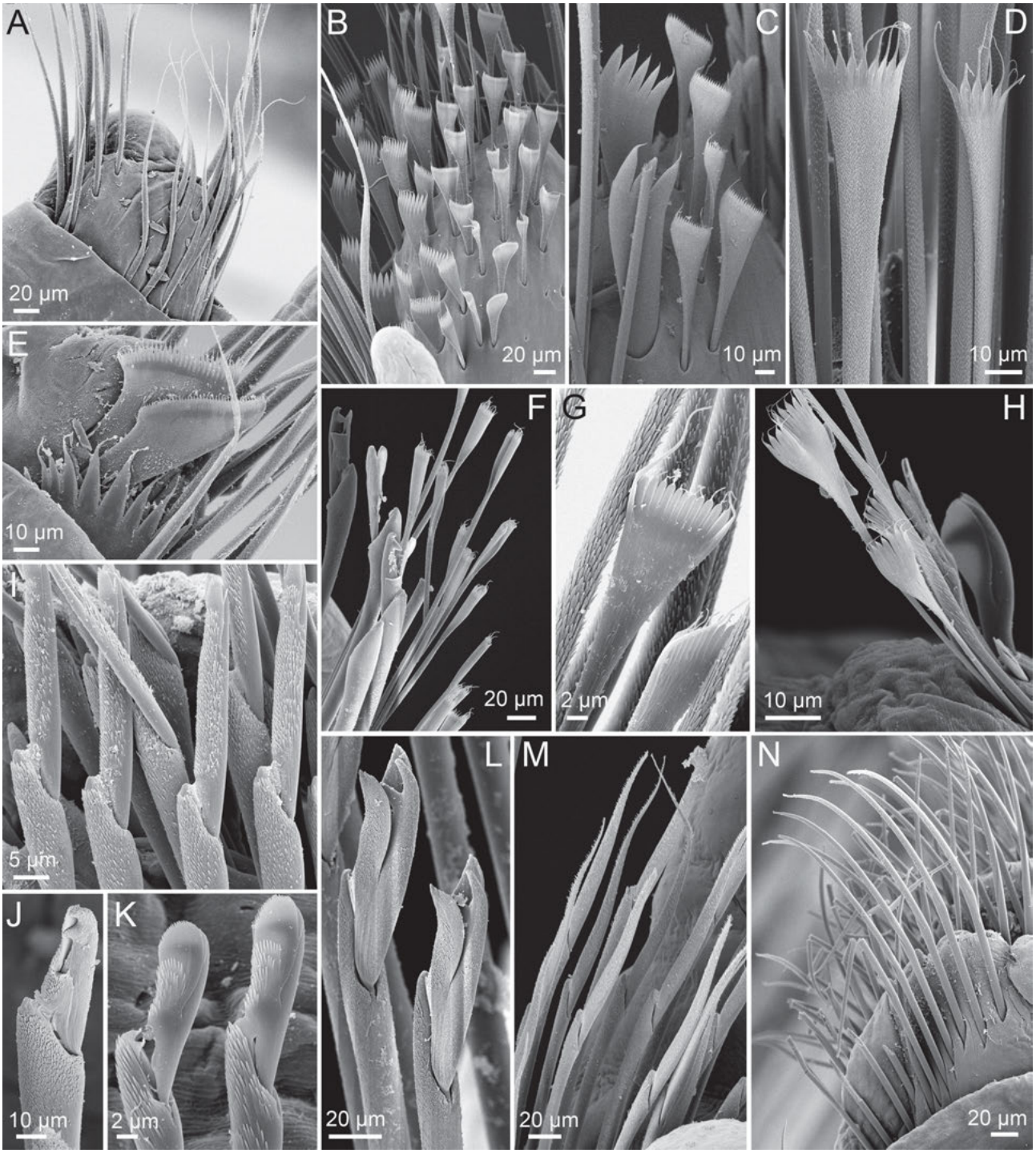


Fig. 7.12.4.6: Morphology of neuropodial compound and pectinate chaetae. A, *Marphysa mossambica*, limbate chaetae; B, *Marphysa sanguinea*, thick and thin pectinate chaetae; C, *Marphysa* sp., thick with wide teeth and thin isodont pectinate chaetae; D, *Eunice violaceomaculata*, thin anodont pectinaeta chaetae; E, *M. mossambica*, thick pectinate chaetae with narrow and wide teeth; F. *Eunice denticulata*, curved thin pectinate chaetae; G, *Marphysa fallax*, thin heterodont pectinate chaetae; H, *Lysidice unicornis*, thin anodont pectinate chaetae; I, *M. fallax,* compound falcigers; J, *Leodice antennata*, compound bidentate falciger; K, *L. unicornis*, compound falcigers covered with guards; L, *E. violaceomaculata*, compound bidentate falcigers; M, *M. sanguinea*, compound spinigers; N, *Euniphysa aciculata*, pseudocompound spinigers.

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longest chaetae, tapering toward the distal end and may have serrations along one margin. The number of limbate chaetae per parapodium decreases toward the posterior end. *Marphysa* species lacking compound chaetae have limbate chaetae also in subacicular bundles. These chaetae have been named capillaries in some studies (e.g., Bobin 1944). The name limbate is retained here because it is the most commonly used term in the current literature (Fauchald 1992a).

Pectinate chaetae are placed anterior or dorsal in relation to the limbate chaetae, and they are usually shorter than the latter (Fig. 7.12.4.6B–H). They are typically present along the whole body but are more numerous in median and posterior chaetigers. In some species, pectinate chaetae are absent or inconspicuous in most anterior chaetigers. The blade of pectinate chaetae has distal teeth, giving a comb-like appearance, and tapers to a shaft at the proximal end. Blades are symmetric or asymmetric (*sensu* Steiner and Amaral 2000, asymmetric referrred to as oblique by Zanol et al. 2016), narrow or wide (*sensu* Molina-Acevedo and Carrera-Parra 2015), flat, slightly, or strongly curved, and have fine or coarse teeth. All teeth may be of equal length (anodont *sensu* Carrera-Parra and Salazar-Vallejo 1998) (Fig. 7.12.4.6D, E, H), both, or just one of the outer teeth may be longer than inner teeth (isodont and heterodont *sensu* Carrera-Parra and Salazar-Vallejo 1998, respectively) (Fig. 7.12.4.6B, C, G). Teeth may taper evenly or abruptly. Outer teeth may be as wide as or wider than inner teeth. In some pectinate chaetae of *Marphysa* and *Paucibranchia* species, inner teeth have the same height at distal end but increasingly deeper proximal ends from margins to center; the longest inner teeth, those with deepest proximal end, are off center (spatula-shaped pectinate chaetae *sensu* Zanol et al. 2007). In most species, pectinate chaetae shafts are thinner than limbate chaetae (narrow pectinate *sensu* Zanol et al. 2014 and thin pectinate *sensu* Zanol et al. 2016) (Fig. 7.12.4.6B–D, F–H). Some *Marphysa* species have a second kind of pectinate chaetae with shaft as thick as or thicker than limbate chaetae, which is not present in most anterior chaetigers (wide pectinate *sensu* Zanol et al. 2014 and thick pectinate *sensu* Zanol et al. 2016) (Fig. 7.12.4.6B, C, E). As "narrow and wide" have also been used to describe the blade width, the use of the terms "thin and thick" pectinate chaetae (*sensu* Zanol et al. 2016) describing the thickness of the shaft in relation to limbate chaetae of the same parapodium is preferred. Thin and thick pectinate chaetae have been hypothesized as different evolutionary lineages of pectinate chaetae due to the similarities in distribution along the body within each lineage (Zanol et al. 2014). Thin pectinates are usually present from most anterior to median or posterior chaetigers. Thick pectinate chaetae are usually present from median to posterior chaetigers. Both thin and thick pectinates may be present at some chaetigers. More than one kind of thin and thick pectinate chaetae may be present. Fan-shaped chaetae (*sensu* Fauchald 1987) is a kind of thick pectinate chaetae.

Compound and pseudocompound chaetae may be present along the whole body. They are both composed of an appendage and a shaft and differ in the articulation between those parts. In compound chaetae, appendage (article *sensu* Zanol et al. 2014 and blade *sensu* Glasby and Hutchings 2010, Molina-Acevedo and Carrera-Parra 2015) and shaft are articulated, both edges of the proximal end of the appendage are connected to the shaft by ligament and the longest edge fits into a socket in the shaft (Fig. 7.12.4.6I–M). Pseudocompound chaetae lack articulation between appendage and shaft, and the fracture between these parts runs only halfway through the chaetae (Fig. 7.12.4.6N). Appendages may taper to fine tip at the distal end (compound spinigers) (Fig. 7.12.4.6M) or have two to three teeth (compound falcigers) (Fig. 7.12.4.6J–L). Tridentate compound falcigers are present only in some *Leodice* species, usually at the posteriormost body region. Teeth may be inconspicuous (Zanol et al. 2014). The length of the appendages as well as relative length and shape of teeth may vary along the body and among species. Convex sheets on both sides of appendages of compound falcigers are named guards (hoods *sensu* Fauchald 1970) (Fig. 7.12.4.6J–L). The name "guard" has been preferred because the sheets are not distally fused as in hoods. Guards may be distally round or tapering and bear mucro. Shafts may be distally narrow or expanded. A third type of compound chaetae, spinifalciger, has a long appendage with an attached bidentate distal appendage, which lacks double guards (*sensu* Molina-Acevedo and Carrera-Parra 2017). These chaetae are present in low numbers, restricted to anterior chaetigers and exclusive to *Treadwellphysa*.

Despite being described as subacicular, compound chaetae may not be placed completely ventral in relation to aciculae (Zanol et al. 2014): (1) compound chaetae of the most anterior row may be as dorsal as aciculae, (2) compound chaetae may be on both dorsal and ventral sides of aciculae, and (3) compound chaetae may be in rows anterior and posterior to aciculae. Most species of the family representing all genera have only compound falcigers. Some *Eunice*, *Euniphysa*, *Marphysa*, *Paucibranchia*, and *Treadwellphysa* species have both compound falcigers and spinigers. Some *Marphysa* and *Euniphysa* species have only compound spinigers. Usually, when both compound falcigers and spinigers are present, spinigers are mainly present in anterior chaetigers and falcigers appear

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later along the body, and at least few transitional chaetigers usually bear both types of chaetae or both may continue present until the end of the body.

Neuroaciculae always support neuropodia and vary in number, shape of distal end, and color. Anterior parapodia usually have more numerous neuroaciculae, which decrease in number posteriorly. Single neuroacicula may be placed in the center or off-center of the chaetal lobe. Numerous neuroaciculae are usually distributed in the chaetal lobe in a dorsal to ventral direction. However, at least in some *Marphysa* species, they are distributed in an oblique row, and the anteriormost neuroaciculae are also dorsalmost in each chaetal lobe. Neuroaciculae are usually the largest chaetae in the parapodium. They may have different shape and color along the body or even in the same parapodium. Neuroaciculae taper from the proximal to the distal end, which is straight or bent. The shape of the distal end varies as blunt-tipped, conical, irregularly knobbed, hammer-headed, bidentate, or mucronate. Color may be translucent, yellow (light), amber, brown, and black (dark). In brown and black aciculae, core and sheaths may be distinct, with core being darker than sheaths and the latter may even be clear. The color of aciculae varies along the body without a clear pattern or following different patterns in different species and even genera. The recorded patterns of color variation are as follows: (1) anteriormost aciculae lightest with the same color shade as more posterior ones (exclusive to some *Leodice* species with dark aciculae), (2) anteriormost aciculae lightest with color shade considerably different from more posterior ones, (3) posteriormost aciculae lightest with the same color shade as more anterior ones, (4) posteriormost aciculae lightest with color shade considerably different from more anterior ones, (5) anteriormost and posteriormost aciculae lightest with the same color shade as median ones, (6) anteriormost and posteriormost aciculae lightest with color shade considerably different from median ones, and (7) anteriormost aciculae darkest.

Subacicular hooks are the most ventral and anterior chaetae in the chaetal lobe, except in *Palola*, which lacks this type of chaetae. They are inserted at an angle, not parallel to aciculae (Fauchald 1992a, Zanol et al. 2007). They are usually as large as aciculae, but in large specimens they become disproportionally smaller, sometimes as thin as compound chaetae (Fauchald 1992a, Zanol and Bettoso 2006). In all species, subacicular hooks are not present in at least the first 10 chaetigers, except in *Fauchaldius* in which subacicular hook are first present in the second chaetiger. The chaetiger subacicular hook first appears is a taxonomic feature, but it varies, usually within a range of 10 to 20 chaetigers, with the size of the specimen (e.g., Parapar et al. 1993, Lu and Fauchald 2000). In larger specimens, subacicular hooks tend to have a later start. In most species, subacicular hooks are present in all chaetigers after first appearance. However, in large specimens, they may be missing in several chaetigers (Fauchald 1992a). In general, just one subacicular hook is present per parapodium, but some species may have several. The number may vary along the body. In species with just one subacicular hook per parapodium, a second, usually a replacement hook, is eventually present in some parapodia.

The main variable features of subacicular hooks are the shape of the distal end and the color. The distal end may lack teeth (referred to as falcate, unidentate, simple, or spine-like), have two (bidentate) or three (tridentate) teeth (Fig. 7.12.4.7A–E). Falcate and bidentate subacicular hooks may be present in the same specimen. Sometimes, subacicular hooks described as falcate have two inconspicuous teeth, which become clear under SEM (e.g., Zanol et al. 2014). At least in some cases, falcate subacicular hooks appear to be worn-down bidentate subacicular hooks. The shape and relative position of proximal and distal teeth have interspecific variation but, in some cases, also along the body and intraspecific (Zanol et al. 2017). Teeth of tridentate subacicular hooks are most commonly arranged in crest, but few species have it in tandem. Bidentate subacicular hooks are the most widespread form being present in all genera. Falcate subacicular hooks have been described in species of *Eunice* and *Marphysa*. Tridentate crested subacicular hooks are restricted to species of *Leodice*. Tridentate tandem subacicular hooks have been described for *Eunice* and *Leodice* species. A pair of guards is present on each side of the distal end covering the proximal tooth or all teeth (Fig. 7.12.4.7A–D). Often, it cannot be observed because it is broken. Guards in the majority of Eunicidae are sheet-like structures, but in *Fauchaldius* they are disassociated fibrils (Fig. 7.12.4.12C) similar to beard of Arenicolidae larval uncini in Hausen (2005).

Colors recorded for subacicular hooks are translucent, yellow, amber, brown, dark brown, or black (Fig. 7.12.4.7F, G). Traditionally, these have been referred to as shades of light or dark subacicular hooks. Color varies along the body; usually, the darkest color is the one described. In some species, the variation is slight, and no clear pattern is present, this is mostly common in light-colored subacicular hooks. In other species, posteriormost subacicular hooks are the lightest and may have (1) the same color shade as more anterior hooks and (2) a different color shade from more anterior hooks. The core and sheaths of subacicular hooks may be distinct. This is most commonly observed in dark hooks, which may even have a black core and a clear sheath. In dark hooks, the darkest shade may have different patterns along the hook, it may be (1) near distal end, (2) on

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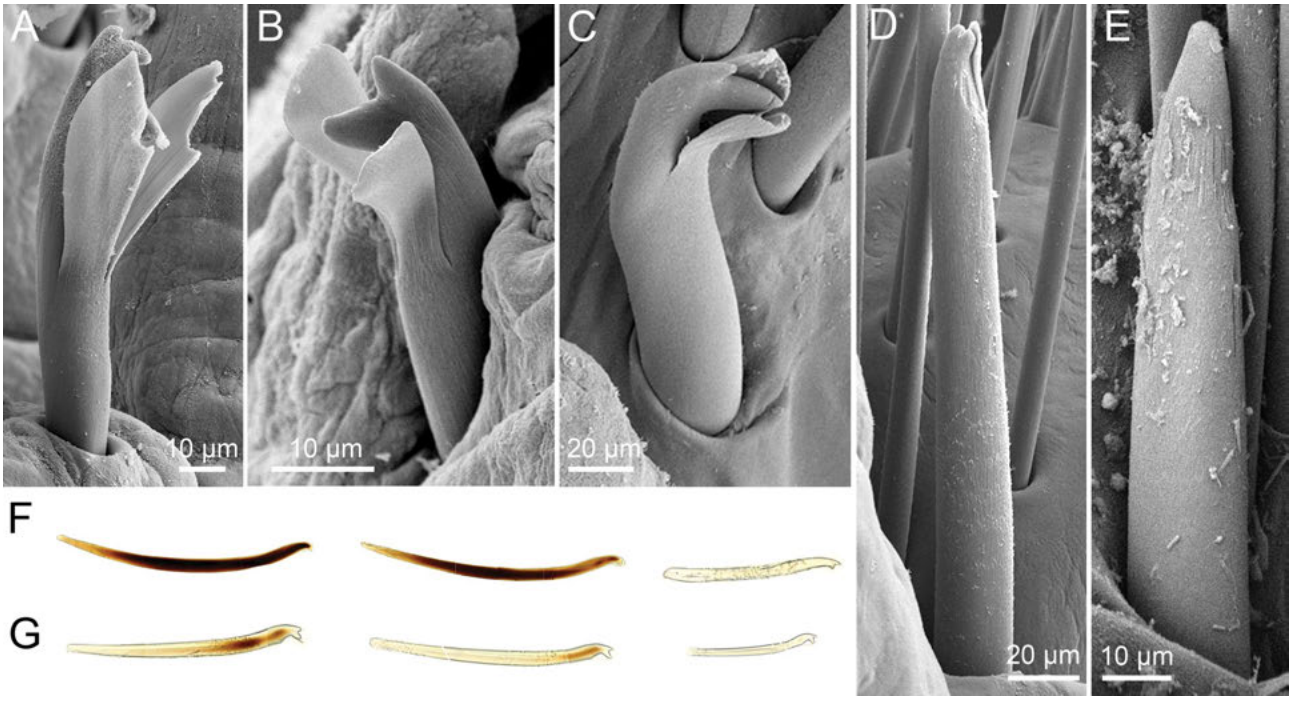


Fig. 7.12.4.7: Morphology and coloration of subacicular hooks in Eunicidae. A–E, SEM micrographs. A, *Leodice antennata*, tridentate hook; B, *Marphysa fallax*, bidentate hook; C, *Eunice violaceomaculata*, bidentate hook; D, *Marphysa sanguinea*, bidentate hook; E, *Marphysa* sp., simple falcate hook; F, G, Pattern of dark color on subacicular hooks, columns correspond to different regions along the body; F, *Eunice norvegica,* darkest color present on most of the length of the hook, but color more concentrated toward proximal end; G, *Nicidion cariboea*, darkest color present near the distal end of the hook; A, F, G, Modified from Zanol et al. (2014).

most of the length of hook but more concentrated toward proximal end, and (3) on the distal half. The darkest color on the distal half or near-distal end of subacicular hooks along most of its distribution appears to be an exclusive feature of *Nicidion* species (Zanol et al. 2014).

The color and shape of subacicular hooks have been used to subdivide the genus *Eunice* in taxonomically informal groups of species bearing certain subacicular hooks (Ehlers 1868, Hartman 1944, Fauchald 1970): (A) group flavus-bidentate has light bidentate subacicular hooks, (B) group fuscus-bidentate has dark bidentate subacicular hooks, (C) group flavus-tridentate has light tridentate subacicular hooks, and (D) group fuscus-unidentate has light falcate subacicular hooks. These groups are paraphyletic and do not hold with reinstatement of *Leodice* and *Nicidion* (Zanol et al. 2014). *Eunice*, as currently accepted, includes only species of groups B and D. *Leodice* has species of groups A to C. *Nicidion* has species of group B only.

Pygidium

The pygidium bears the anus and one or two pairs of pygidial cirri (anal cirri) (e.g., Hartman 1944) (Fig. 7.12.4.8). Pygidial cirri connect directly to the pygidium or to a ventral expansion of the pygidium (ventral shield *sensu* Zanol et al. 2014). Their shape is tapering, digitiform, or club-shaped (clavate). They are smooth, irregularly or regularly articulated. In species with two pairs of pygidial cirri, the pairs are placed in a dorsal to ventral position. The dorsal pair is usually the longest. Many descriptions are based on incomplete specimens and thus lack information on the pygidium morphology.

Chromosomes

The karyotype has only been described for one species of *Marphysa* from Japan. The diploid number is 32. All chromosome are similar and acrocentric (Hayashi et al. 1996).

Biology and ecology

Distribution and habitat

Eunicids inhabit diverse marine and estuarine habitats worldwide from intertidal to deep-sea bottoms. Most species are exclusively marine, but certain species of

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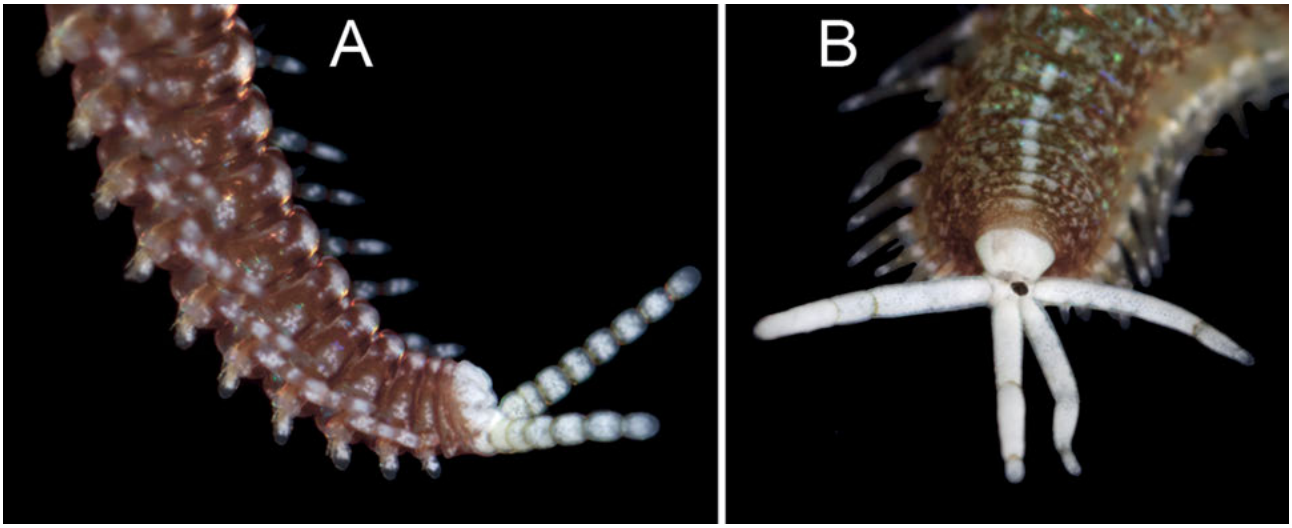


Fig. 7.12.4.8: Morphology of eunicid pygidia, live photographs. A, With two pygidial cirri; B, With four pygidial cirri. © A. Semenov.

Marphysa may also be found in brackish water, being able to withstand great salinity variation (e.g., Garcês and Pereira 2011). Shallow tropical and subtropical habitats bear the highest diversity of eunicid species. Genera *Eunice*, *Leodice*, *Marphysa*, and *Nicidion* and even some species such as *Leodice websteri* Fauchald, 1969 inhabit both shallow and deep waters (Treadwell 1921, Hartmann-Schröder 1998, Hartmann-Schröder and Zibrowius 1998, Molodtsova and Budaeva 2007). Only *Aciculomarphysa* and *Fauchaldius*, which have not been reported since their original descriptions, appear to be exclusive deep-water genera.

Worldwide distribution has been suggested for some species such as *Eunice aphroditois*, *Leodice antennata* Lamarck, 1818, *Lysidice ninetta* Audouin & Milne Edwards, 1833a, *Marphysa sanguinea* (Montagu, 1813), *Nicidion cariboea* (Grube, 1856), and *Palola viridis* Gray in Stair, 1847. However, those species subjected to more detailed studies turned out to be the sets of cryptic species with narrower distribution (e.g., *L. ninetta* in Iannotta et al. 2009, *M. sanguinea* in Hutchings and Karageorgopoulos 2003, Zanol et al. 2016, Hutchings and Kupriyanova 2017, and *P. viridis* in Schulze 2006, Schulze and Timm 2011).

Most genera and some species are present in both soft and hard bottoms (e.g., *Leodice antennata* in Kurt-Şahin and Çinar 2009). The exception among genera is *Euniphysa*, which is restricted to soft bottoms (Lu and Fauchald 2000). *Eunice*, *Leodice*, *Lysidice*, *Nicidion*, and *Palola* are most diverse in hard bottoms, especially dead hard corals, limestones, and calcareous algae in which they burrow or live in their crevices. These genera as well as *Marphysa* may also be present in rocky bottoms or associated with other biogenic habitats such as sponges, seagrasses, cnidarians, vermetid colonies, and kelp holdfasts (Treadwell 1921, Hartman 1938, Gambi 2002, Molodtsova and Budaeva 2007). Association with a specific biogenic habitat does not seem to happen in most species. However, there may be some exceptions, such as (1) *Lysidice thalassicola* Carrera-Parra, Fauchald & Gambi, 2011 associated with seagrass *Thalassia testudinum* and (2) *F. cyrtauloni* Carrera-Parra & Salazar-Vallejo, 1998 associated with hexactinellid sponge *Cyrtaulon sigsbeii*. Eunicid species may also be members of plastic-associated and driftwood rafting communities (Thiel and Gutow 2005, Goldstein et al. 2014).

Species crawl on the bottom, build burrows or tubes, and are commonly gregarious. Burrow shape and individual placement within it are variable. Whereas some species keep their head close to the tube opening, others, such as some soft substrate-burrowing *Marphysa* species, appear to keep their head down (Treadwell 1921, Pillai 1958, Day 1967, Zanol et al. 2016). *Lysidice* and *Palola* species inhabiting hard substrates are probably able to burrow using their jaws (Crossland 1904, McIntosh 1910). However, Hauenschild et al. (1968) suggested that the branching burrows used by the *Palola* in Samoa were constructed by sipunculans, an opinion not shared by Caspers (1984). Some species of *Lysidice* and *Marphysa* burrow in seagrass sheaths (remains of leaf bases at the rhizome) of *Posidonia oceanica* and *T. testudinum*, which they also feed on (Gambi et al. 2003). The burrows of some *Palola* may be lined with parchment-like material and branching (Crossland 1904), whereas mucous lines the burrows of some large *Eunice* (see Lachat and Haag-Wackernagel 2016). Burrows of *Marphysa borradailei* Pillai, 1958 are branched and connected to those of different specimens.

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They are recognized from the outside by the piles of feces close to the opening (Pillai 1958).

Tubes are known for *Eunice* and *Leodice* species only. They are most commonly built of parchment-like material stiff or malleable, simple or branching. Tubes may also be fragile and made by sand, stone, and shells kept together by a thin delicate organic matrix under rocks (e.g., *Leodice rubrivittata* Treadwell, 1921 and *Leodice unifrons* Verrill, 1900). Malleable parchment-like tubes are found under rocks (Pettibone 1963), within sponges and corals (Treadwell 1921). Stiff parchment-like tubes attach to rocks, shells, and also soft substrate. They may be covered by biodetrital material and restricted to the structures they are attached to (e.g., *Lysidice pennata*) (Winsnes 1989). However, they commonly extend above the substrate and have a zigzag appearance, similar to those described as *Tibiana* (see Taxonomy section for further discussion). These tubes are usually covered by epibionts such as algae, bivalves, ascidians, bryozoans, cnidarians, and sponges, which may shelter other errant species (Day 1967, Clavier 1990). In species such as *Leodice metatropos* (Hanley, 1986) and *Eunice cultrifera* Zanol, Hutchings & Fauchald, 2020 from Jervis Bay (Australia), stiff tubes of different specimens entwine at the base and diverge distally, giving a gorgonian or tree-like appearance to the structure, which can be as tall as 3.6 m (Hanley 1986, Jacoby et al. 1995). Individuals of these species appear to exhibit cooperative tube-building behavior to construct such large structures. Groupings of tubes of several individuals have also been reported for *Eunice tubifex* Crossland, 1904 (as *Euniphysa tubifex* in Clavier 1990), but these were less common than isolated tubes (Clavier 1990). In New Caledonia, *E. tubifex* tubes attach to soft substrate by a J-shaped end (Clavier 1990).

Sponge-associated species usually inhabit the channels of sponges (Neves and Omena 2003), but some are found in the sediment accumulated within vase sponges (Prentiss and Harris 2011). Association is not size restricted, and the length of species found in sponges ranges from millimeters (e.g., *Fauchaldius*) to 60 cm (personal observation).

Eunicid species are associated with at least 17 species of cnidarians [scleractinian corals, black corals (anthipatharias), zoantharias (*Epizoanthus* spp.), and stylasterids hydrozoans] (Kise and Reimer 2016, Molodtsova et al. 2016). Species associated with scleractinian corals are traditionally associated with bioerosion due to borrowing activity (Hutchings 1986). However, some species also play a role in assembling coral reefs (Chisholm and Kelley 2001, Roberts 2005). Specimens of eunicids are able to move and aggregate coral fragments, improving reef growth condition, rate, and strength. Also, cnidarian species such as *Desmophyllum pertusum* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758 calcify over previously built eunicid tubes, which are probably significant in determining reef framework (Roberts 2005). Specimens of *Eunice norvegica* living within tube overgrown by coral *D. pertusum* have great importance in ecosystem functioning. The interaction between both species has been classified as symbiosis because it improves feeding efficiency and thus the growth of the eunicid and calcification of the coral, facilitating growth and strengthening of the reef (Mueller et al. 2013). The eunicids steal food from the coral but also clean polyps and protect them through territorial behavior (Mortensen 2001). Black corals (anthipatharias) also overgrow eunicid tubes, giving protection and food to the worm. However, in this relationship, corals appear not to benefit because the colonies with eunicid tubes do not look healthy, bearing naked spinules and eroded spines (Molodtsova and Budaeva 2007). Some *Epizoanthus* spp. are obligatory epibionts of eunicid tubes containing live worms (Kise and Reimer 2016). They grow on simple and branching zigzag eunicid tubes coming out of the substrate, making it easier to mistake the tubes with cnidarians.

Feeding biology

Information on feeding biology of the family is based on the knowledge from few species restricted to genera *Eunice*, *Lysidice*, and *Marphysa*. Eunicids are generally classified as omnivorous and include macrophagous and microphagous (surface and subsurface deposit-feeders) species (Jumars et al. 2015). However, some macrophagous species appear to have more restricted diets. *Leodice pennata* is carnivorous based on gut content (Winsnes 1989). Measures of stable nitrogen isotopes have classified *Lysidice ninetta*, *Paucibranchia bellii* (Audouin & Milne Edwards, 1833), and *Marphysa* cf. *sanguinea* also as carnivores (Jumars et al. 2015). *Marphysa formosa* Steiner & Amaral, 2000 fed exclusively on algae and rejected invertebrates in laboratory experiments (Pardo and Amaral 2006).

Carnivorous and omnivorous species consume a variety of invertebrate and vertebrate species. *Eunice* cf. *aphroditois* is a sit-wait predator of fish, octopus, and other invertebrates. It waits for the prey with jaws open and prostomial appendages radially arranged at the tube opening. These structures are burrowed during the day and protruded at night (Lachat and Haag-Wackernagel 2016). Once the prey comes close to the tube opening, they snatch the prey and bring it back to the tube. Many species of macrophagous and microphagous surface deposit-feeders also come partially out of their tubes to feed (Winsnes 1989). Prostomial appendages are the main sensory structure in localizing food, but at night eyes appear to be important as well (Winsnes 1989, Lachat and Haag-Wackernagel 2016). In the

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case of *Eunice* cf. *aphroditois*, prostomial appendages may also lure the prey with worm-like movements (Lachat and Haag-Wackernagel 2016). Cannibalism has been observed in juveniles and adults of different species kept in laboratory cultures (Lewis and Karageorgopoulos 2008, Garcês and Pereira 2011).

Herbivorous diet includes the consumption of encrusting algae, macroalgae, and seagrasses (Jumars et al. 2015). The consumers of the latter are the species of *Lysidice* and *Marphysa* that bore in seagrass sheaths. These species appear to have an important ecological role, making seagrass organic matter available to other organisms and facilitating microbial colonization (Gambi 2002). Enzymatic cellulase activity has been reported in the gut of these boring *Lysidice* species as well as in *Eunice* cf. *aphroditois* (Yokoe and Yasumasu 1964, Cigliano et al. 2003).

Reproduction and development

Information on reproduction and development is known for about 20 species of the genera *Eunice*, *Leodice*, *Lysidice*, *Marphysa*, and *Palola*. All studied species are iteroparous and gonochoric, and sexual dimorphism is unknown. Gametes are usually distributed along most of the body, starting at chaetigers posterior to the initial 20 to 60 chaetigers and missing in posteriormost chaetigers. Ripe individuals can be sexed based on the shape and color of the gametes, which are visible through the body wall.

Ripe females are usually yellow, green, or purple due to the color of gametes. Mature oocytes vary in diameter from 100 to 300 µm. Oogenesis is extraovarian, gonads are attached to the posterior septum of the chaetiger, but previtellogenic oocytes move to the coelom where they undergo vitellogenesis (e.g., *M.* cf. *sanguinea* in Prevedelli et al. 2007, El Barhoumi et al. 2013). Ripe males usually have beige and pinkish gametes. Sperm are usually round ect-aquasperm (Gambi and Cigliano 2006, Lewis and Karageorgopoulos 2008, Carrera-Parra et al. 2011), but elongated sperm are also present (e.g., *Marphysa elityeni* Lewis & Karageorgopoulos, 2008). Male gonads are in similar position to those of females and release immature gametes (clusters of primary spermatocytes) into the coelomic cavity (e.g., *Marphysa* cf. *sanguinea* in Prevedelli et al. 2007, El Barhoumi et al. 2013). In studied species, spawning periodicity is highly variable, but generally not all mature gametes are released and specimens with mature oocytes can be found year-round. The release of gametes happens through nephridiopores; however, light and physical stimuli can lead to harsh swimming and breaking of the cuticle as in *Eunice fucata* (Mayer 1902).

Free spawning in the water column followed by planktonic larval development is the most common mode reported for the family. Epitoky has been described for several species of *Eunice*, *Leodice*, *Lysidice*, and *Palola* in different oceans, Caribbean Sea, East Atlantic Ocean, Mediterranean Sea, and Pacific Ocean (Horst 1902, Mayer 1902, Herpin 1925, Gravier and Dantan 1928, Allen 1957, Richards 1967, Schulze and Timm 2011, Pamungkas 2015). In *Palola* and at least in *Eunice fucata*, the epitoke form is the ripe posterior end, which breaks off from the benthic anterior end and swims to the water column. Atoke anterior ends remain in the benthos and regenerate posterior ends. The main external modification described for *Palola* epitokes is the development of ventral eyespot in chaetigers (Hauenschild et al. 1968). In some *Eunice* spp. and *Lysidice* spp., the epitoke form is the complete specimen (Horst 1902, Gambi and Cigliano 2006, Carrera-Parra et al. 2011, Pamungkas 2015). *Lysidice* spp. epitokes have prostomial eyes several times larger than those of the atoke form. Epitokes usually swarm near the surface of water column synchronously at night in one or few dates along the year. Stimuli triggering the swarming are not clear, they may be connected to lunar and tidal cycles or to the spawning of other organisms, such as corals (Caspers 1984, Schulze and Timm 2011). Swarms may contain more than one species (e.g., Martens et al. 1995, Pamungkas 2015).

In estuarine *Marphysa* species, spawning can happen inside the burrows, where initial development also takes place until the trochophore stage (Prevedelli et al. 2007) or can be followed by the formation of gelatinous egg masses attached to the burrows where embryos develop until late metatrochophore or early nectochaetae stage (Southern 1921, Aiyar 1931, Pillai 1958, Pettibone 1963, Malathi et al. 2011). The gelatinous egg masses appear to be formed during the night containing fertilized eggs. Egg masses appear to confer antimicrobial, osmotic, and thermal protection to developing individuals and to prevent them from dispersing (Aiyar 1931, Malathi et al. 2011, 2017). It has been suggested that they could also be a source of nutrients, but *Marphysa* larvae do not feed while in the egg mass (Malathi et al. 2011).

There is no unambiguous record of feeding eunicid larvae (Rouse 2000). All studied eunicid larvae are lecitotrophic. Also, no mature oocyte smaller than 100 µm in diameter has been recorded, indicating that lecitotrophy is widespread in the family. The first larval stage (trochophore) has a pair of eyes, a ciliary band covering the entire presegmental region, a telotroch, and, in some species, an apical tuft. The following stage (metatrochophore *sensu* Aiyar 1931, Pillai 1958) has chaetae and ciliary bands in at least two patterns: (1) apical tuft,

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presegmental ciliary band, and telotroch (Aiyar 1931, Pillai 1958, Prevedelli et al. 2007) and (2) akrotroch, prototroch, metatroch, neurotroch, and telotroch (Åkesson 1967, Rouse 1999). In *Leodice valens* Camberlin, 1919 (as *Eunice kobiensis* McIntosh, 1885 in Åkesson 1967), larvae settle at this stage, secrete tubes, and already exhibit gregarious tendency as observed in adults of this species. In *Marphysa* species, settlement happens at the following stage (nectochaeta), which lacks ciliary bands and bears chaetae, a pair of pygidial cirri, and rudimentary jaws. Late metatrochophores leaving egg mass swim for 6 to 12 hours, settle close to egg masses as nectochaetae, form aggregations, and secrete a stick mucous mat (Pillai 1958). Early nectochaetae, when free from the egg mass, sink settling close to parental individuals (Aiyar 1931, Malathi et al. 2011). Larval settlement age varies from about 10 days [*Leodice harassii* (Audouin & Milne Edwards, 1833a) (see Herpin 1925), *Marphysa gravelyi* Southern, 1921 (see Malathi et al. 2011), and *Marphysa* cf. *sanguinea* (see Prevedelli et al. 2007)] to 20 days in *L. valens* (see Åkesson 1967).

Development timing and order of events vary among species. However, it is usually synchronous in the same cohort. Also in all species, the median antenna is always the first anterior appendage to develop followed by the lateral antennae, palps, and peristomial cirri (Herpin 1925, Pillai 1958, Åkesson 1967, Giangrande 1989). The maxillae are shed and replaced along the development, but the mandibles have continuous growth (Herpin 1925, Giangrande 1989, Cassai and Prevedelli 1998). Thus, the number of growth lines in the mandibles appears to be a good estimator of the age in *Lysidice harassii*, but the same is not true for *Marphysa* cf. *sanguinea*, which has no linear growth (Giangrande 1989, Cassai and Prevedelli 1998). Even in species with linear growth, the use of mandible as an age estimator may be challenging due to the difficulty in counting lines and interferences resulting from breakage, wear-off, and metabolism (Giangrande 1989).

Autotomy is common, and several eunicid species regenerate anterior and posterior sections of the body (Fauvel 1923, Bely 2006). In *Lysidice pennata*, posterior regeneration may start from as early as chaetiger 30 (Winsnes 1989). *Palola viridis* and *Eunice fucata* regenerate their reproductive posterior region after losing it during the reproductive period (Mayer 1902, Hofmann 1969). Populations of *Nicidion insularis* (Nogueira et al., 2001) have high rates of anterior and posterior regeneration (personal observation). To the best of our knowledge, asexual reproduction has not been reported for the family.

Bioluminescence

Bioluminescence is very poorly known in Eunicidae. It lights up as blue along both sides of the body when the individual suffers from physical disturbance. In *Eunice afra* Peters, 1854 from the Suez Channel, bioluminescence appears to come from the inflated bases of the ventral cirri, and the secreted mucous also lights up (Crossland in McIntosh 1910). *Eunice afra* from Maldives (Indian Ocean) and Nicobar Island (Andaman Sea), *Nicidion* spp. from Abrolhos Atoll (Southwest Atlantic Ocean) and Belize (Caribbean Sea), and *Palola siciliensis* (Grube, 1840) from unknown locality also exhibit bioluminescence (Crossland in McIntosh 1910, Tampi and Rangarajan 1964, personal observations).

Respiratory pigments

Extracellular hemoglobin (erythrocruorins *sensu* Weber 1978) is present at least in *Eunice* and *Marphysa*. Species from all genera have red blood; thus, such pigments are probably more widespread. The oxygen affinity of these pigments varies among species and appears to be connected to life mode, being higher in *Marphysa* cf. *sanguinea* living in a muddy environment than in *Eunice* cf. *aphroditois* (Bannister et al. 1976, Weber et al. 1978). Five putative noncirculating hemerythrin genes are expressed in *L. pennata* (Costa-Paiva et al. 2017). In *Marphysa* cf. *sanguinea*, a hemerythrin gene named *msHemerycin* has an antimicrobial function and might be an innate immune response of the species (Seo et al. 2016).

Commercial and cultural value

Different species, mostly intertidal, of *Eunice* and *Marphysa* are used as bait. *Eunice* species used as baits are large reaching more than 1 m in length. *Eunice sebastiani* Nonato, 1965, an endemic species from southeast Brazil, was collected by recreational fishermen until its population decrease led to its inclusion in the Brazilian Red List of Endangered Species (Amaral and Jablonski 2005). *Eunice roussaei* Quatrefages, 1866 is exploited as bait in the Adriatic Sea (as *E. aphroditois*) (see Gambi 1994, Bettoso et al. 1998). This is the only subtidal species used as bait caught by traps placed by the opening of the burrow (Bettoso et al. 1998).

Species of the genus *Marphysa*, most of them traditionally identified as *M. sanguinea*, are used as baits in the different parts of the world: Australia, China, France, India, Italy, Japan, Kenya, Korea, Malaysia, Portugal, South Africa, Spain, Tanzania, and Tunisia (Crossland 1903, Gambi 1994, Lewis and Karageorgopoulos 2008, Glasby and Hutchings 2010, Malathi et al. 2011, Garcês and Pereira 2011, El Barhoumi et al. 2013, Saito et al. 2014, Idris et al. 2014, Parandavar et al. 2015, Zanol et al. 2016, Kihia et al. 2017, Lavesque et al. 2017, Liu et al. 2017). In most places, recreational fishermen collect them by digging. They also may be used by professional fishermen and commercialized locally. In some places, such as China and

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France, species are commercially exploited and shipped live to other localities (Lavesque et al. 2017, Liu et al. 2017).

The trade of live worms imposes the risk of introducing nonindigenous species in the places where they are commercialized (Sá et al. 2017). The release of unused baits by fishermen resulted in a human-mediated introduction of a *Marphysa* species in Japan (Iwasaki et al. 2004 after Saito et al. 2014). The trade of "live rock" by the aquarium industry results in unwanted species introduction in tanks (Schulze 2011). Commonly reported cases are those of large eunicids (>1 m), which are voracious predators destroying the fauna in the tank and becoming a nuisance to the owners.

The digging to collect *Marphysa* may impact the targeted species as well as other organisms and may lead to overexploitation of the resource. Thus, studies have been undertaken to offer subsidies for resource management plans (Kihia et al. 2017) and for aquaculture of *Marphysa* species (e.g., Imai 1975, Garcês and Pereira 2011, Parandavar et al. 2015, Kim et al. 2017, Martin et al. 2020). However, a first challenge that has to be met for a sustainable exploitation and the establishment of such aquacultures is the correct identification of the species. Most studies are probably dealing with different species, although they identify the species as *M. sanguinea* (Zanol et al. 2016, Elgetany et al. 2018, Lavesque et al. 2019).

The cultural value of eunicids comes from the use of epitoke forms as food by locals in South Pacific Islands (e.g., Samoa, Tonga, and Fiji), Indonesia, and East Timor. At least in Ambon (Indonesia), epitoke swarming is composed of several species, including several *Eunice* spp. and *Lysidice oele* Horst, 1902, but it is dominated by *Palola* sp. (Martens et al. 1995, Pamungkas 2015). *Palola* epitokes are considered a delicacy. Locals are able to estimate the swarming dates, which happens once or twice a year between October and December in South Pacific Islands and February to April (at the highest tide of the year) in Indonesia and East Timor (Schulze 2006, Pamungkas 2015). On those dates, locals gather to collect the epitokes and prepare specialty dishes, which have a high nutritious value, as protein make up more than half of epitokes biomass content (Pamungkas 2015).

Phylogeny and taxonomy

Phylogeny

The monophyly of Eunicidae (*sensu* Hartman 1944) has been controversial in phylogenetic hypotheses based on morphological characters (Zanol et al. 2007) or just 18S rDNA data (Struck et al. 2006), which retrieved Onuphidae within Eunicidae. However, Eunicidae is supported as a monophyletic group with Onuphidae as its sister group in most recent hypotheses based on morphological and molecular data (cytochrome oxidase I, 16S rDNA, 18S rDNA, and 28S rDNA) (Fig. 7.12.4.9) (Struck et al. 2006, Zanol et al. 2010, 2014, Budaeva et al. 2016). The eunicid clade is supported by unique and nonhomoplasious synapomorphies, such as dorsal buccal lip fused to the dorsal side of the prostomium (Fig. 7.12.4.3G, H) and anterior extensions of the dorsolateral fold medially connected (Fig. 7.12.4.3I) (Zanol et al. 2014). Such features are included in the current diagnosis of the family, making it more precise and evolutionarily meaningful.

Traditionally, the identification of genera within the family has focused on the shape of the prostomium (bilobed, four-lobed, or completely round) (e.g., Kinberg 1865, Ehlers 1868, the mandibles (flat or curved) (e.g., Hartman 1944, Fauchald 1970) and the number of prostomial appendages (one, three, or five), the latter being considered as the main and unambiguous feature (e.g., Kinberg 1865, Ehlers 1868, Gravier 1900, Hartman 1944, Gathof 1984). Some authors (e.g., Kinberg 1865, Ehlers 1868) also have considered the presence or absence of branchiae as an informative feature for generic-level taxonomy. However, this may not be consistent even for species-level taxonomy (Nogueira et al. 2001).

Thirty extant genera and one extinct genus have been described for Eunicidae. Of those, only the extant genera *Aciculomarphysa* Hartmann-Schröder, 1998 in Hartmann-Schröder and Zibrowius 1998 (1 species), *Eunice* Cuvier, 1817 (240 species), *Euniphysa* Wesenberg-Lund, 1949 (11 species), *Fauchaldius* Carrera-Parra & Salazar-Vallejo, 1998 (2 species), *Leodice* Lamarck, 1818 (35 species), *Lysidice* Lamarck, 1818 (30 species), *Marphysa* Quatrefages, 1865 (74 species), *Nicidion* Kinberg, 1865 (14 species), *Palola* Gray in Stair, 1847 (14 species), *Paucibranchia* Molina-Acevedo, 2018 (19 species), and *Treadwellphysa* Molina-Acevedo & Carrera-Parra, 2017 (8 species) and the extinct genus *Esconites* Thompson & Johnson, 1977 (1 species) are considered valid.

Both *Aciculomarphysa* and *Fauchaldius* have been described for small specimens associated with antipatharian coral from the Southwest Pacific Ocean (460–490 m deep) and hexactinellid sponges from the Caribbean Sea (151 m deep), respectively. Their species are only known from the original descriptions. All other valid genera, with the exception of *Eunice*, *Paucibranchia*, and *Treadwellphysa*, are monophyletic groups (Lu and Fauchald 2000, Schulze 2006, Schulze and Timm 2011, Zanol et al. 2014). *Euniphysa* and *Palola* are monophyletic in their original definitions. The others have been emended to reconcile

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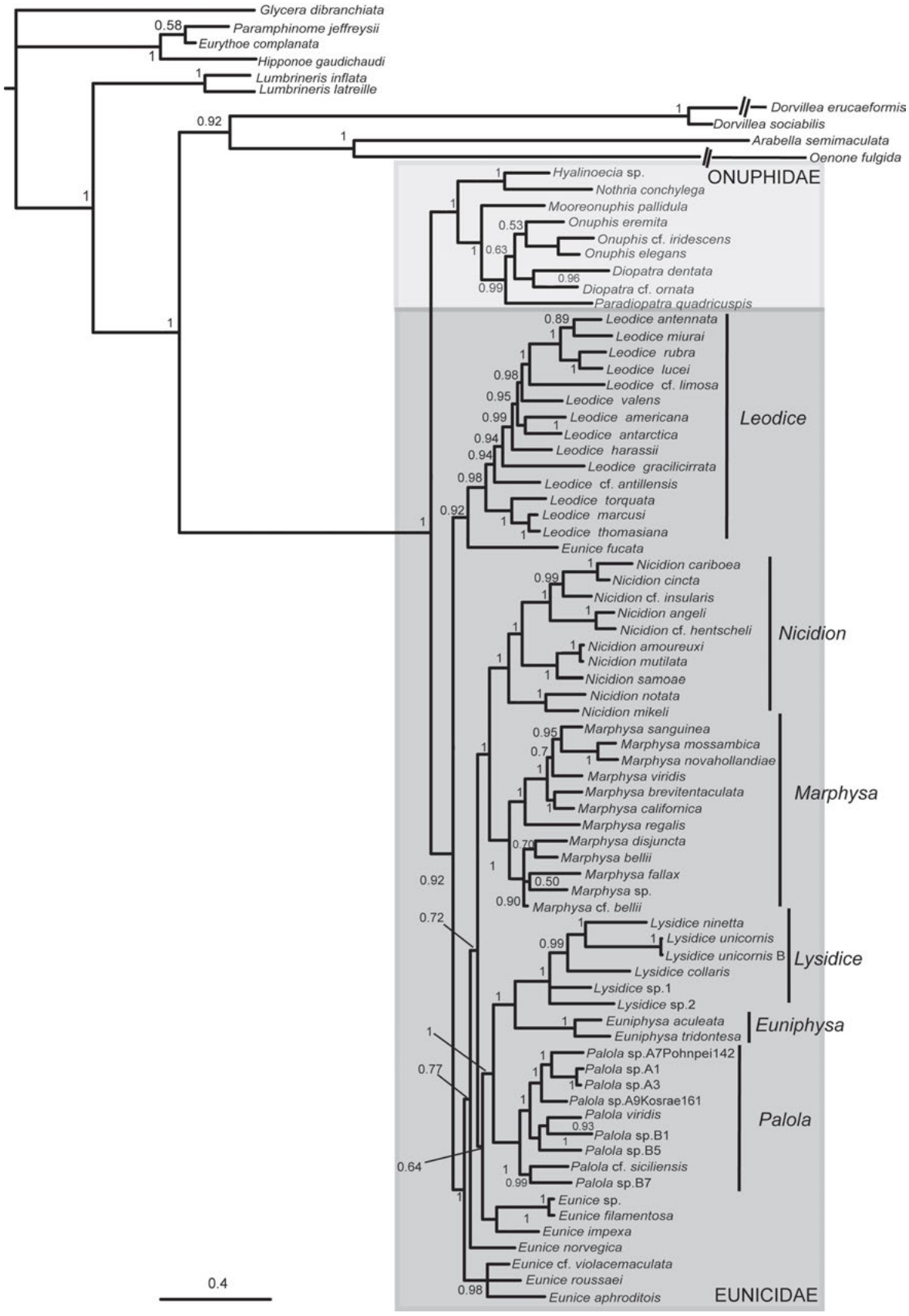


Fig. 7.12.4.9: Phylogeny of Eunicidae. Bayesian tree of combined evidence data set, 80 terminals. The genus name for each clade is on the right. Posterior probability values are placed on the branches. Modified from Zanol et al. (2014).

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evolutionary lineages (Zanol et al. 2014). The monophyly of *Paucibranchia* and *Treadwellphysa* has not been tested.

Eunice has historically been a genus defined by plesiomorphies, which included species that did not fit any other genus. In the most recent phylogenetic hypotheses, it was consistently recovered polyphyletic, with species being grouped in three different clades (Zanol et al. 2007, 2010, 2014). The phylogenetic placement of *E. aphroditois*, the type species of the genus, is not consistent in different hypotheses, not allowing for a reliable redefinition of the genus and its species composition. *Eunice aphroditois* always groups with *Eunice roussaei* and *Eunice violaceomaculata* Ehlers, 1887, species that are morphologically very similar; sometimes, *E. norvegica* is also placed in the clade. In some phylogenetic hypotheses, this clade is sister to another clade of *Eunice* species, *Eunice filamentosa* Grube, 1856, *Eunice* sp., and *Eunice impexa* Grube, 1878, which may represent a distinct monophyletic genus (Zanol et al. 2014). This latter clade has unique features, such as MxIV running from dorsal to ventral with teeth restricted to the dorsal quarter and compound falcigers bidentate with teeth inconspicuous in parapodia from anteriormost chaetigers (P1) and from around the first 1/8 of the chaetigers (P2). Due to the inconsistent placement of this clade in different phylogenetic hypotheses (Zanol et al. 2010, 2014), these species were maintained in *Eunice*.

Leodice and *Nicidion* were resurrected by Zanol et al. (2014) as two of the clades of *Eunice* species consistently recovered and that contained their type species, respectively. The names *Leodice* and *Eunice* were used interchangeably for the same taxon until the beginning of the 20th century despite the proposition of *Leodice* as junior synonym of *Eunice* by Audouin and Milne Edwards (1833a) and Grube (1850). *Leodice* became in disuse by the studies of Hartman (1944, 1959), a status confirmed in Fauchald (1992a). *Nicidion*, described as a genus in Kinberg (1865) characterized by the same features as *Eunice* but lacking branchiae, was consistently used as subgenus (Hartman 1944, Fauchald 1970). *Nicidion* was synonymized to *Eunice* on the basis that solely the presence or absence of branchiae should not be considered a valid generic character (Fauchald 1992a).

Original diagnoses of *Lysidice* (presence of median and lateral antennae, palps absent, and peristomial cirri absent) and *Marphysa* (presence of median and lateral antennae, palps absent, and peristomial cirri absent) delimit paraphyletic groups (Zanol et al. 2014). The clade of *Lysidice* species also includes species with only the median antennae as prostomial appendage (feature of the genus *Nematonereis*). *Nematonereis* has been synonymized to *Lysidice*; thus, the current definition of the genus also includes species with only median antennae (Zanol et al. 2014). The original diagnostic features of *Marphysa* are also present in some *Nicidion* species. Thus, it has also been redefined to comprise a monophyletic group. However, considering *Paucibranchia* and *Treadwellphysa* apart from *Marphysa* may make the latter paraphyletic. Species of *Treadwellphysa* share a feature that resulted as unique to *Marphysa* in the phylogenetic hypotheses, which is the presence of thick pectinate chaetae.

Esconites Thompson & Johnson, 1977 was described for common and well-preserved fossil specimens from the Pennsylvanian Essex fauna (318.1–299 million years ago), named *Esconites zelus* Thompson & Johnson, 1977. In the original description, the only distinction between *Esconites* and recent Eunicidae with five prostomial appendages, flat mandible, and pectinate branchiae with several filaments are the parapodia, biramous and subbiramous, respectively. Paxton (1986) reinterpreted *Esconites* parapodia as subbiramous. Thus, currently, there is no distinction between this extinct genus and extant genera *Eunice*, *Leodice*, *Nicidion*, and *Marphysa*.

Hartman (1944) presented the first hypothesis of affinity among eunicid genera. *Palola* would be the most distinct lineage due to the lack of pectinate chaetae and subacicular hooks, separating from the other genera first. The major lineage, containing the remaining genera, would contain two lineages according to absence or presence of peristomial cirri. In the lineage lacking peristomial cirri, the evolution would have followed a gradual addition of prostomial appendages as observed in the ontogeny of *Eunice* and *Marphysa* species (Herpin 1925, Pillai 1958, Åkesson 1967, Giangrande 1989), from *Nematonereis* (median antenna only) to *Lysidice* (median and lateral antennae) and finally to *Marphysa* and *Paramarphysa* (median and lateral antennae and palps). The lineage containing peristomial cirri would include *Eunice* and *Nicidion* and thus only forms with median and lateral antennae and palps.

An opposite interpretation of the evolution of features and thus of the phylogenetic relationships among genera was presented by Orensanz (1990) and supported by phylogenetic hypotheses for the family based on morphological and molecular data (Zanol et al. 2010, 2014). The most plesiomorphic forms of eunicids had median and lateral antennae, palps, peristomial cirri, flat mandibles, branchiae, pectinate chaetae, and subacicular hooks. Losses include palps, lateral antennae, peristomial cirri, pectinate chaetae, compound chaetae, and subacicular hooks.

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In the most recent phylogenetic hypothesis, the *Leodice* clade is sister to all other eunicids (Fig. 7.12.4.9) (Zanol et al. 2014). The major eunicid clade contains two main sister lineages: (1) *Nicidion* and *Marphysa* as sister groups and (2) *Palola* sister group to the clade containing *Lysidice* and *Euniphysa* as sister groups. The inconsistent placement of *Eunice* species varies from sister of the major clade to sister of the *Palola*, *Euniphysa*, and *Lysidice* clade.

Taxonomy

Eunicidae Berthold, 1827
Lycidicea Kinberg, 1865: 565
Leodicidae Treadwell, 1921: 4
Euniphysidae Shen & Wu, 1991: 765
Type genus: *Eunice*
Diagnosis: Prostomium with dorsal buccal lips fused (Fig. 7.12.4.3G); ventral buccal lip with median transverse groove. Median antenna present. Lateral antennae, palps, and peristomial cirri present or absent. Double-ringed peristomium. Anterior extension of the dorsolateral fold medially fused (Fig. 7.12.4.3I). Asymmetric eulabidognath maxillae with four or five paired plates and one unpaired plate. Ventral mandible flat or curved. Subbiramous parapodia, notopodial cirri present. Limbate chaetae and aciculae present. Pectinate chaetae, compound chaetae, and subacicular hooks present or absent. One or two pairs of pygidial cirri.

Diagnoses of extant genera:
Aciculomarphysa Hartmann-Schröder, 1998 in Hartmann-Schröder and Zibrowius 1998 (Fig. 7.12.4.10)
Aciculomarphysa Hartmann-Schröder & Zibrowius, 1998: 41
Type species: *Aciculomarphysa comes* Hartmann-Schröder, 1998
Diagnosis: Short with about 30 chaetigers. Median, lateral antennae and palps present (Fig. 7.12.4.10A). Peristomial cirri absent. First chaetiger lacking chaetae in adults (Fig. 7.12.4.10B). Maxillae with four paired plates and one unpaired plate. Mandibles flat. Only limbate chaetae and acicular chaetae present (Fig. 7.12.4.10C, D). Pectinate chaetae and compound chaetae absent. Acicular chaetae falcate or bidentate. Dorsal and ventral pygidial cirri present.
Remarks: The presence of only limbate chaetae and acicular chaetae is unique to the species of *Aciculomarphysa*. Hartmann-Schröder and Zibrowius (1998) could not distinguish aciculae and subacicular hooks and thus named similar chaetae as acicular chaetae. In some of the original illustrations, falcate and bidentate acicular chaetae appear to be aciculae and subacicular hook, respectively. However, in one figure, one bidentate acicular chaeta is illustrated

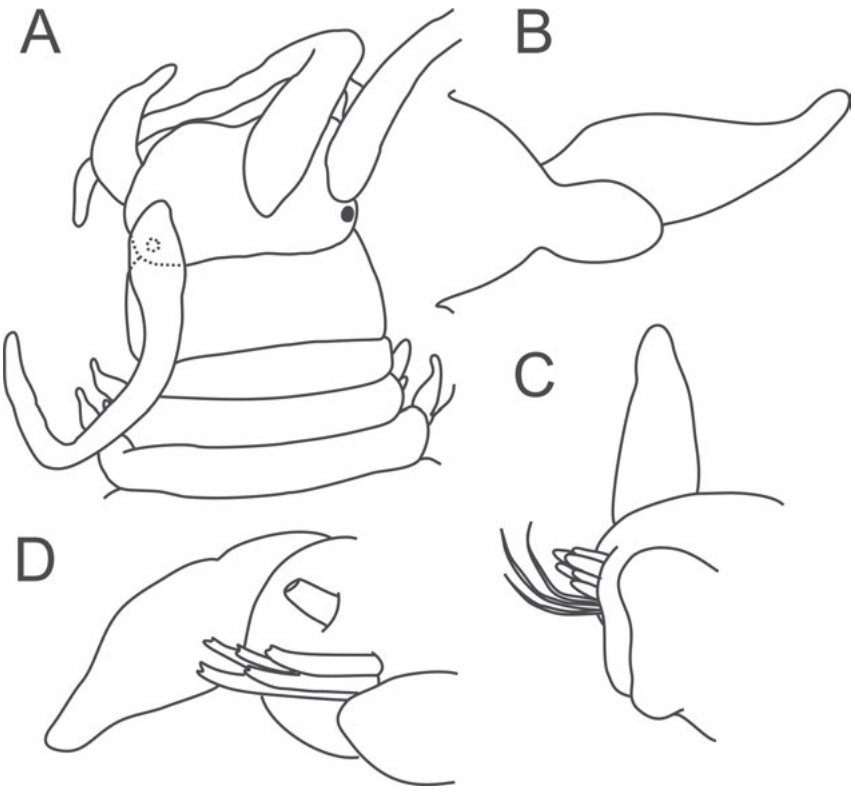


Fig. 7.12.4.10: Morphology of *Aciculomarphysa comes*, A, Anterior body region, dorsal view; B, Parapodium from chaetiger 1, ventral view; C, Parapodium from chaetiger 8, ventral view; D, Parapodium from chaetiger 29, ventral view. Modified from Hartmann-Schröder and Zibrowius (1998).

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in a supra-acicular position (Hartmann-Schröder and Zibrowius, 1998: 42, fig. 38). For this reason, we keep the term "acicular chaetae" in the diagnosis.

The genus is monospecific. It was described based on three individuals associated with Antipatharia (Anthozoa, Cnidaria) from deep sea Loyalty Islands (New Caledonia). Holotype is an ovigerous female. The smallest paratype has acicular chaetae in the first chaetiger.

Eunice Cuvier, 1817
Eunice Cuvier, 1817: 524
Tibiana Lamarck, 1816: 148
Eriphyle Kinberg, 1865: 561
Type species: *Nereis aphroditois* Pallas, 1788
Diagnosis: Median antenna, lateral antennae and palps present. Peristomial cirri present. Maxillae with four or five paired plates and one unpaired plate (Fig. 7.12.4.4G). Mandibles flat (Fig. 7.12.4.4H). Limbate chaetae, thin pectinate chaetae, compound bidentate falcigers or spinigers (Fig. 7.12.4.6L, M), aciculae, and subacicular hooks present. Subacicular hooks dark, falcate or bidentate (Fig. 7.12.4.7C, F).
Remarks: Traditionally, *Eunice* has been diagnosed based on plesiomorphic features, such as the presence of median and lateral antennae, a pair of palps, a pair of peristomial cirri, aciculae, subacicular hooks, limbate, pectinate, and compound chaetae (Orensanz 1990). It is currently recognized as polyphyletic. However, it could not be emended to represent a monophyletic group due to the inconsistent placement of the type species in different phylogenetic hypotheses (Zanol et al. 2014). Thus, *Eunice* continues to be identified by the plesiomorphic features listed above. It is not yet possible to give a precise diagnosis for the genus.

In the key to the different genera of Eunicidae in Molina-Acevedo and Carrera-Parra (2017), they restricted *Eunice* to species with similar MxI to those of the type species, MxI with falcal arch not extended and without a curvature at the internal basal edge. However, species that are still part of this genus have contrasting MxI, which have falcal arch extended and a curvature at the internal basal edge. Thus, these features are not compatible diagnostic features with our current knowledge about *Eunice*.

Euniphysa Wesenberg-Lund, 1949 (Fig. 7.12.4.11)
Euniphysa Wesenberg-Lund, 1949: 305, Miura, 1986: 312–313, Lu & Fauchald, 2000: 1011–1014
Paraeuniphysa Wu & He, 1988: 123
Heterophysa Shen & Wu, 1990: 765, Shen & Wu, 1991: 138
Type species: *Euniphysa aculeata* Wesenberg-Lund, 1949
Diagnosis: Median, lateral antennae and palps present; all slender, without articulation (Fig. 7.12.4.11A, B). Peristomial cirri present. Maxillae with five paired plates and one unpaired plate, MxIII to MxV with fang-like teeth (Fig. 7.12.4.11E). Mandibles flat (Fig. 7.12.4.11F). Dorsal fleshy knob present in neuropodial chaetal lobes (Fig. 7.12.4.11G). Limbate chaetae, thin pectinate chaetae (Fig. 7.12.4.11D), aciculae, compound spinigers (Fig. 7.12.4.11C), and subacicular hooks present. Compound bidentate falcigers and pseudocompound spinigers (Figs. 7.12.4.6N, 7.12.4.11G) present or absent.
Remarks: Features unique to species of *Euniphysa* are MxIII to MxV with fang-like teeth and pseudocompound spinigers.

Fauchaldius Carrera-Parra & Salazar-Vallejo, 1998 (Fig. 7.12.4.12)
Fauchaldius Carrera-Parra & Salazar-Vallejo, 1998: 148
Type species: *Fauchaldius cyrtauloni* Carrera-Parra & Salazar-Vallejo, 1998
Diagnosis: Median antenna, lateral antennae and palps present (Figs. 7.12.4.3D, 7.12.4.12A, B). Peristomial cirri present. Maxillae with five paired plates. Mandibles flat. Aciculae and subacicular hooks present. Subacicular hook guards as disassociated fibrils (Fig. 7.12.4.12C). Limbate chaetae, pectinate chaetae, and compound chaetae absent.
Remarks: The presence of only aciculae and subacicular hooks is unique to species of *Fauchaldius*. The genus includes two species *F. cyrtauloni* and *Fauchaldius insolita* Amoureux, 1977. It was described based on several individuals associated with hexactinellid sponge *Cyrtaulon sigsbeei* Schmidt, 1880a, b from off Quintana Roo (Mexico).

Leodice Lamarck, 1818 (Fig. 7.12.4.13)
Type species: *Leodice antennata* Lamarck, 1818
Diagnosis: Median, lateral antennae and palps present with regular (Figs. 7.12.4.2C, 7.12.4.3B, 7.12.4.13A) or irregular articulations. Prostomium steep truncate (Figs. 7.12.4.2C) or round. Peristomial cirri present. Maxillae with four or five paired plates and one unpaired plate (Fig. 7.12.4.13C). Mandibles flat (Fig. 7.12.4.13D). Limbate chaetae, thin pectinate chaetae, compound bidentate (Fig. 7.12.4.6J) or tridentate falcigers, aciculae, and subacicular hooks present. Aciculae light or dark. Dark aciculae vary in color along body; anteriormost always lightest but maintain same color shade. Subacicular hooks light or dark, bidentate or tridentate (Fig. 7.12.4.7A). Lateral black dots between parapodia present or absent.
Remarks: *Leodice* includes species previously assigned to *Eunice* having at least one of these features that are exclusive to the genus: regularly articulated prostomial appendages, tridentate compound falcigers, tridentate subacicular hooks, light subacicular hooks (groups A and C

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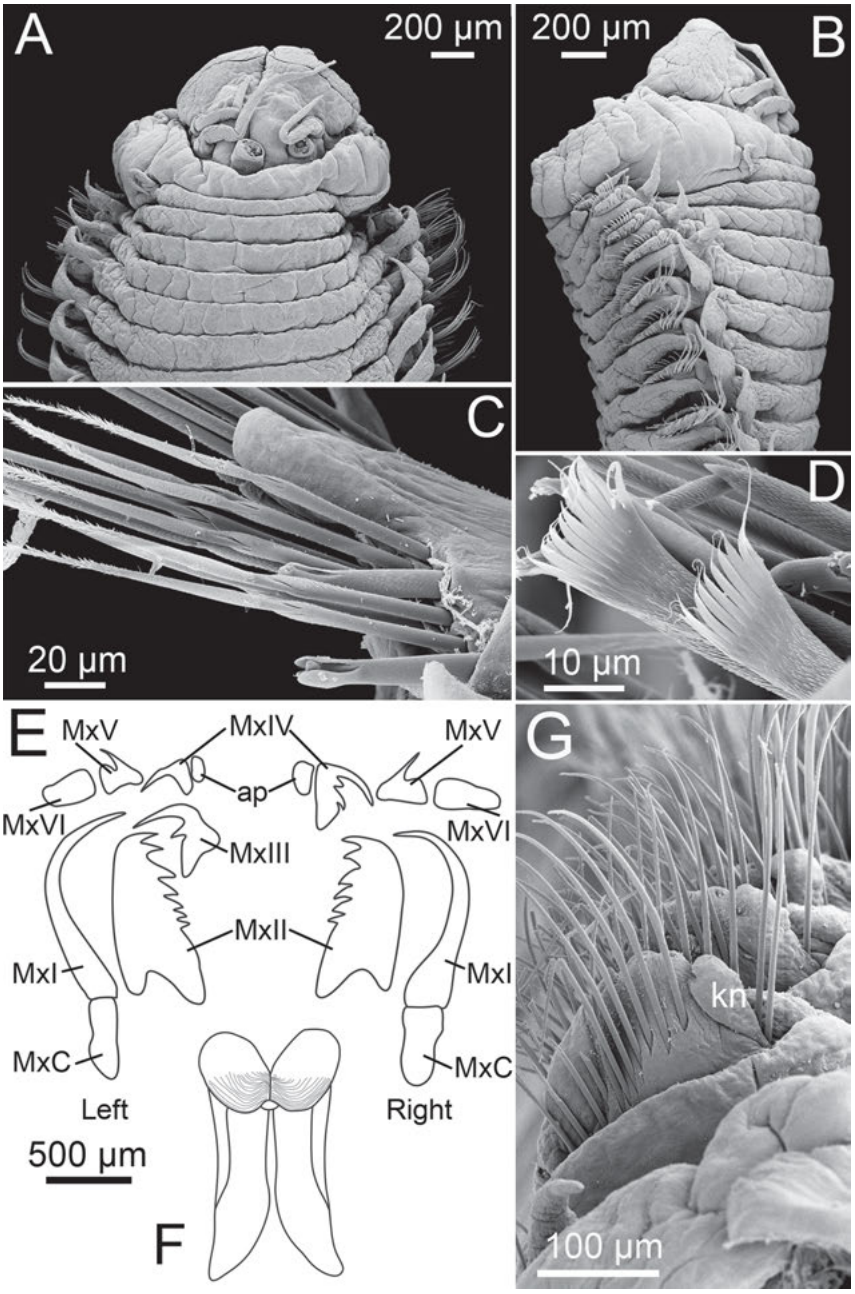


Fig. 7.12.4.11: Morphology of *Euniphysa*. A–D, G, *Euniphysa aculeata*; A, anterior region of the body, dorsal view, median and right lateral antennae incomplete; B, Same as A, but lateral view; C, Compound spinigers; D, Pectinate chaetae; E, *Euniphysa auriculata*, maxillae with MxIII to MxV bearing fang-like teeth; F, *Euniphysa spinea*, mandibles; G, Parapodia with dorsal fleshy knob. kn, knob. E, Modified from Lu and Fauchald (2000); F, Modified from Miura (1977).

sensu Fauchald 1970), aciculae from anterior neuropodia lightest but with the same color shade as median and posterior ones, or a lateral black dot present between posterior parapodia. Despite being exclusive to the *Leodice*, not all of these features are present in all species of the genus.

Molina-Acevedo and Carrera-Parra (2017) restricted *Leodice* to species with moniliform prostomial appendages, tridentate subacicular hooks, and T-shaped aciculae in some parapodia. Nonetheless, these do not represent the diversity of species included in the clade that justified the resurrection of the genus. Thus, the diagnosis included here maintains a broader definition of the genus.

Lysidice Lamarck, 1818 (Fig. 7.12.4.14)
Lysidice Lamarck, 1818: 324
Nereidice Blainville, 1828: 474
Nematonereis Schmarda, 1861: 119
Blainvillea Quatrefages, 1866: 370
Type species: *Lysidice ninetta* Audouin & Milne Edwards 1833a
Diagnosis: Median antenna present. Lateral antennae present or absent (Figs. 7.12.4.2D, 7.12.4.3E, F, 7.12.4.14A). Palps absent. Peristomial cirri absent. Maxillae with four paired plates and one unpaired plate (Fig. 7.12.4.14C). Mandibles curved with diverging shafts, X-shaped (Fig. 7.12.4.14D, E).

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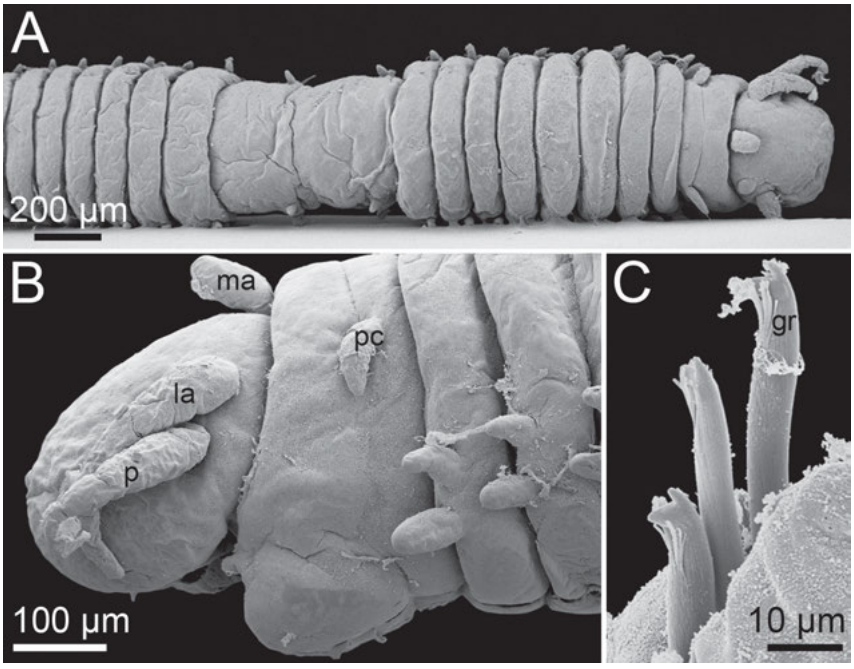


Fig. 7.12.4.12: Morphology of *Fauchaldius cyrtauloni*. A, Anterior region of the body, dorsal view; B, Prostomium and peristomium, lateral view; C, Subacicular hooks with guards as dissociated fibrils. gr, guards; la, lateral antenna; ma, median antenna; p, palp; pc, peristomial cirrus.

Muscle fiber complex F1 + F2 placed between mandible shafts (Fig. 7.12.4.14B). Limbate chaetae, thin pectinate chaetae (Fig. 7.12.4.6H), bidentate compound falcigers (Fig. 7.12.4.6K), aciculae, and subacicular hooks present.

Remarks: Features unique to species of *Lysidice* are the presence of only the median antenna in some species, lack of palps, shape of the mandibles, and placement of muscle fiber complex F1 + F2.

Nematonereis was considered a distinct genus from *Lysidice* by Molina-Acevedo and Carrera-Parra (2017) without any discussion and justification on their decision. Thus, we here maintain *Nematonereis* as a junior synonym of *Lysidice*, which translates the current knowledge about the phylogeny of the family (Zanol et al. 2014).

Marphysa Quatrefages, 1865
Marphysa Quatrefages, 1865: 593, 1866: 331
Amphiro Kinberg, 1865: 565
Nauphanta Kinberg, 1865: 564
Macduffia McIntosh, 1885: 303
Aphelothrix Chamberlin, 1919: 231
Type species: *Nereis sanguinea* Montagu, 1813
Diagnosis: Median antenna, lateral antennae and palps present (Figs. 7.12.4.2A, E). Peristomial cirri absent. Maxillae with four paired plates and one unpaired plate. MxI falcal arch extended rectangular; basal inner edge lacking a curvature (Fig. 7.12.4.15A). Mandibles flat. Branchiae distributed along most of the body. Neuropodial postchaetal lobes longer than chaetal lobes at least in anteriormost parapodia (Fig. 7.12.4.5A, E) Limbate chaetae (Fig. 7.12.4.6A), pectinate chaetae, aciculae, and subacicular hooks present; bidentate falcigers (Fig. 7.12.4.6I) and spinigers (Fig. 7.12.4.6M) present or absent (Fig. 7.12.4.6A, I, M). Thin pectinate chaetae with both outer teeth longer than inner teeth; inner teeth of equal length (Fig. 7.12.4.6B, C, G). Thick pectinate chaetae present (Fig. 7.12.4.6B, C, E). Subacicular hooks light or dark, falcate or bidentate (Fig. 7.12.4.7B, D, E).

Remarks: The unique shapes of MxI falcal arch and the basal inner edge are useful diagnostic features of *Marphysa* (Molina-Acevedo and Carrera-Parra, 2017). However, other diagnostic features suggested by the same authors appear more variable within the genus. These are (1) the curve on MxI basal outer edge, which seems to be absent in the type species of the genus *M. sanguinea* (Lavesque et al. 2019), and (2) the presence of compound chaetae, which may also be absent, as species of the synonymized genus *Nauphanta* lack compound chaetae (Glasby and Hutchings 2010).

In *Marphysa*, the kind of pectinate chaetae varies along the body. In anteriormost chaetigers, when pectinate chaetae are present, these are thin. Thin pectinate chaetae may be present until the end of the body and co-occur with thick pectinate chaetae.

The presence of median and lateral antennae and palps combined with the lack of peristomial cirri is not unique to *Marphysa* as traditionally considered (Zanol et al. 2014) and defined a paraphyletic genus. The diagnosis of the genus was emended in order to define a monophyletic genus. Based on this, the unique features of the genus, despite not being present in all species, were (1) thin pectinate chaetae always with outer teeth longer

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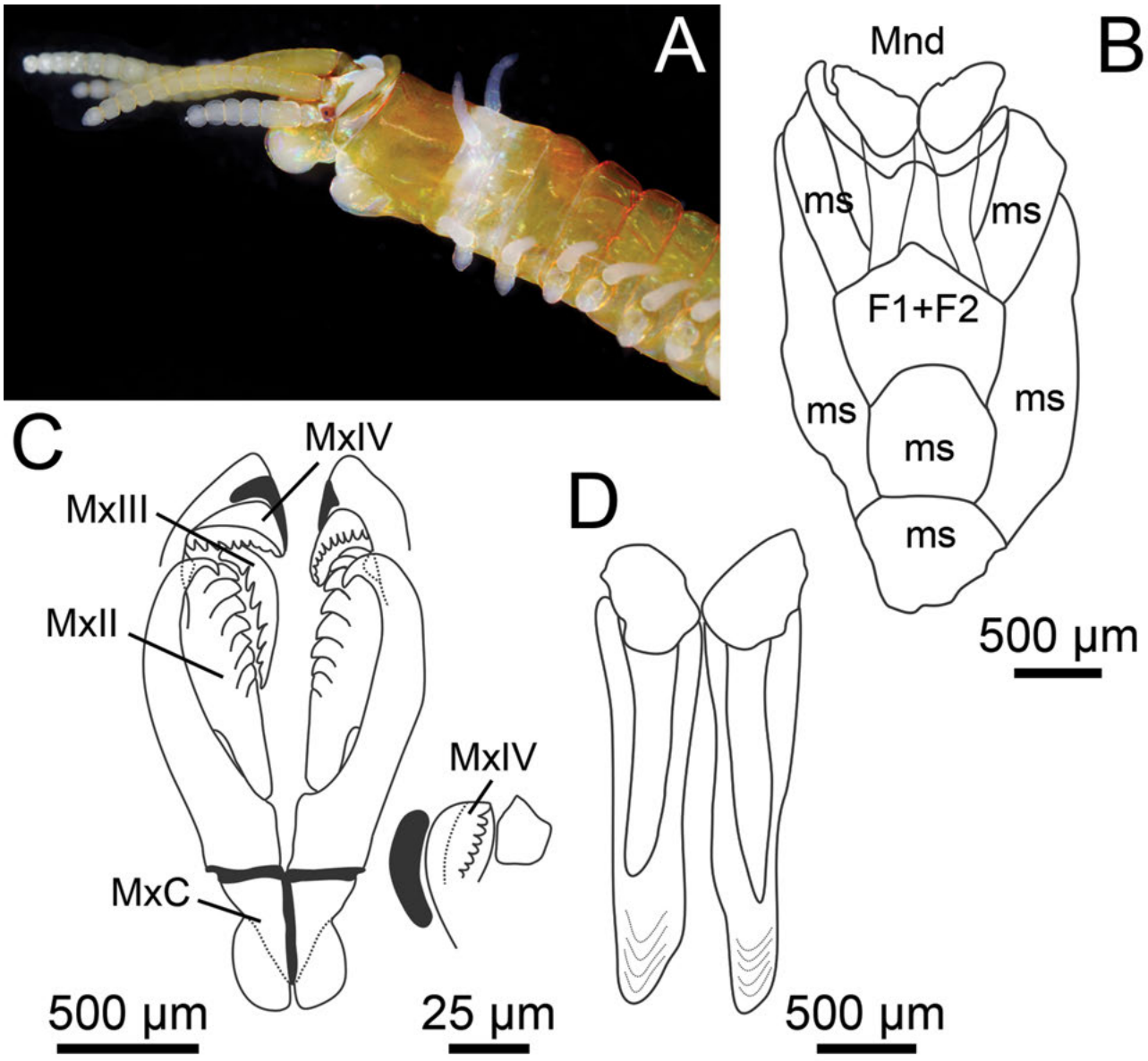


Fig. 7.12.4.13: Morphology of *Leodice*. A, *Leodice* sp., live photograph (© A. Semenov), anterior region of the body, lateral view; B, *Leodice* cf. *torquata*, pharyngeal bulb musculature, ventral view. C, *Leodice rubra*, maxillae, dorsal view; D, *L. rubra*, mandibles, ventral view. ms, muscles; Mnd, mandibles; Mx, maxillae; F1 + F2, muscle fiber complex F1 + F2. B–D, Modified from Zanol et al. (2007).

than inner teeth, (2) thin pectinate chaetae with inner teeth of unequal length, and (3) thick pectinate chaetae (Zanol et al. 2014). *Marphysa* was further restricted with the description of *Paucibranchia* and *Treadwellphysa*, which include species previously identified as *Marphysa* (Molina-Acevedo and Carrera-Parra 2017, Molina-Acevedo 2018). *Paucibranchia* includes all species with thin pectinate chaetae with inner teeth of unequal length, and *Treadwellphysa* includes some of the species with thick pectinate chaetae. In all of three genera, thin pectinate chaetae always have outer teeth longer than inner teeth. The monophyletic status of the current definition of these three genera has not been tested.

Nicidion Kinberg, 1865 (Fig. 7.12.4.16)
Nicidion Kinberg, 1865: 564
Paramarphysa Ehlers, 1887: 99
Type species: *Nicidion cincta* Kinberg, 1865
Diagnosis: Median antenna, lateral antennae and palps present (Figs. 7.12.4.2B, 7.12.4.3A, 7.12.4.16A). Peristomial cirri present or absent. Maxillae with four paired plates and one unpaired plate. Mandibles flat. Neuropodial chaetal lobes pointed from second quarter to posterior end of the body. Limbate chaetae, thin pectinate chaetae, bidentate compound falcigers, aciculae, and subacicular hook present. Thin pectinate chaetae in median and posterior chaetigers with wide blade and dorsal to aciculae.

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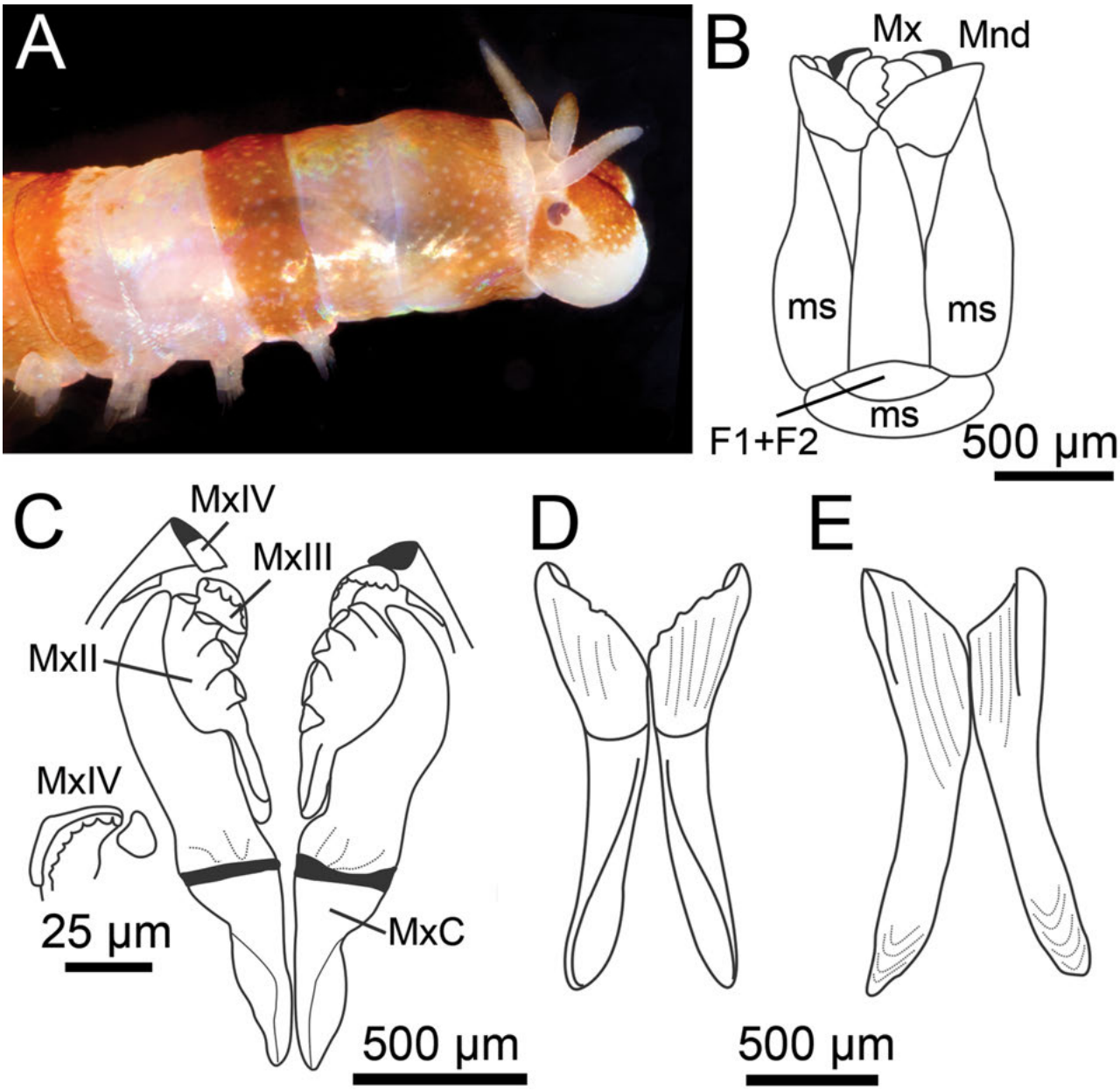


Fig. 7.12.4.14: Morphology of *Lysidice*. A, *Lysidice* sp., live photograph (© A. Semenov), anterior region of the body, lateral view; *Lysidice ninetta*: B, Pharyngeal bulb musculature, ventral view; C, Maxillae, dorsal view; D, Mandibles, ventral view; E, Same as D, but dorsal view. ms, muscles; Mnd, mandibles; Mx, maxillae; F1 + F2, muscle fiber complex F1 + F2. B–E, Modified from Zanol et al. (2007).

Aciculae dark. Bidentate subacicular hooks dark in more anterior region and light on posteriormost region. Dark subacicular hooks not evenly colored, most commonly darkest color shade placed at distal half or distal end of hook (Fig. 7.12.4.7G).

Remarks: The location of the darkest color shade along the subacicular hook is the feature unique to species of *Nicidion* despite not being present in all species. In most species of the genus, parapodia, notopodial, and ventral cirri decrease in size toward the posterior end. Thus, aciculae and subacicular hooks stand out, giving a characteristic look to the posterior end (Fig. 7.12.4.16B). The absence of branchiae, as traditionally considered, is not diagnostic feature of the genus (Zanol et al. 2014). This feature has been found to vary even within species (e.g., Nogueira et al. 2001).

Peristomial cirri may be absent even in adult specimens of *Nicidion*. Specimens of *Nicidion angeli* Carrera-Parra and Salazar-Vallejo, 1998 and *Nicidion* cf. *hentscheli* Augener, 1931 examined by Zanol et al. (2014) lack peristomial cirri and are not juveniles as assumed by Molina-Acevedo and Carrera-Parra (2017).

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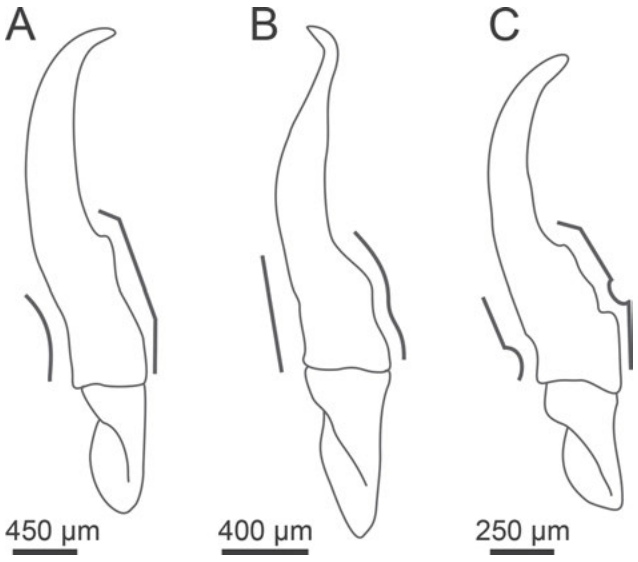


Fig. 7.12.4.15: Schematic drawing of left MxI and maxillary carrier. A, *Marphysa viridis*, MxI falcal arch extended rectangular, basal outer edge arched, basal inner edge lacking a curvature; B, *Paucibranchia disjuncta*, MxI falcal arch extended rounded, basal outer edge straight, basal inner edge with curvature where MxII posteriormost end fits; C, *Treadwellphysa yucatanensis*, MxI falcal arch extended rectangular, basal outer edge with anterior half straight and base arched, basal inner edge with curvature where MxII posteriormost end fits. Modified from Molina-Acevedo (2018).

The curvature at the proximal end of MxI where MxII fits as reported by Molina-Acevedo and Carrera-Parra (2017) for 7 of the 10 species of *Nicidion* may be a useful diagnostic feature to distinguish *Nicidion* from *Marphysa* and *Treadwellphysa* as suggested by the authors. However, it is not informative in differentiating *Nicidion* and *Eunice* as used in the key of the same study. Some *Eunice* and *Leodice* species also have the curvature at the proximal end of MxI where MxII fits (e.g., Wolf 1980).

Palola Gray in Stair, 1847 (Fig. 7.12.4.17)
Palola Gray in Stair, 1847: 409
Lithognatha Stewart, 1881: 717
Type species: *Palola viridis* Gray in Stair, 1847
Diagnosis: Median antenna, lateral antennae and palps present (Fig. 7.12.4.17A). Peristomial cirri present. Maxillae with four or five paired plates and one unpaired plate (Fig. 7.12.4.17C). Mandibles curved, scoop-shaped; plates fused anteriorly; heavily calcified; with parallel shafts (Fig. 7.12.4.17D, E). Muscle fiber complex F1 + F2 covers mandible shafts (Fig. 7.12.4.17B). Limbate chaetae, bidentate compound falcigers, and aciculae present. Pectinate chaetae and subacicular hooks absent.
Remarks: Features unique to species of *Palola* are the shape of mandibles, position of muscle fiber complex F1 + F2 in relation to mandible shafts, and lack of subacicular hooks.

Paucibranchia Molina-Acevedo, 2018
Type species: *Eunice bellii* Audouin & Milne-Edwards, 1833b
Diagnosis: Modified after Molina-Acevedo (2018). Median and lateral antennae and palps present (Fig. 7.12.4.3C). Peristomial cirri absent. Maxillae with four paired plates and one unpaired plate. MxI falcal arch extended rounded; basal inner edge with curvature where MxII posteriormost end fits (Fig. 7.12.4.15B). Mandibles flat. Branchiae present in few anterior chaetigers, branchial filaments tapering. Notopodial cirri longest at branchial region. Inflated base of ventral cirri present only in the anterior region of the body. Postchaetal lobes long at wide base and tapering tips at branchial region. Limbate chaetae, thin pectinate chaetae, aciculae, compound chaetae, and subacicular hook present. Thin pectinate chaetae with both outer teeth longer than inner teeth; inner teeth of equal or unequal length, short or long, in transverse or oblique distribution. Compound spinigers and bidentate falcigers present or absent. Subacicular hooks unidentate or bidentate; translucent or amber at the distal end or along the whole length of the hook or reddish at proximal end.
Remarks: *Paucibranchia* is the most recent genus described for the family. It includes species with branchiae distributed in the short anterior region of the body and with only compound spiniger chaetae, with only compound falciger chaetae, or with both kinds of compound chaetae, which correspond to *Marphysa* informal groups B1, C1, and D1 (*sensu* Fauchald 1970) or part of groups Sanguinea, Aenea, and Bellii (*sensu* Glasby and Hutchings 2010). Species of *Paucibranchia* formed a poorly supported monophyletic group sister to a clade with all other *Marphysa* species included in an analysis of combined morphological and molecular data (Zanol et al. 2014).

Treadwellphysa Molina-Acevedo & Carrera-Parra, 2017
Type species: *Treadwellphysa yucatanensis* Molina-Acevedo & Carrera-Parra, 2017
Diagnosis: Modified after Molina-Acevedo and Carrera-Parra (2017). Median and lateral antennae and palps present. Peristomial cirri absent. Maxillae with four paired plates and one unpaired plate. MxI falcal arch extended rectangular; basal inner edge with curvature where MxII posteriormost end fits (Fig. 7.12.4.15C). Dorsal projection present at posterior end of base of MxII. Mandibles flat. Branchiae start posterior to chaetiger 15 distributed along most of the body. Inflated base of ventral cirri transverse welt with short digitiform tip. Limbate chaetae, pectinate chaetae, aciculae, compound chaetae, and subacicular hook present. Pectinate chaetae thin, thick or both. Compound spinigers present or absent, bidentate falcigers present in all chaetigers, spinifalcigers present in anterior chaetigers. Subacicular hooks bidentate.

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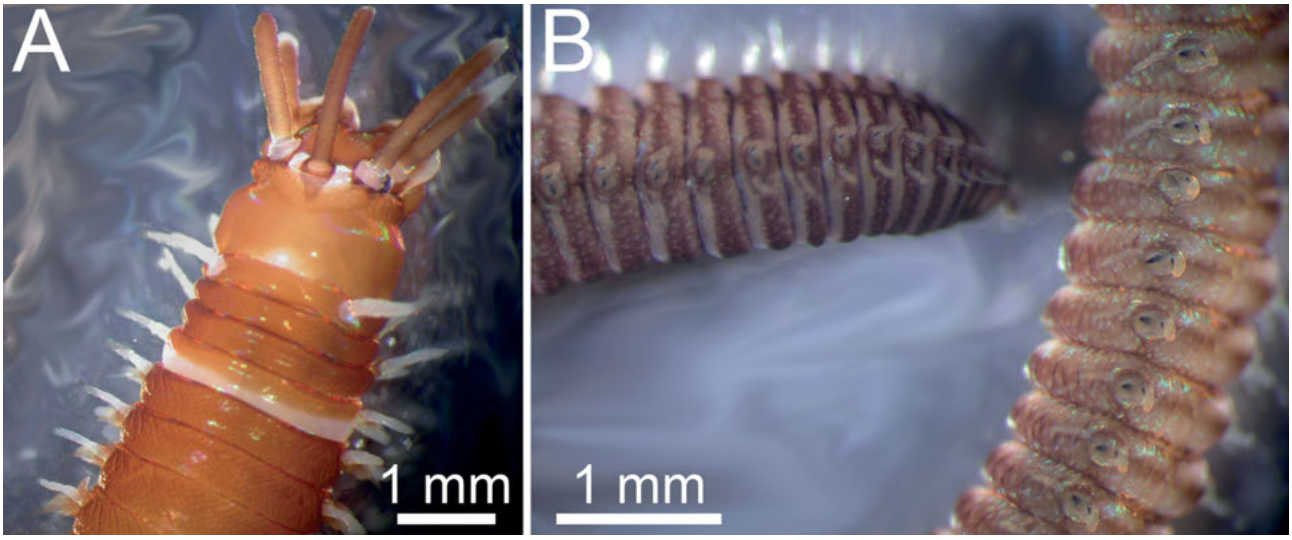


Fig. 7.12.4.16: Morphology of *Nicidion mutilata*. A, Live photograph, anterior region of the body, dorsal view; B, Live photograph, median and posterior regions of the body with dark subacicular hooks, lateral view. Modified from Zanol et al. (2014).

Remarks: The genus was described for species that otherwise would be identified as *Marphysa*. *Treadwellphysa* species can be distinguished from all other eunicids by the shape of MxI and inflated base of ventral cirri and the presence of compound spinifalcigers in anterior chaetigers of some species (Molina-Acevedo and Carrera-Parra 2017, Molina-Acevedo 2019).

Invalid genera:

1. *Amphiro* Kinberg, 1865 characterized by the presence of three prostomial appendages. However, five prostomial appendages are present in the type specimen and peristomial cirri are absent. Type species: *Amphiro atlantica* Kinberg, 1865. Type locality: La Plata, Argentina. Current status: junior synonym of *Marphysa* (Hartman 1948).
2. *Aphelothrix* Chamberlin, 1919 characterized by the presence of five prostomial appendages and the lack of peristomial cirri and compound chaetae. Type species: *Eunice mossambica* Peters, 1854. Type locality: Mozambique. Current status: junior synonym of *Marphysa* (Hartman 1959).
3. *Blainvillea* Quatrefages, 1866 characterized by the presence of only median antennae. It was synonymized to *Nematonereis* (Hartman 1959). Species: *Blainvillea elongata* Quatrefages, 1866 and *Blainvillea filum* Quatrefages, 1866. Type locality: France. Current status: junior synonym of *Lysidice*.
4. *Eriphyle* Kinberg, 1865 characterized by a four-lobed prostomium, five prostomial appendages, peristomial cirri and branchiae. Type species: *Eriphyle capensis* Kinberg, 1865. Type locality: Cape of Good Hope, South Africa. Current status: junior synonym of *Eunice* (Malmgren 1867, Hartman 1959, Fauchald 1992a).
5. *Heteromarphysa* Verrill, 1900. Described for juvenile specimen with four eyes. Type species: *Heteromarphysa tenuis* Verrill, 1900. Type locality: Bermuda. Current status: indeterminable.
6. *Heterophysa* Shen & Wu, 1991 characterized by five prostomial appendages, a pair of peristomial cirri, fang-shaped maxillary teeth, MxI with three teeth, and compound chaetae starting at chaetiger 7. Type species: *Heterophysa tridontesa* Shen & Wu, 1991. Type locality: Beibu Gulf, China. Current status: junior synonym of *Euniphysa* (Lu and Fauchald 2000).
7. *Lithognatha* Stewart, 1881 characterized by curved mandible. Type species: *Lithognatha worslei* Stewart, 1881. Type locality: Singapore. Current status: junior synonym of *Palola* (Fauchald 1970).
8. *Lysibranchia* Cantone, 1983 characterized by three antenna, lack of peristomial cirri, and few branchiae in anterior chaetigers; might be a juvenile of *M. bellii* (Audouin & Milne Edwards, 1833b) (Çinar 2005). Type species: *Lysibranchia paucibranchiata* Cantone, 1983. Type locality: Sicily, Italy. Current status: indeterminable, described on a juvenile of unconfirmed species.
9. *Macduffia* McIntosh, 1885 characterized by prostomium anteriorly round, five prostomial appendages, lack of peristomium cirri, and branchiae restricted to anterior chaetigers. Type species: *Macduffia bonhardi* McIntosh, 1885. Type locality: Off Saint Thomas, U.S. Virgin Islands. Current status: junior synonym of *Marphysa* (Hartman 1959).

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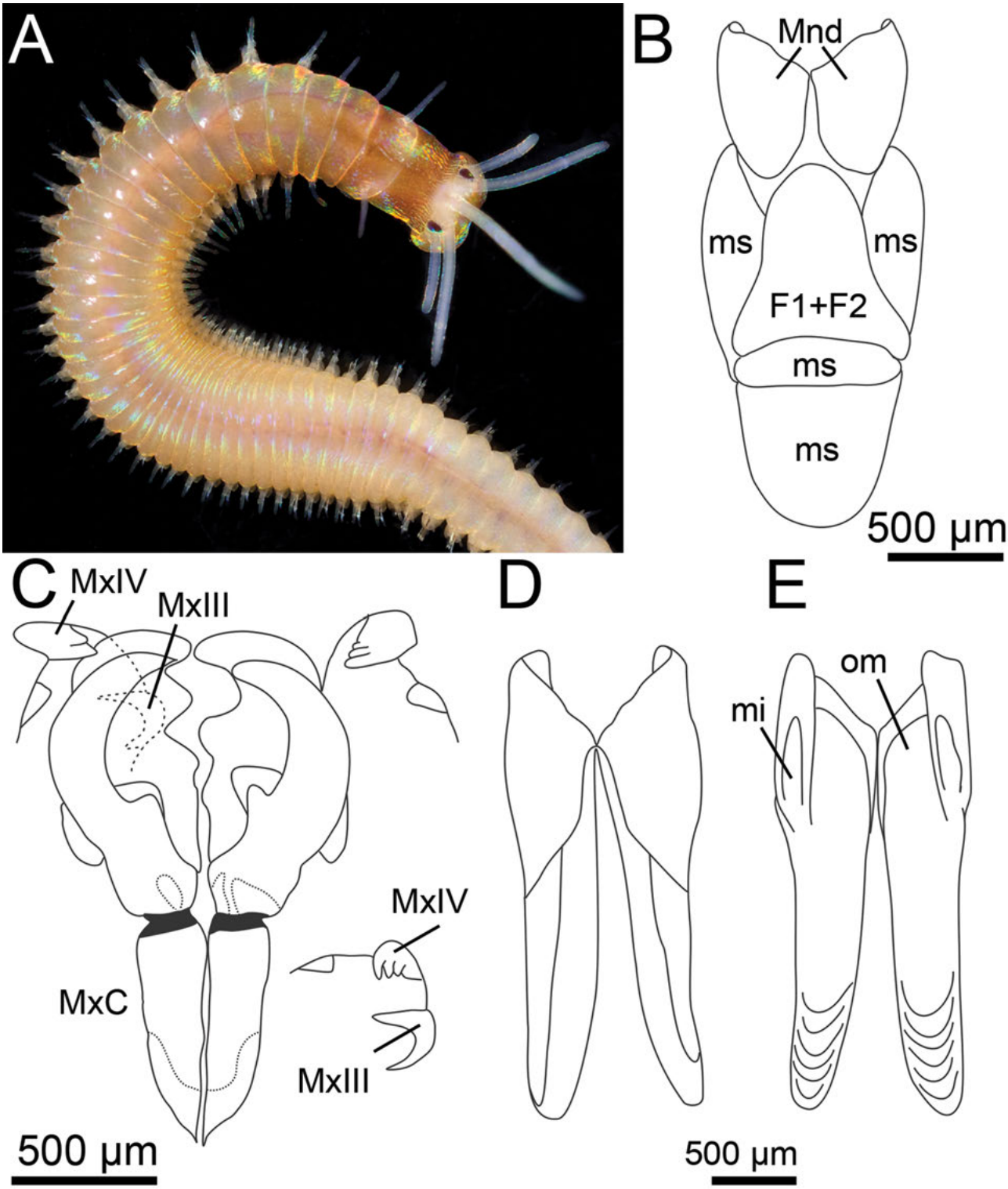


Fig. 7.12.4.17: Morphology of *Palola*. A, *Palola* sp., live photograph (© A. Semenov), anterior body region, dorsal view; *Palola brasiliensis*: B, Pharyngeal bulb musculature, ventral view; C, Maxillae, dorsal view; D, Mandibles, ventral view; E, Same as D, but dorsal view. mi, muscle insertion; ms, muscles; Mnd, mandibles; Mx, maxillae; F1 + F2, muscle fiber complex F1 + F2; om, outline of organic matrix. B–E, Modified from Zanol et al. (2007).

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10. *Mayeria* Verrill, 1900. Described for posterior end of *E. fucata* Mayer, 1902. Type species: *Staurocephalus gregaricus* Mayer, 1900. Type locality: Florida, USA. Current status: junior synonym of *Eunice* (Mayer 1902).
11. *Nauphanta* Kinberg, 1865 characterized by five prostomial appendages, lack of peristomium cirri, wide pectinate chaetae, and lack of compound chaetae. Type species: *Nauphanta novaehollandiae* Kinberg, 1865. Type locality: Sydney, Australia. Current status: junior synonym of *Marphysa* (Glasby and Hutchings 2010).
12. *Nausicaa* Kinberg, 1865 characterized by five prostomial appendages, lack of peristomium cirri, and single filament branchiae. Type species: *Nausicaa striata* Kinberg, 1865 indeterminable. Type locality: San Jose Island, Panama. Current status: *nomen nudum* (Molina-Acevedo 2018).
13. *Nematonereis* Schmarda, 1861 characterized by one median antenna and lack of lateral antennae, palps, and peristomial cirri. Type species: *Nematonereis unicornis* Schmarda, 1861. Type locality: Atlantic Ocean. Current status: junior synonym of *Lysidice* (Zanol et al. 2014).
14. *Nereidice* Blainville, 1828 characterized by three prostomial appendages and lack of peristomium cirri. Described as an alternative name to the genus *Lysidice*. Current status: junior synonym of *Lysidice* (Hartman 1959).
15. *Nereidonta* Blainville, 1828 characterized by five prostomial appendages. Described for species current assigned to genera *Eunice*, *Leodice*, and *Marphysa*. Current status: indeterminable.
16. *Palpiglossus* Wagner, 1885 No description available. Type species: *Palpiglossus labiatus* Wagner, 1885. Type locality: unknown. Current status: *nomen nudum*.
17. *Paraeuniphysa* Wu & He, 1988 characterized by five prostomial appendages, a pair of peristomial cirri, fang-shaped maxillary teeth, and compound chaetae starting at chaetiger 11. Type species: *Paraeuniphysa taiwanensis* Wu & He, 1988. Type locality: Taiwan Strait. Current status: junior synonym of *Euniphysa* (see Lu and Fauchald 2000).
18. *Paramarphysa* Ehlers, 1887 characterized by prostomium with anteromedian incision, five prostomial appendages, and lack of peristomial cirri and branchiae. Type species: *Paramarphysa longula* Ehlers, 1887. Type locality: Off Havana, Cuba. Current status: junior synonym of *Nicidion* (Molina-Acevedo and Carrera-Parra 2017).
19. *Tibiana* Lamarck, 1816 described to name empty tubes of *Eunice* species thought to be corals. Species named at the original description: *Tibiana fasciculata* Lamarck, 1816 (from France) and *Tibiana ramosa* Lamarck, 1816 (from Australia), both indeterminable species.

References

Aiyar, R.G. (1931): An account of the development and breeding habits of a brackish water Polychaete worm of the genus *Marphysa*. *Journal of the Linnean Society of London* 37: 387–403.

Åkesson, B. (1967): The embryology of the Polychaete *Eunice kobiensis*. *Acta Zoologica (Stockholm)* 48: 141–192.

Allen, M.J. (1957): The breeding of polychaetous annelids near Parguera, Puerto Rico. *Biological Bulletin* 113: 49–57.

Amaral, A.C.Z. & Jablonski, S. (2005): Conservation of marine and coastal biodiversity in Brazil. *Conservation Biology* 19: 625–631.

Amoureux, L. (1877): Annélides polychètes profondes de Madagascar. Description deux nouvelles espèces (Collections Crosnier et Jouannic). *Bulletin du Muséum d'Histoire Naturelle, Paris* 495: 1093–1109.

Andrews, E.A. (1892): On the eyes of polychaetous annelids. *Journal of Morphology* 7: 169–222.

Audouin, J.V. & Milne Edwards, H. (1833a): Classification des Annélides, et description de celles qui habitent les côtes de la France. *Annales des sciences naturelles, Paris sér. 1* 28: 187–247.

Audouin, J.V. & Milne Edwards, H. (1833b): Classification des Annélides, et description de celles qui habitent les côtes de la France. *Annales des sciences naturelles, Paris sér. 1* 30: 411–425.

Audouin, J.V. & Milne Edwards, H. (1834): *Recherches pour servir à l'histoire naturelle du littoral de la France, ou recueil de mémoires sur l'anatomie, la physiologie, la classification et les moeurs des animaux de nos côtes; ouvrage accompagné de planches faites d'après nature, 2: Annélides*. Paris: Crochard Libraire. 290 pp.

Augener, H. (1931): Die bodensässigen Polychäten nebst einer Hirudinee der Meteor-Fahrt. *Mitteilungen des Zooologischen Staatsinstituts und zoologischen Museums, Hamburg* 44: 279–313.

Bannister, J.V., Bannister, W.H., Anastasi, A. & Wood, J. (1976): Isolation, characterization and oxygen equilibrium of an extracellular haemoglobin from *Eunice aphroditois* (Pallas). *Biochemical Journal* 159: 35–42.

Bartolomaeus, T. & Quast, B. (2005): Structure and development of nephridia in Annelida and related taxa. *Hydrobiologia* 535/536: 139–165.

Bely, A.E. (2006): Distribution of segment regeneration ability in the Annelida. *Integrative and Comparative Biology* 46: 508–518.

Berthold, A.A. (1827): *Latreille's Natürliche Familien des Thierreichs*. Verlag Landes-Industrie-Comptoirs, Weimar: 606 pp.

Bettoso, N., Faverio, G. & Orel, G. (1998): Note sulla biologia e sulla pesca del verme de rimini (*Eunice aphroditois* Pallas) in alto Adriatico. *Hydrore*s 16: 24–34.

Blainville, H. de (1828): *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des differens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connaisance, soit relativement a l'utilité qu'en peuvent retirer la médicine, l'agriculture, le commerce et les arts; suivi dune biographie des plus cilibres naturalistes*. F.G. Levrault, Strasbourg, Paris: 628 pp.

Bobin, G. (1944): Morphogénèse des soies chez les Annélides Polychètes. *Annales de l'Institut Océanographique* 22: 1–106.

Budaeva, N., Schepetov, D., Zanol, J., Neretina, T. & Willassen, E. (2016): When molecules support morphology: Phylogenetic reconstruction of the family Onuphidae (Eunicida, Annelida) based on 16S rDNA and 18S rDNA. *Molecular Phylogenetics and Evolution* 94: 791–801.

Cantone, G. (1983): Un nuovo genere di Eunicidae (Annelida: Polychaeta) del Golfo di Catania. *Animalia* 10: 81–86.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Carrera-Parra, L.F. & Salazar-Vallejo, S.I. (1998): A new genus and 12 new species of Eunicidae (Polychaeta) from the Caribbean Sea. *Journal of the Marine Biological Association of the United Kingdom* 78: 145–182.

Carrera-Parra, L.F., Fauchald, K. & Gambi, M.C. (2011): Revision of the taxonomic status of *Lysidice* (Polychaeta, Eunicidae) in the western Caribbean Sea with observation on species reproductive features and habitat preference. *Italian Journal of Zoology* 78: 27–40.

Caspers, H. (1984): Spawning periodicity and habitat of the palolo worm *Eunice viridis* (Polychaeta: Eunicidae) in the Samoan Islands. *Marine Biology* 79: 229–236.

Cassai, C. & Prevedelli, D. (1998): Reproductive effort, fecundity and energy allocation in *Marphysa sanguinea* (Polychaeta: Eunicidae). *Invertebrate Reproduction and Development* 34: 133–138.

Chamberlin, R.V. (1919): The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48: 1–514.

Chisholm, J.R.M. & Kelley, R. (2001): Worms start reef-building process. *Nature* 409: 152.

Cigliano, M., Manini, E. & Gambi, M.C. (2003): First data on cellulolytic enzyme activity in polychaete borers associated to *Posidonia oceanica* sheaths. *Biologia Marina Mediterranea* 10: 388–391.

Çinar, M.E. (2005): Polychaetes from the coast of northern Cyprus (eastern Mediterranean Sea), with two new records for the Mediterranean Sea. *Cahiers de Biologie Marine* 46: 143–159.

Claparède, É. (1868): Les Annélides Chétopodes du Golfe de Naples, Premiere Partie. *Mémoires de la Société de physique et d'histoire naturelle de Genève* 19: 313–584.

Clark, L.B. & Hess, W.N. (1940): The reactions of the Atlantic *Palolo*, *Leodice fucata*, to light. III. *Papers from the Tortugas Laboratory, Carnegie Institution* 33: 71–81.

Clavier, J. (1990): Preliminary data on the biology dnd ecology of *Euniphysa tubifex* (Annelida: Polychaeta) in the south-west lagoon of New Caledonia. *Proceedings ISRS, Nouméa*: 47–52.

Colbath, G.K. (1986): Jaw mineralogy in Eunicean polychaetes (Annelida). *Micropaleontology* 32: 186–189.

Costa-Paiva, E.M., Whelan, N.V., Waits, D.S., Santos, S.R., Schrago, C.G. & Halanych, K.M. (2017): Discovery and evolution of novel hemerythrin genes in annelid worms. *BMC Evolutionary Biology* 17: 85.

Crossland, C. (1903): On the marine fauna of Zanzibar and British East Africa, from collections made by Cyril Crossland in the years 1901 and 1902. Polychaeta, Part II. *Proceedings of the Zoological Society of London* 2: 129–144.

Crossland, C. (1904): On the marine fauna of Zanzibar and British East Africa, from collections made by Cyril Crossland in the years 1901 and 1902. Polychaeta, Part III. With which is incorporated the account made in the Maldive archipelago in the year 1899. *Proceedings of the Zoological Society of London* 1: 287–330.

Cuvier, G. (1817): *Le régne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Volume 4*. Deterville, Paris: 255 pp.

Day, J.H. (1967): *A monograph on the Polychaeta of Southern Africa. Part I. Errantia*. Trustees of the British Museum (Natural History), London: 458 pp.

Desière, M. (1967): Morphologie de l'organe buccal ventral de *Marphysa bellii* (Audouin and Edwards) (Polychete, Eunicidae). *Annales de la Société Royale Zoologique de Belgique* 97: 65–90.

Eakin, R.M. & Hermans, C.O. (1988): Eyes. *Microfauna Marina* 4: 135–156.

Ehlers, E. (1868): *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Volume II*. Wilhelm Engelmann, Leipzig: 269–748.

Ehlers, E. (1887): Reports on the results of dredging, under the direction of L. F. Pourtales, during the years 1868–1870, and of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea (1878–79), in the U.S. Coast Survey Steamer Blake: Report on the Annelida. *Memoirs of the Museum of Comparative Zoology at Harvard College* 15: 1–335.

El Barhoumi, M., Scaps, P. & Zghal, F. (2013): Reproductive cycle of *Marphysa sanguinea* (Montagu, 1815) (Polychaeta: Eunicidae) in the Lagoon of Tunis. *The Scientific World Journal* 2013: ID624197.

Elgetany, A.H., El-Ghobashy, A.E., Ghoneim, A.M. & Struck, T.H. (2018): Description of a new species of the genus *Marphysa* (Eunicidae), *Marphysa aegypti* sp.n., based on molecular and morphological evidence. *Invertebrate Zoology* 15: 71–84.

Fauchald, K. (1969): A revision of six species of the flavus-bidentatus group of *Eunice* (Eunicidae: Polychaeta). *Smithsonian Contributions to Zoology* 6: 1–15.

Fauchald, K. (1970): Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in Marine Biology* 5: 1–335.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–188.

Fauchald, K. (1987): Redescription of the genus *Nauphanta* Kinberg, 1865 (Polychaeta, Eunicidae). *Proceedings of the Biological Society of Washington* 100: 375–380.

Fauchald, K. (1992a): A review of the genus *Eunice* (Eunicidae: Polychaeta) based upon type material. *Smithsonian Contributions to Zoology* 523: 1–422.

Fauchald, K. (1992b): Review of the types of *Palola* (Eunicidae: Polychaeta). *Journal of Natural History* 26: 1177–1225.

Fauvel, P. (1923): *Faune de France. 5. Polychètes Errantes.* Paris: Paul Lechevalier. 488 pp.

Gambi, M.C. (1994): Polychaetes of commercial and applied interest in Italy: An overview. *Mémoires du Muséum National D'histoire Naturelle* 162: 593–601.

Gambi, M.C. (2002): Spatio-temporal distribution and ecological role of polychaete borers of *Posidonia oceanica* (L.) Delile scales. *Bulletin of Marine Science* 71: 1323–1331.

Gambi, M.C. & Cigliano, A. (2006): Observations on reproductive features of three species of Eunicidae (Polychaeta) associated with *Posidonia oceanica* seagrass meadows in the Mediterranean Sea. *Scientia Marina* 70: 301–308.

Gambi, M.C., van Tussenbroek, B.I. & Brearley, A. (2003): Mesofaunal borers in seagrasses: World-wide occurrence and a new record of boring polychaetes in the Mexican Caribbean. *Aquatic Botany* 76: 65–77.

Garcês, J.P. & Pereira, J. (2011): Effect of salinity on survival and growth of *Marphysa sanguinea* Montagu (1813) juveniles. *Aquaculture International* 19: 523–530.

Gathof, J.M. (1984): Family Eunicidae Savigny, 1818. In: Uebelacker, J.M. & Johnson, P.G. (eds.) *Polychaetes of the Northern Gulf of Mexico*. U.S. Department of the Interior Mineral Management Service Gulf of Mexico OCS, Metairie: 6: 1–31.

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Giangrande, A. (1989): Observations on recruitment and growth of *Eunice harassii* Audouin & Milne Edwards (Polychaeta, Eunicidae) in the Mediterranean Sea. *Vie Milieu* 39: 135–141.

Glasby, C.J. & Hutchings, P.A. (2010): A new species of *Marphysa* Quatrefages, 1865 (Polychaeta: Eunicida: Eunicidae) including the genus *Nauphanta* Kinberg, 1865. *Zootaxa* 45: 29–45.

Goldstein, M.C., Carson, H.S. & Eriksen, M. (2014): Relationship of diversity and habitat area in North Pacific plastic-associated rafting communities. *Marine Biology* 161: 1441–1453.

Goodrich, E.S. (1945): The study of nephridia and genital ducts since 1895. *Quarterly Journal of Microscopical Science, London* 86: 113–392.

Graber, V. (1880): Morphologische Untersuchungen über die Augen der freilebenden marinen Borstenwürmer. *Archiv für mikroskopische Anatomie* 17: 243–324.

Gravier, C. (1900): Contribution à l'étude des Annélides Polychètes de la Mer Rouge. Première partie. *Nouvelles Archives du Muséum d'Histoire Naturelle Paris* 2: 137–282.

Gravier, C. & Dantan, J.L. (1928): Peches nocturnes a la lumiere dans la Baie d'Alger. Annelides polychetes. *Annales de l'Institut Océanographique, Paris* 5: 1–187.

Grube, A.E. (1840): *Actinien, Echinodermen und Würmer des Adriatischen und Mittelmeers nach eigenen Sammlungen beschrieben*. J.H. Bon, Königsberg: 92 pp.

Grube, A.E. (1850): Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin* 16: 249–364.

Grube, A.E. (1856): Annulata Örstediana. Enumeratio Annulatorum, quae in itinere per Indiam occidentalem et Americam centralem annis 1845–1848 suscepto legit cl. A.S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad Americam meridionalem collectis. *Vidensk. Meddelelser fra Dansk naturhistorisk Foren. i Kobenhavn* 1: 44–62.

Grube, A.E. (1878): Untersuchungen über die Familie Eunicea. *Schlesische Gesellschaft für vaterländische Cultur. Jahres-Bericht* 55: 79–104.

Hanley, J.R. (1986): Co-operative effort in a new species of tube dwelling worm, *Eunice metatropos* (Polychaeta: Eunicidae). *The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences* 3: 215–221.

Hartman, O. (1938): Descriptions of new species and new generic records of polychaetous annelids from California of the families Glyceridae, Eunicidae, Stauronereidae, and Opheliidae. *University of California Publications in Zoology* 43: 93–111.

Hartman, O. (1944): Polychaetous Annelids. Part V. Eunicea. *Allan Hancock Pacific Expeditions* 10: 1–237.

Hartman, O. (1948): The marine annelids erected by Kinberg. With some notes on some other types in the Swedish State Museum. *Arkiv för Zoologi* 42A: 1–137.

Hartman, O. (1959): Catalogue ot the polychaetous annelids of the world Part I. *Allan Hancock Foundation Publications, Ocasional Paper* 23: 1–353.

Hartmann-Schröder, G. (1984): Die Polychaeten der antiborealen Südküste Australiens (zwischen Albany im Westen und Ceduna im Osten). Teil 10. In: Hartmann-Schröder G, Hartmann G, editors. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 81: 7–62.

Hartmann-Schröder, G. (1998): Remarks on *Tibiana* and description of species *Eunice* with zigzag-shaped tubes (Polychaeta: Eunicidae). *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 95: 45–48.

Hartmann-Schröder, G. & Zibrowius, H. (1998): Polychaeta associated with Antipatharia (Cnidaria: Anthozoa): description of Polynoidae and Eunicidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 95: 29–44.

Hauenschild, C., Fischer, A. & Hofmann, D. (1968): Untersuchungen am pazifischen Paolowurm *Eunice viridis* (Polychaeta) in Samoa. *Helgoländer wissenschaftliche Meeresuntersuchungen* 18: 254–295.

Hausen, H. (2005): Chaetae and chaetogenesis in polychaetes (Annelida). *Hydrobiologia* 535/536: 37–52.

Hayashi, I. & Yamane, S. (1994): On a probable sense organ newly found in some eunicid polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 74: 765–770.

Hayashi, K., Miyata, T. & Hamano, T. (1996): Chromosome number of eunicid Polychaete *Marphysa sanguinea*. *Fisheries Science* 62: 329–330.

Heider, K. (1925): Über *Eunice*. Systematisches, Kiefersack, Nervensystems. *Zeitschrift für wissenschaftliche Zoologie* 125: 55–90.

Herpin, R. (1925): Recherches biologiques sur la reproduction et le développement de quelques Annélides polychètes. *Bulletin de la Société des Sciences Naturelles de l'ouest de Frances* 5: 1–250.

Hilbig, B. (1986): Vergleichende licht- und elektronenmikroskopische Untersuchungen an Cuticula, Epidermis and Borsten einiger Eunicida (Polychaeta, Annelida). II. Epidermale Drüsen. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 114: 371–400.

Hofmann, D.K. (1969): Untersuchungen über die Regeneration des Prostomiums und die Hinterenden beim Polychaeten *Eunice viridis* Gray. *Zoologischer Anzeiger* 33: 253–260.

Horst, R. (1902): Over de "wawo" van Rumphius (*Lysidice oele* n. sp.). In: *Rumphius Gedenkboek*. Koloniaal Museum, Haarlem: 105–108.

Hutchings, P.A. (1986): Biological destruction of coral reefs. *Coral Reefs* 4: 239–252.

Hutchings, P.A. & Karageorgopoulos, P. (2003): Designation of a neotype of *Marphysa sanguinea* (Montagu, 1813) and a description of a new species of *Marphysa* from eastern Australia. *Hydrobiologia* 496: 87–94.

Hutchings, P. & Kupriyanova, E. (2017): Cosmopolitan polychaetes — Fact or fiction? Personal and historical perspectives. *Invertebrate Systematics* 31: 1–9.

Iannotta, M.A., Gambi, M.C. & Patti, F.P. (2009): Molecular evidence of intraspecific variability in *Lysidice ninetta* (Polychaeta: Eunicidae) in the Mediterranean Sea. *Aquatic Biology* 6: 121–132.

Idris, I., Hutchings, P. & Arshad, A. (2014): Description of a new species of *Marphysa* Quatrefages, 1865 (Polychaeta: Eunicidae) from the west coast of Peninsular Malaysia and comparisons with species from Marphysa Group A from the Indo-West Pacific and Indian Ocean. *Memoirs of Museum Victoria* 71: 109–121.

Imai, I. (1975): On the development and the spawning behavior of the polychaete worm *Marphysa sanguinea* (Montagu). *Aquaculture* 23: 14–20.

Iwasaki, K., Kimura, T., Kinoshita, K., Yamaguchi, T., Nishikawa, T., Nishi, E., Yamanishi, R., Hayashi, I., Okoshi, K., Kosuge, T., Suzuki, T., Henmi, Y., Furota, T. & Mukai, H. (2004): Human-mediated introduction and dispersal of marine

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

organisms in Japan: Results of a questionnarire survey by the Committee for the Preservation of the Natural Environment, the Japanese Association of Benthology. *Japanese Journal of Benthology* 59: 22–44.

Izuka, A. (1912): The errantiate Polychaeta of Japan. *Journal of the College of Science, Imperial University of Tokyo* 30: 1–262.

Jacoby, C.A., Wallner, B.G., Langtry, S.K. & Hutchings, P.A. (1995): Deepwater fauna and flora. In: Cho, G., Georges, A., Stoutjesdijk, R. & Longmore, R. (eds.), *Jervis Bay — A Place of Cultural, Scientific and Educational Value*. Australian Nature Conservation Agency, Canberra: 157–162.

Jourdan, E. (1887): Études histologiques sur deux espèces du genre *Eunice*. *Annales des sciences naturelles, Zoologie* 2: 239–304.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Kielan-Jaworowska, Z. (1966): Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica* 16: 9–152.

Kihia, C.M., Waigwa, S.W. & Munyaka, J.M. (2017): Polychaete (*Marphysa mosambica*) morphometrics, and their use in the estimation of whole polychaete size and breeding values of bait exploited by artisanal fishers at the Kenyan coastline. *Advances in Ecological and Environmental Research*: 1–13.

Kim, K.H., Kim, B.K., Kim, S.K., Phoo, W.W., Venmathi Maran, B.A. & Kim, C.-H. (2017): Appropriate feeding for early juvenile stages of eunicid polychaete *Marphysa sanguinea*. *Fisheries and Aquatic Sciences* 20: 19.

Kinberg, J.G.H. (1865): Annulata nova. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 21: 559–574.

Kise, H. & Reimer, J.D. (2016): Unexpected diversity and a new species of *Epizoanthus* (Anthozoa, Hexacorallia) attached to eunicid worm tubes from the Pacific Ocean. *Zookeys* 2016: 49–71.

Kott, P. (1951): Nereidae and Eunicidae of south Western Australia; also notes on the ecology of Western Australian limestone reefs. *Journal of the Royal Society of Western Australia* 35: 85–130.

Krishnamoorthi, B. & Krishnaswamy, S. (1966): Physiological studies on *Marphysa gravelyi* Southern. IV. Structure of nephridia. *Journal of Marine Biological Association of India* 8: 244–253.

Kurt Şahin, G.K. & Çinar, M.E. (2009): Eunicidae (Polychaeta) species in and around İskenderun Bay (Levantine Sea , Eastern Mediterranean) with a new alien species for the Mediterranean Sea and a re-description of *Lysidice collaris*. *Turkish Journal of Zoology* 33: 331–347.

Lachat, J. & Haag-Wackernagel, D. (2016): Novel mobbing strategies of a fish population against a sessile annelid predator. *Scientific Reports* 6: 33–187.

Lamarck, J.B. de (1816): *Histoire naturelle des animaux sans vertèbres: présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent: précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie, v. 2*. Deterville Libraire & Verdiere Libraire, Paris: 568 pp.

Lamarck, J.B. de (1818): *Histoire naturelle des animaux sans vertèbres: présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent: précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie, v. 5*. Deterville Libraire & Verdiere Libraire, Paris: 612 pp.

Lavesque, N., Daffe, G., Bonifácio, P. & Hutchings, P. (2017): A new species of the *Marphysa sanguinea* complex from French waters (Bay of Biscay, NE Atlantic) (Annelida, Eunicidae). *Zookeys* 716: 1–17.

Lavesque, N., Daffe, G., Grall, J., Zanol, J., Gouillieux, B. & Hutchings, P. (2019): Guess who? On the importance of using appropriate name: Case study of *Marphysa sanguinea* (Montagu, 1813). *Zookeys* 2019: 1–15.

Lewis, C. & Karageorgopoulos, P. (2008): A new species of *Marphysa* (Eunicidae) from the western Cape of South Africa. *Journal of the Marine Biological Association of the United Kingdom* 88: 277–287.

Linnaeus, C. (1758): *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*. Stockholm 1–824.

Linnaeus, C. (1767): *Systema naturae per regne tria nalurae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*. Stockholm: 533–1327.

Liu, Y., Hutchings, P. & Sun, S. (2017): Three new species of *Marphysa* Quatrefages, 1865 (Polychaeta: Eunicida: Eunicidae) from the south coast of China and redescription of *Marphysa sinensis* Monro, 1934. *Zootaxa* 4263: 228–250.

Lu, H. & Fauchald, K. (2000): A phylogenetic and biogeographic study of *Euniphysa* (Eunicidae, Polychaeta). *Journal of Natural History* 34: 997–1044.

Malathi, E., Sunder Raj, S.K. & Mercy Bai, P. (2011): Larval development of *Marphysa gravelyi* (Polychaeta: Eunicidae) from Pulicat Lake, India. *Italian Journal of Zoology* 78: 249–254.

Malathi, E., Collette, M.J. & Priscilla, A.L. (2017): Biochemical composition and function of jelly masses of *Marphysa gravelyi* (Polychaeta: Eunicidae) from Pulicat Lake, India. *Journal of the Marine Biological Association of the United Kingdom* 97: 1135–1141.

Malmgren, A.J. (1867): Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 24: 127–235.

Martens, J.M., Heuer, U. & Hartmann-Schröder, G. (1995): Massenschwärmen des Südsee-Palolowurms (*Palola viridis* Gray) und weiterer Polychaeten wie *Lysidice oele* Horst und *Lumbrineris natans* n. sp. auf Ambon (Molukken: Inodnesien). *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 92: 7–34.

Martin, D., Gil, J., Zanol, J., Meca, M.A. & Portela, R.P. (2020): Digging the diversity of Iberian bait worms *Marphysa* (Annelida, Eunicidae). *PLoS One* 15: e0226749.

Mayer, A.G. (1900): An Atlantic palolo, *Staurocephalus gregaricus*. *Bulletin of the Museum of Comparative Zoology* 36: 1–14.

Mayer, A.G. (1902): The Atlantic palolo. *The Museum of the Brooklyn Institute of Arts and Sciences Science Bulletin* 1: 93–103.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S.Challenger during the years 1872–76* 12: 1–554.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

McIntosh, W.C. (1910): A monograph of the British annelids. Polychaeta. Syllidae to Ariciidae. *Ray Society of London* 2: 233–524.

Miura, T. (1977): Eunicid polychaetous annelida from Japan — II. La Mer. *Bulletin de la Société Franco-Japonaise d´Océanographie* 15: 61–81.

Miura, T. (1986): Japanese polychaetes of the genera *Eunice* and *Euniphysa*: Taxonomy and branchial distribution patterns. *Publications of the Seto Marine Biological Laboratory* 31: 269–325.

Molina-Acevedo, I.C. (2018): Morphological revision of the Subgroup 1 Fauchald, 1970 of *Marphysa* de Quatrefages, 1865 (Eunicidae: Polychaeta). *Zootaxa* 1: 1–125.

Molina-Acevedo, I.C. (2019): Redescription of two species previously regarded as *Marphysa* de Quatrefages, 1865, with the description of new species of *Treadwellphysa* Molina-Acevedo and Carrera-Parra, 2017. *Journal of Natural History* 53: 517–540.

Molina-Acevedo, I.C. & Carrera-Parra, L.F. (2015): Reinstatement of three species of the *Marphysa sanguinea* complex (Polychaeta: Eunicidae) from the Grand Caribbean Region. *Zootaxa* 3925: 37–55.

Molina-Acevedo, I.C. & Carrera-Parra, L.F. (2017): Revision of *Marphysa* de Quatrefages, 1865 and some species of *Nicidion* Kinberg, 1865 with the erection of a new genus (Polychaeta: Eunicidae) from the Grand Caribbean. *Zootaxa* 4241: 1–62.

Molodtsova, T. & Budaeva, N. (2007): Modifications of corallum morphology in black corals as an effect of associated fauna. *Bulletin of Marine Science* 81: 469-479.

Molodtsova, T.N., Britayev, T.A. & Martin, D. (2016): Cnidarian and their polychaete symbionts. In: Goffredo, S. & Dubinsky, Z. (eds.), *The Cnidaria, Past, Present and Future*. Springer International Publishing, Heidelberg: 387–413.

Montagu, G. (1813): Descriptions of several new or rare animals principally marine, found on the south coast of Devonshire. *Transactions of the Linnean Society of London* 11: 18–21.

Mortensen, P.B. (2001): Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. *Ophelia* 54: 83–104.

Mueller, C.E., Lundälv, T., Middelburg, J.J. & Oevelen, D. van (2013): The symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. *PLoS One* 8: e58660.

Müller, O.F. (1776): *Zoologicae Danicae Prodromus: seu Animalium Daniae et Norvegiae indigenarum characteres nomina; et synonyma imprimis popularium*. Typiis Hallageriis, Hafniae, Copenhagen: 282 pp.

Neves, G. & Omena, E. (2003): Influence of sponge morphology on the composition of the polychaete associated fauna from Rocas Atoll, northeast Brazil. *Coral Reefs* 22: 123–129.

Nogueira, J.M.M., Steiner, T.M. & Amaral, A.C.Z. (2001): Descriptions of two new species of *Eunice* Cuvier, 1817 (Polychaeta: Eunicidae) from coastal islands of the State of Sao Paulo, Brazil. *Scientia Marina* 65: 47–57.

Nonato, E.F. (1965): *Eunice sebastiani* sp. nov. (Annelida, Polychaeta). *Boletim do Instituto Oceanográfico* 14: 133–139.

Orensanz, J.M. (1990): The Eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Antarctic Research Series* 52: 1–183.

Orrhage, L. (1995): On the innervation and homologues of the anterior end appendages of the Eunicea (Polychaeta), with a tentative outline of the fundamental constitution of the cephalic nervous system of the Polychaetes. *Acta Zoologica* 76: 229–248.

Pallas, P.S. (1788): Marina varia nova et rariora. *Nova Acta Academiae Scientiarum imperialis Petropolitanea* 2: 229–249.

Pamungkas, J. (2015): Species richness and macronutrient content of wawo worms (Polychaeta, Annelida) from Ambonese waters, Maluku, Indonesia. *Biodiveristy Data Journal* 3: e4251.

Parandavar, H., Kim, K.H. & Kim, C.H. (2015): Effects of rearing density on growth of the polychaete rockworm *Marphysa sanguinea*. *Fisheries and Aquatic Science* 18: 57–63.

Parapar, J., Freire, J., Urgorri, V. & Besteiro, C. (1993): Morphological variability in *Eunice vittata* (Chiaje, 1828) (Polychaeta, Eunicidae) in the Ría de Ferrol (Galicia, NW Spain). *Ophelia* 37: 117–125.

Pardo, E.V. & Amaral, A.C.Z. (2006): Foraging and mobility in three species of Aciculata (Annelida: Polychaeta). *Brazilian Journal of Biology* 66: 1065–1072.

Paxton, H. (1986): Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). *Records of the Australian Museum* 38: 1–74.

Paxton, H. (1998): The *Diopatra chiliensis* confusion — redescription of *D. chiliensis* (Polychaeta, Onuphidae) and implicated species. *Zoologica Scripta* 27: 31–48.

Paxton, H. (2009): Phylogeny of Eunicida (Annelida) based on morphology of jaws. *Zoosymposia* 264: 241–264.

Paxton, H. & Eriksson, M.E. (2012): Ghosts from the past — Ancestral features reflected in the jaw ontogeny of the polychaetous annelids *Marphysa fauchaldi* (Eunicidae) and *Diopatra aciculata* (Onuphidae). *Gff* 134: 309–316.

Peters, W.C.H. (1854): Über die Gattung *Bdella*, Savigny (Limnatis, Moquin-Tandon) und die in Mossambique beobachteten Anneliden, wovon hier eine Mittheilung folgt [informal title in meeting report]. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* 1854: 607–614.

Pettibone, M.H. (1963): Marine polychate worms of the New England region Part 1. Aphroditidae through Trochochetidae. *United States National Museum Bulletin* 227: 1–356.

Pillai, T.G. (1958): Studies on a brackish-water polychaetous annelid, *Marphysa borradailei*, sp. n. from Ceylon. *Ceylon Journal of Science (Biological Sciences)* 1: 94–106.

Prentiss, N.K. & Harris, L.H. (2011): Polychaete fauna inhabiting sediments associated with the stinking vase sponge (*Ircinia campana* Lamarck, 1814), St. John, United States Virgin Islands. *Italian Journal of Zoology* 78: 317–323.

Prevedelli, D., N'siala, G.M., Ansaloni, I. & Simonini, R. (2007): Life cycle of *Marphysa sanguinea* (Polychaeta: Eunicidae) in the Venice Lagoon (Italy). *Marine Ecology* 28: 1–10.

Pruvot, G. (1885): Recherches anatomiques et morphologiques sur le système nerveux des annélides polychètes. *Archives de Zoologie Expérimentale et Générale* 3: 211–326.

Pruvot, G. & Racovitza, É.G. (1895): Matériaux pour la faune des annélides de Banyuls. *Archives de Zoologie Expérimentale et Générale* 3: 339–342.

Purschke, G. (1988): Pharynx. *Microfauna Marina* 4: 177–197.

Purschke, G. (2005): Sense organs in polychaetes (Annelida). *Hydrobiologia* 5353/536: 53–78.

Purschke, G. & Hausen, H. (2007): Lateral organs in sedentary polychaetes (Annelida) — Ultrastructure and phylogenetic significance of an insufficiently known sense organ. *Acta Zoologica* 39: 23–39.

Quatrefages, A. de (1865): Note sur la classification des Annélides. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 60: 586–600.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

Quatrefages, A. de (1866): *Histoire naturelle des Annelés marins et d'eau douce: Annélides et Géphyriens. Tome 1*. Librarie Encyclopédique de Roret, Paris: 588 pp.

Read, G.B. (2019): A history of annelid research. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.), *The Handbook of Zoology. Annelida. Volume 1: Annelida. Basal Groups and Pleistoannelida, Sedentaria I*. DeGruyter, Berlin: 3–36.

Richards, T.L. (1967): Reproduction and development of the polychaete *Stauronereis rudolphi*, including a summary of development in the superfamily Eunicea. *Marine Biology* 1: 124–133.

Roberts, J.M. (2005): Reef-aggregating behaviour by symbiotic eunicid polychaetes from cold-water corals: Do worms assemble reefs? *Journal of the Marine Biological Association of the United Kingdom* 85: 813–819.

Rouse, G.W. (1999): Trochophore concepts: Ciliary bands and the evolution of larvae in spiralian Metazoa. *Biological Journal of the Linnean Society* 66: 411–464.

Rouse, G.W. (2000): Bias? What bias? The evolution of downstream larval-feeding in animals. *Zoologica Scripta* 29: 213–236.

Sá, E., Costa, P.F. e, Fonseca, L.C. da, Alves, A.S., Castro, N., Cabral, S. dos S., Chainho, P., Canning-Clode, J., Melo, P., Pombo, A.M. & Costa, J.L. (2017): Trade of live bait in Portugal and risks of introduction of non-indigenous species associated to importation. *Ocean and Coastal Management* 146: 121–128.

Saito, H., Kawai, K., Umino, T. & Imabayashi, H. (2014): Fishing bait worm supplies in Japan in relation to their physiological traits. *Memoirs of Museum Victoria* 71: 279–287.

Salazar-Vallejo, S.I., Carrera-Parra, L.F. & León-González, J.A. De (2011): Giant Eunicid Polychaetes (Annelida) in shallow tropical and temperate seas. *Revista de Biologia Tropical* 59: 1463–1474.

Savigny, J.C. (1820): Systeme des annelides, principalement de celles des cotes de l'Egypte et de la Syrie, offrant les caracteres tant distinctifs que naturels des ordres, families et genres, avec la description des especes. *Description de l'Egypte Histoire Naturelle, Paris* 1: 1–128.

Schmarda, L.K. (1861): *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise un die Erde 1853 bis 1857. Erster Band (zweite Hälfte) Turbellarien, Rotatorien und Anneliden*. Wilhelm Engelmann, Leipzig: 164 pp.

Schmidt, O. (1880a): Die Spongien des Meerbusen von Mexico (Und des caraibischen Meeres). Heft II. Abtheilung II. Hexactinelliden. In: *Reports on the Dredging under the Supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS 'Blake'*. Gustav Fischer, Jena: 33–90.

Schmidt, O. (1880b): Die Spongien des Meerbusen von Mexico (Und des caraibischen Meeres). Heft II. Abtheilung III. Tetractinelliden. In: *Reports on the Dredging under the Supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS 'Blake'*. Gustav Fischer, Jena: 33–90.

Schulze, A. (2006): Phylogeny and genetic diversity of Palolo worms (*Palola*, Eunicidae) from the tropical North Pacific. *Biological Bulletin* 210: 25–37.

Schulze, A. (2011): The Bobbit worm dilemma: A case for DNA. *Revista de Biologia Tropical* 59: 1475–1477.

Schulze, A. & Timm, L.E. (2011): *Palolo* and *un*: Distinct clades in the genus *Palola* (Eunicidae: Polychaeta). *Marine Biodiversity* 42: 161–171.

Seo, J.K., Nam, B.H., Go, H.J., Jeong, M., Lee, K.Y., Cho, S.M., Lee, I.A. & Park, N.G. (2016): Hemerythrin-related antimicrobial peptide, msHemerycin, purified from the body of the lugworm, *Marphysa sanguinea*. *Shellfish, Fish & Immunology* 57: 49–59.

Shen, S. & Wu, B.L. (1990): A new family of Polychaeta. *Acta Oceanologica Sinica* 12: 765–772. [in Chinese]

Shen, S. & Wu, B.L. (1991): A new family of Polychaeta-Euniphysidae. *Acta Oceanologica Sinica* 10: 129–140. [English version of the 1990 paper]

Southern, R. (1921): Polychaeta of the Chilka Lake and also of fresh and brackish water in other parts of India. *Memoirs of the Indian Museum* 4: 563–659.

Stair, J.B. (1847): An account of *Palolo*, a sea-worm eaten in the Navigator Islands, with a description by J.E. Gray. *Proceedings of the Zoological Society of London* 15: 17–18.

Steiner, T. & Amaral, A.C.Z. (2000): Two new species of *Marphysa* Quatrefages, 1865 (Eunicidae, Polychaeta) from intertidal sandy beaches of the São Sebastião Channel, State of São Paulo (Brazil). *Bulletin of Marine Science* 67: 479–489.

Stewart, C. (1881): On a supposed new boring annelid. *Journal of the Royal Microscopical Society* 1: 717–719.

Struck, T.H., Purschke, G. & Halanych, K.M. (2006): Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach. *Systematic Biology* 55: 1–20.

Suschenko, D. & Purschke, G. (2009): Ultrastructure of pigmented adult eyes in errant polychaetes (Annelida): Implications for annelid evolution. *Zoomorphology* 128: 75–96.

Tampi, P.R.S. (1949): On the eyes of polychaetes. *Proceedings of the Indian Academy of Science Section B* 29: 129–147.

Tampi, P.R.S. & Rangarajan, K. (1964): Some polychaetous annelids from the Andaman waters. *Journal of Marine Biological Association of India* 6: 98–123.

Thiel, M. & Gutow, L. (2005): The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review* 43: 279–418.

Thompson, I. & Johnson, R.G. (1977): New fossil polychaete from Essex, Illinois. *Fieldiana Geology* 33: 471–487.

Treadwell, A.L. (1921): Leodicidae of the West Indian region. *Carnegie Institute of Washington Publication* 15: 1–131.

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535/536: 199–225.

Verrill, A.E. (1900): Additions to the Turbellaria, Nemertina, and Annelida of the Bermudas, with revisions of some New England genera and species. *Transactions of the Connecticut Academy of Arts and Sciences* 10: 595–671.

Von Haffner, K. (1959): Über den Bau und den Zusammenhang der wichtigsten Organe des Kopfendes von *Hyalinoecia tubicola* Malmgren (Polychaeta, Euncidae, Onuphidinae), mit Berücksichtigung der Gattung *Eunice*. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 77: 133–192.

Von Haffner, K. (1961): Der Bau und die Verwandschaftsbeziehungen des Palolowurmes *Eunice viridis* Gray (Polychaeta, Eunicidae). *Internationale Revue der gesammten Hydrobiologie* 46: 184–204.

Von Haffner, K. (1962): Über die Abhängigkeit des Gehirnbaues von den Sinnesorganen. Vergleichende Untersuchungen an Euniciden (Polychaeta). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 80: 159–212.

EBSCOhost - printed on 2/13/2023 2:51 PM via . All use subject to https://www.ebsco.com/terms-of-use

von Palubitzki, T. & Purschke, G. (2020): Ultrastructure of pigmented eyes in Onuphidae and Eunicidae (Annelida: Errantia: Eunicida) and its importance in understanding the evolution of eyes in Annelida. *Zoomorphology* 139: 1–19.
Wagner, N. (1885): *Die Wirbellosen des Weissen Meeres. Zoologische Forschungen an der Kueste des Solowetzkischen Meeresbusens in dem Sommermonaten der Jahre 1877, 1879 und 1882. Volume 1.* Wilhelm Engelman, Leipzig: 171 pp.
Weber, R.E. (1978): Respiratory pigments. In: Mill, P.J. (ed.), *Physiology of Annelids*. Academic Press, London: 393–446.
Weber, R.E., Bonaventura, J., Sullivan, B. & Bonaventura, C. (1978): Oxygen equilibria and ligand-binding kinetics of erythrocruorins from two burrowing polychaetes of different modes of life, *Marphysa sanguinea* and *Diopatra cuprea*. *Journal of Comparative Physiology* 123: 177–184.
Wesenberg-Lund, E. (1949): Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran* 4: 247–400.
Winsnes, I.M. (1989): Eunicid polychaetes (Annelida) from Scandinavian and adjacent waters. Family Eunicidae. *Zoologica Scripta* 18: 483–500.
Wolf, G. (1980): Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). *Senckenbergiana maritima* 12: 1–182.
Wu, Q.Q. & He, M.H. (1988): A new genus and new species of Eunicidae from Taiwan Strait. *Acta Zootaxonomica Sinica* 13: 123–126.
Yokoe, Y. & Yasumasu, I. (1964): The distribution of cellulase in invertebrates. *Comparative Biochemistry and Physiology* 13: 323–338.
Zanol, J. (2010): Homology of prostomial and pharyngeal structures in Eunicida (Annelida) based on innervation and morphological similarities. *Journal of Morphology* 271: 1023–1043.
Zanol, J. & Bettoso, N. (2006): Identity of *Eunice roussaei* (Eunicidae: Polychaeta: Annelida) from the Adriatic and Mediterranean seas. *Journal of the Marine Biological Association of the United Kingdom* 86: 1017–1024.
Zanol, J., Fauchald, K. & Paiva, P.C. (2007): A phylogenetic analysis of the genus *Eunice* (Eunicidae, polychaete, Annelida). *Zoological Journal of the Linnean Society* 150: 413–434.
Zanol, J., Halanych, K.M., Struck, T.H. & Fauchald, K. (2010): Phylogeny of the bristle worm family Eunicidae (Eunicida, Annelida) and the phylogenetic utility of noncongruent 16S, COI and 18S in combined analyses. *Molecular Phylogenetics and Evolution* 55: 660–676.
Zanol, J., Halanych, K.M. & Fauchald, K. (2014): Reconciling taxonomy and phylogeny in the bristleworm family Eunicidae (polychaete, Annelida). *Zoologica Scripta* 43: 79–100.
Zanol, J., Silva, T. dos S.C. da & Hutchings, P. (2016): *Marphysa* (Eunicidae, polychaete, Annelida) species of the Sanguinea group from Australia, with comments on pseudo-cryptic species. *Invertebrate Biology* 135: 328–344.
Zanol, J., Silva, T. dos S.C. da & Hutchings, P. (2017): One new species and two redescriptions of *Marphysa* (Eunicidae, Annelida) species of the Aenea-group from Australia. *Zootaxa* 4268: 411–426.
Zanol, J., Hutchings, P.A. & Fauchald, K. (2020). *Eunice sensu latu* (Annelida: Eunicidae) from Australia: description of seven new species and comments on previously reported species of the genera *Eunice*, *Leodice* and *Nicidion*. *Zootaxa* 4748: 1–43.

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7.12.5 Histriobdellidae Claus & Moquin-Tandon, 1884

Introduction

Histriobdellidae, the so-called "Charlie Chaplin worms," represent a group of minute marine or limnic commensal annelids that live on different crustaceans (lobsters, isopods, crayfish, etc.). On their hosts, histriobdellids mainly populate the branchial filaments, the pleopods, and/or the egg masses. Adult histriobdellids are transparent, range in size from 0.7 to about 1.5 mm, and exhibit well-developed, pigmented jaws as well as a variable segment number (9 in *Histriobdella* Van Beneden, 1858 and probably 10 or more in *Stratiodrilus* Haswell, 1900). Furthermore, a body annulation of six or more prominent regions is obvious during contraction of the animal. Currently, three genera with 13 described species are known.

Morphology

In Histriobdellidae, the anterior end bears a prominent head structure formed by the fused prostomium and peristomium (Fig. 7.12.5.1A–C). The head bears five appendages that, by definition, resemble the two laterally located sensory palps and three antennae (Fig. 7.12.5.1C). Notably, in some taxa, the antennae can be articulated (Rouse and Pleijel 2001).

Besides these five anteriormost appendages, histriobdellids bear a further pair of appendages. In the peristomial part of the head region, two adhesive muscular papillae are present (Fig. 7.12.5.1A–C). Those papillae can be retractable (in *Stratiodrilus* and *Steineridrilus* Zhang, 2014) or nonretractable (in *Histriobdella*). In general, the anterior papillae represent locomotory appendages with a well-developed adhesive duo-gland system and prominent gland openings (Fig. 7.12.5.1E) (Gelder and Jennings 1975, Gelder and Tyler 1986). In addition to the head appendages, histriobdellids show cirrus-like structures along the body. In both *Steineridrilus* and *Stratiodrilus*, the external segments 2 and 3 possess two pairs of cirrus-like appendages, whereas on segment 5 only one pair can be found (Rouse and Pleijel 2001). Although comparative morphological investigations are still pending, these cirrus-like structures might be homologous to the parapodial cirri of other annelid groups (Rouse and Pleijel 2001). In males, another type of distinct body appendage — the

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paired claspers — is present (Fig. 7.12.5.1G). Those claspers are situated laterally at segment 4, can be everted at least in *Histriobdella homari*, and are used during the process of copulation. Remarkably, those male claspers show similarities to the anterior papillae based on external features (Haswell 1900, Shearer 1910, Harrison 1928).

The foot-like structures at the posterior end of the body is another distinct type of appendages present in all histriobdellids (Fig. 7.12.5.1A, B). Similar to the anterior appendages, they are also used for locomotion and bear an adhesive duo-gland system with external glandular openings (Gelder and Tyler 1986). Nevertheless, the homology of the feet-like structures is unclear and needs further investigations. In *Histriobdella*, small nonarticulated cirrus-like appendages (sometimes called tubercles) are situated at each foot-like appendage (Fig. 7.12.5.1B, D). In *Steineridrilus* and *Stratiodrilus*, there can be up to four such tubercles (e.g., Amato 2001). The anus of histriobdellids is located between the posterior appendages, but the site of the pygidium is unknown so far.

The central nervous system of Histriobdellidae consists of an anterior distinct brain, esophageal connectives, and the ventral nerve cord formed out of two neurite bundles (Fig. 7.12.5.2B). The ventral nerve cord displays distinct ganglia in intervals representing more or less the external annulation of the body (Fig. 7.12.5.2D) (Foettinger 1884, Haswell 1900, 1916, Shearer 1910, Gelder and Jennings 1975). The number of described ganglia differs between 9 in *Histriobdella homari* (see Gelder and Jennings 1975) and at least 10 in *Stratiodrilus* (see Haswell 1900, Lang 1949).

Because body appendages, such as the anterior antennae and palps as well as the various cirrus-like structures along the body, are well innervated via neurite bundles (and possess putative sensory cilia in most cases) (Fig. 7.12.5.2B), these structures should be classified as sensory organs (Shearer 1910, Gelder and Jennings 1975). Furthermore, Shearer (1910) described numerous putative sensory cilia-bearing cells distributed over the entire body of the animals.

Nuchal organs are present as well (Foettinger 1884, Shearer 1910, Gelder and Jennings 1975). The latter form densely ciliated pits close to the dorsolateral posterior brain boundaries. These pits are situated anterior to the dorsal bases of the anterior papillae and show a strong neuronal innervation. In all histriobdellids investigated so far, eyes are absent.

The musculature of histriobdellids has been well described by Foettinger (1884) and Haswell (1900); additional details have been added by Shearer (1910). The body wall musculature consists of four distinct bundles of longitudinal muscle fibers running along the entire body (Fig. 7.12.5.2C). Consisting of up to 30 muscle fibers, the two dorsal and two ventral bundles appear flattened dorsoventrally. Furthermore, they split up in the anterior and posterior regions and send muscle fibers innervating the jaws as well as the anterior papillae and posterior locomotory appendages. The buccal apparatus as well as the locomotory appendages bear an additional own set of muscle fibers (Fig. 7.12.5.2C). According to Shearer (1910), the body wall musculature appears reduced in *Histriobdella*, whereas *Stratiodrilus* resembles a more complex muscular system. In both cases, true circular body wall muscles are absent, but few oblique muscle bundles are located in regular intervals along the body (Tzetlin and Filippova 2005).

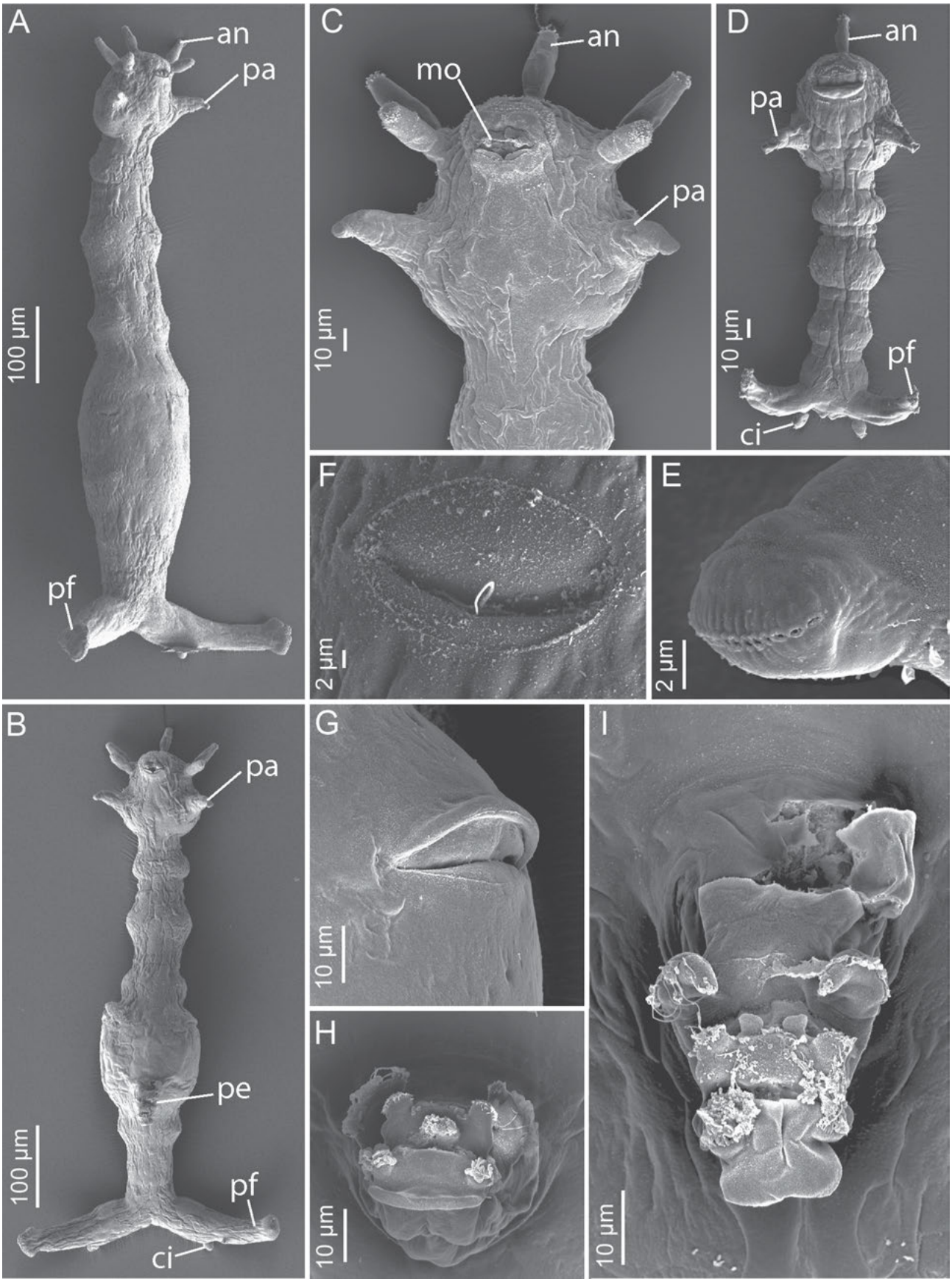
The excretory system is represented by paired protonephridia in segments 1 to 4 (in *Histriobdella*) (Fig. 7.12.5.2B) or segments 1, 2, and 5 (in *Stratiodrilus*) (Haswell 1900, 1916, Shearer 1910). The nephridial system does not seem to be related to the reproductive system.

Another character visible in Histriobdellidae is the buccal apparatus. The ventral muscular pharynx (Fig. 7.12.5.2C) is equipped with distinct eversible jaws (Fig. 7.12.5.2A). These jaws consist of ventral mandibles (Fig. 7.12.5.3B) and dorsal maxillae as typical for Eunicida (Fig. 7.12.5.3A) (see chapter Eunicida, pp. 353 ff.) (Budaeva and Zanol 2020). Although several investigations described the jaw morphology in the past, the final decision concerning the type of jaws and detailed analyses are still pending. In previous investigations, histriobdellid maxillae are called eunicid-like (Mesnil and Caullery 1922), a prionognath (Rouse and Pleijel 2001) or a ctenognath type (Tzetlin 1980), whereas Paxton (2009) suggested that the histriobdellid jaw apparatus is unlike any other.

Reproduction and development

Histriobdellids are dioecious organisms with sexual dimorphism. For sperm transfer, the males embrace the females, penetrate the female body wall using their penis, and inject sperm into the coelom. The median penis itself is situated at the ventral surface of adult animals, between segments 4 and 5 (Fig. 7.12.5.1B). Whereas in *Stratiodrilus* the penis is represented by an eversible chitinous needle-like spine with a sloped tip (Fig. 7.12.5.3C, D) (Haswell 1900), the penis in *Histriobdella homari* is exhibited by a nonchitinous but paired structure including a central duct (Fig. 7.12.5.1H, I). All histriobdellids investigated so far possess long filiform sperm cells that lack a flagellum.

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Instead, a long acrosome is accompanied by four (*Stratiodrilus*) to eight or nine (*Histriobdella*) mitochondria, which are arranged around the anterior end of a cylindrical nucleus (Jamieson et al. 1985). In histriobdellid females, the paired ovaries and oviducts lead to ventrolateral openings in segment 5 (Fig. 7.12.5.1F) (Shearer 1910). According to Shearer (1910), copulation is possible anywhere at the female body. Haswell (1900, 1913) described the transfer of spermatophores, but this observation could not be verified by other authors so far. In all cases, the mature eggs are ellipsoidal with a diameter of 100 to 213 µm (Haswell 1916, Vila and Véliz 2014). Egg-case-secreting glands are associated with the oviducts (Haswell 1916). The fertilized eggs are deposited before the onset of the first cleavage (Rouse and Pleijel 2001). Covered in a shell-like egg case, they are glued on to the branchial filaments of the hosts, coxal bases, and between the hosts' eggs (Vila and Véliz 2014, Øresland 2019).

Histriobdellids do not have free-swimming larvae. Instead, the development of the yolk-rich embryos is direct, and juveniles even possess well-developed jaws early in ontogenesis (Haswell 1916, Vila and Veliz 2014). After hatching, juveniles of *H. homari* reach a size of about 200 µm and resemble the adult worms. The only obvious differences are the body size and the lesser number of segments and anterior body appendages (Fig. 7.12.5.1D) (Shearer 1910). According to Shearer (1910) and Gelder and Jennings (1975), the development is rapid, and the juveniles reach adulthood soon after hatching.

Biology and ecology

Although first thought to be harmful parasites, Histriobdellidae are shown to be epizoic, microphagous symbionts that feed on bacterial and algal biofilms (Jennings and Gelder 1976, Cannon and Jennings 1987) and as important cleaners of their host. For *Histriobdella homari*, it was assumed that high numbers of histriobdellids could reduce the lobster hatching success (Brattey and Campbell 1985), but this view was neglected by various authors afterwards.

Histriobdella homari is known to migrate from the host's gill chambers to the female egg masses. According to Lerch and Uglem (1996), this fact is reasoned by the abundant and fast-growing bacterial fauna located at the host's eggs and larvae. Further on, a migration of *Histriobdella* is also known between different lobsters (Simon 1968). Although reported for lobsters in captivity, no investigations exist for wild populations.

For the freshwater taxon *Stratiodrilus novaehollandiae*, densities of up to 70 specimens per host are reported so far (Cannon and Jennings 1987). For the marine taxon *H. homari*, up to several thousand specimens are described per lobster (Lerch and Uglem 1996, Øresland 2019). Infection rates for the latter reach up to 100% (Uzmann 1967).

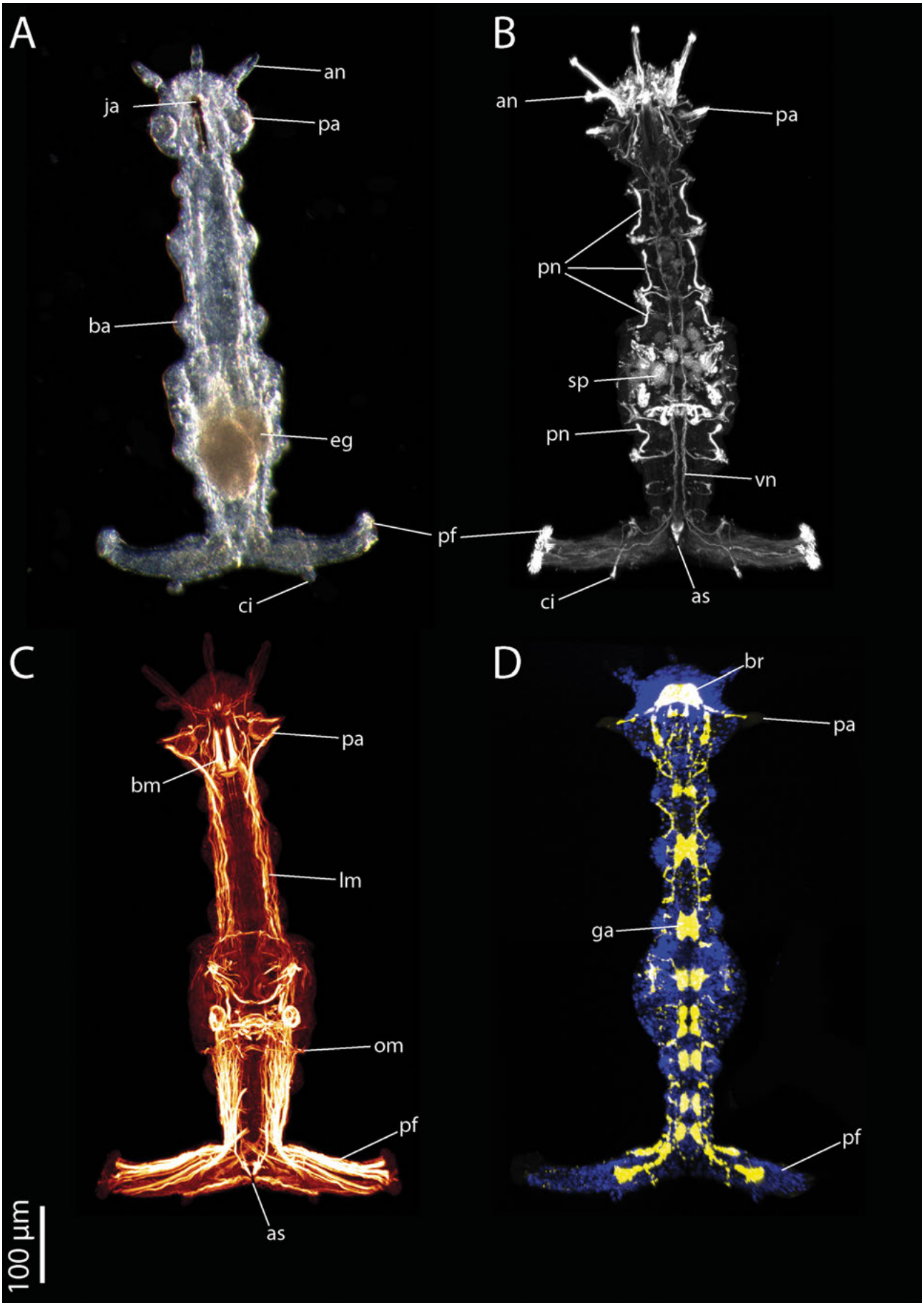
Systematics and distribution

The family name Histriobdellidae was established by Claus and Moquin-Tandon (1884) for the species *Histriobdella homari* Van Beneden, 1858 earlier described as a leech. The name was subsequently accepted by Vaillant (1890), who has been erroneously cited as the author of the family name in many publications on histriobdellids.

Due to bizarre external morphology, histriobdellids have been treated as serpulid larvae (Van Beneden 1853), leeches (Van Beneden 1858), and rotiferans (Haswell 1900, Shearer 1910) and finally placed within "archiannelids" with no clear affinity to any of the existing major annelid groups (Foettinger 1884, Haswell 1900, Hermans 1969). The affinity of histriobdellids to Eunicida has been suggested several times throughout history (Hatschek 1888, Mesnil and Caullery 1922, Jennings and Gelder 1976, Fauchald and Rouse 1997) mainly based on the presence of the complex jaw apparatus resembling that of other eunicidan families (see Paxton 2009 for review). It has become a widely accepted view, although the phylogenetic placement of Histriobdellidae within Eunicida remains unknown with very little molecular data are publicly available. Morphology-based cladistic analysis

◂ **Fig. 7.12.5.1:** External features of *Histriobdella homari* investigated via scanning electron microscopy (SEM). Anterior is up in all images. A, B, Adult female (A) and male (B) specimens exhibiting all main types of histriobdellid body appendages; C, The head is composed of the prostomium and peristomium; D, Juvenile hatchling bear fewer segments and a reduced number of head appendages; E, The anterior papillae show distinct openings of the gland system; F, The female oviduct opening in segment 5; G, The male claspers in *Histriobdella* are evertable; H, The penis in *Histriobdella* is situated ventrally between segments 4 and 5; I, The penis is evertable. an, antennae; ci, cirrus; pa, papillae; pe, penis; pf, posterior foot-like appendage; mo, mouth opening.

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by Fauchald and Rouse (1997) resulted in the placement of Histriobdellidae as sister to Diurodrilidae and basally branching relative to all other taxa, which the authors themselves considered being incorrect. Molecular phylogenetic analyses including histriobdellids as well as other eunicid families are still pending.

Current classification

Up to date, histriobdellids comprise 13 species grouped in three genera. *Histriobdella* is a monotypic genus widely spread in marine environments in the Northern Hemisphere, inhabiting both American and European lobsters (*Homarus* and *Nephrops*). *Stratiodrilus* is the largest (11 species) genus described to represent freshwater histriobdellids from the Southern Hemisphere (Tasmania, Australia, Madagascar, Chile, Argentina, Uruguay, and Brazil). The species of *Stratiodrilus* are mostly known from freshwater decapods (Steiner and Amaral 1999, Da Silva Rosa et al. 2018). Another marine monotypic genus, *Dayus* Steiner & Amaral, 1999, was proposed for the species found in isopods from a lagoon in South Africa but subsequently was shown to be a junior homonym of an earlier described insect (Cicadellidae). The taxon received the new genus name *Steineridrilus*, accommodating the only knowns species, *Steineridrilus cirolanae* Führ, 1971. The diagnoses for the family and all accepted genera are given below.

Histriobdellidae Claus & Moquin-Tandon, 1884

Diagnosis: Small and delicate, up to 1.5 mm in length. Worm-like body with indistinct and irregular annulation. Body divided into head, trunk, and posterior region. Head with prostomium rounded frontally and fused with peristomium. Eyes absent. Nuchal organs present. Five anterior appendages: single median and two lateral antennae and two palps. One pair of (partly) retractable anterior appendages, located lateroventrally on the middle part of the head; with distal adhesive glands. Trunk with five segments, last four segments with or without lateral cirri. Chaetae and aciculae absent. Posterior region composed of fused segments. Two posterior locomotory appendages with adhesive glands and cirri. Antennae, cirri, and tubercles may bear sensory cilia at distal ends. Complex symmetrical jaw apparatus black and chitinous; enclosed in ventral pharyngeal sac. Ventral mandibles and dorsal maxillae. Dioecious and sexually dimorphic. Males with one pair of lateral claspers close to fourth trunk segment and chitinous or muscular penis at the ventral side of the body. Females with one pair of lateral oviduct openings.

Histriobdella Van Beneden, 1858

Type species: *Histriobdella homari* Van Beneden, 1958
1 species.
Diagnosis: Unsegmented antennae and palps, short and with equal length; Anterior appendages not retractable. Ventral mouth. Lateral cirri absent. Posterior end composed of three fused segments with unsegmented cirri; eggs attached to host with one end.

Stratiodrilus Haswell, 1900

Type species: *Stratiodrilus tasmanicus* Haswell, 1900
11 species.
Diagnosis: Median antenna unsegmented and shorter than lateral antennae. Lateral antennae usually bisegmented; palps always longest and usually bisegmented. Anterior appendages retractable. Anterior mouth. Lateral cirri present, simple and often bisegmented; forked in one species. Posterior end composed of five fused segments, often with cirri and tubercles. Antennae, palps, cirri, and tubercles with distal sensory cilia. Eggs attached to host by their sides.

Steineridrilus Zang, 2014

Type species: *Steineridrilus cirolana*e (Führ, 1971) as *Stratiodrilus cirolanae* Führ, 1971
1 species.
Diagnosis: Median antenna bisegmented, lateral antennae unsegmented and short, palps bisegmented and

◂ **Fig. 7.12.5.2:** External and internal anatomical features of *Histriobdella homari*. A, Light microscopic image; B–D, Confocal maximum projections. The immunohistochemical images show stainings against acetylated α-tubulin (B), f-actin (C), and synapsin (D). All images are of the same scale with anterior up. A, Light microscopy reveals the body annulation (ba) and the distinct jaw apparatus (ja); B, Staining against acetylated α-tubulin shows the ventral nerve cord (vn) and the strong neuronal innervation of all body appendages; furthermore, four pairs of protonephridia are visible; C, The staining of the musculature shows the prominent longitudinal muscle fibers and the lack of circular fibers; D, Anti-synapsin staining sheds light on synaptic regions in histriobdellids, with several ganglia visible along the bod of adult animals. an, antennae; as, anus; ba, body annulation; bm, buccal musculature; br, brain; ci, cirrus; eg, egg; ga, ganglion; ja, jaw apparatus; lm, longitudinal muscle bundles; om, oblique musculture; pa, papillae; pf, posterior foot-like appendage; pn, protonephridia; sp, sperm cells; vn, ventral nerve cord.

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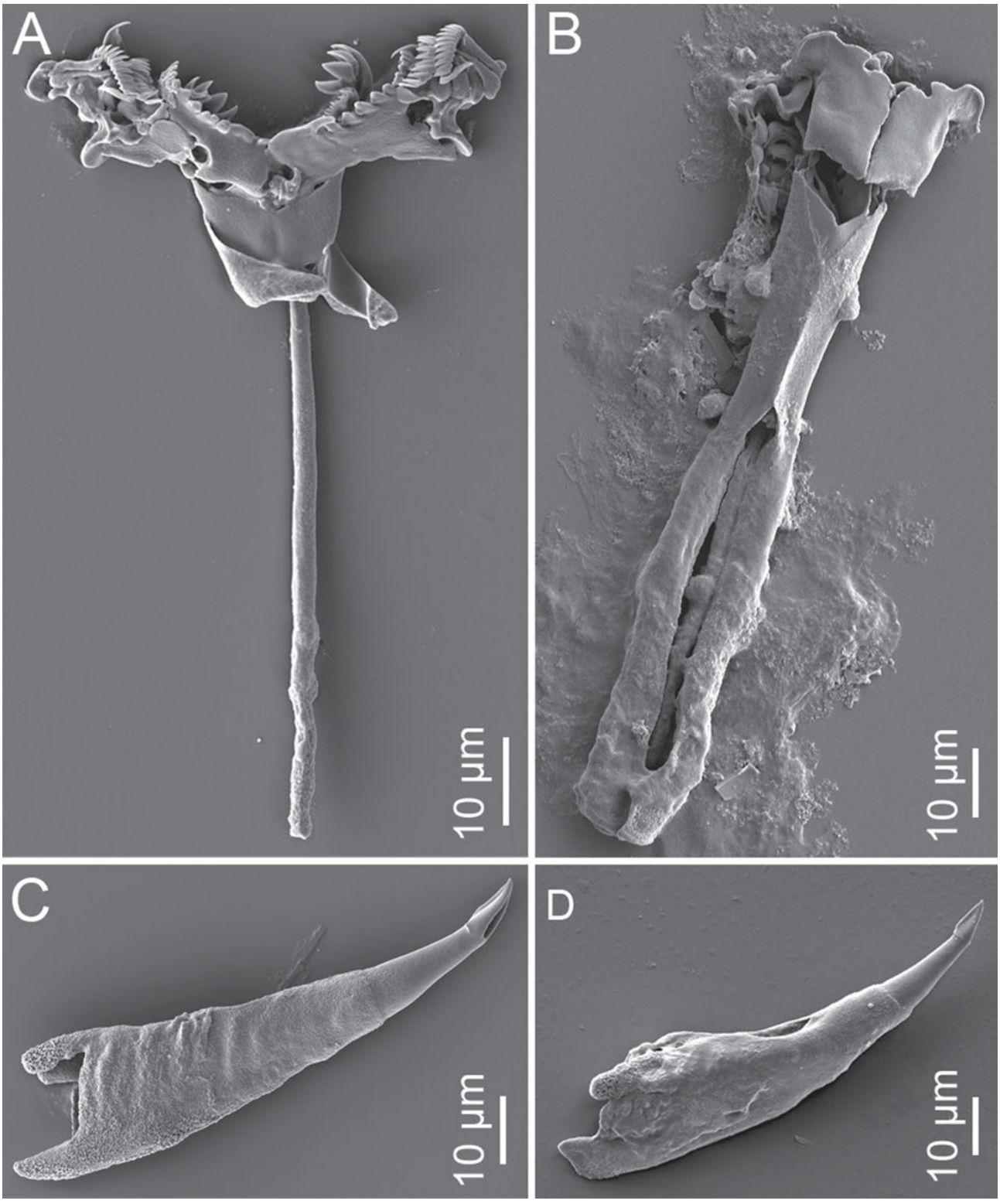


Fig. 7.12.5.3: SEM images of the jaw apparatus (A, B) and the penis spine (C, D) in *Stratiodrilus aeglaphilus* Vila & Bahamonde, 1985. Anterior is up in (A, B). The jaw apparatus is characterized by symmetrical maxillae (A) and paired fused mandibles (B, shown in ventral view). (C, D) *Stratiodrilus* bears a chitinous penis spine with two distinct openings, which is used for copulation and sperm transfer.

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longest. Lateral cirri simple, unsegmented, and partly paired (C1 and C2). Posterior end composed of two fused segments. Eggs attached to host with one end.

References

Amato, J.F.R. (2001): A new species of *Stratiodrilus* (Polychaeta, Histriobdellidae) from freshwater crayfishes of Southern Brazil. *Iheringia, Série Zoologia* 90: 37–44.

Brattey, J. & Campbell, A. (1985): Occurrence of *Histriobdella homari* (Annelida: Polychaeta) on the American lobster in the Canadian maritimes. *Canadian Journal of Zoology* 63: 392–395.

Cannon, L.R.G. & Jennings, J.B. (1987): Occurrence and nutritional relationships of four ectosymbiotes of the freshwater crayfish *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea: Decapoda) in Queensland. *Marine and Freshwater Research* 38: 419–427.

Claus, C. & Moquin-Tandon, G. (1884): *Traité de Zoologie* (2nd ed.). Librairie F. Savy, Paris.

Da Silva Rosa, J.J., MarÇal, I.C., Teixeira, G.M. & Aguiar, A. (2018): Checklist of species of *Stratiodrilus* Haswell, 1900 (Annelida: Histriobdellidae), and new host records from southern Brazil. *Zootaxa* 4399: 412–422.

Fauchald, K. & Rouse, G. (1997): Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71–138.

Foettinger, A. (1884): Recherches sur l'organisation de *Histriobdella homari*, P.-J. van Beneden rapportée aux Archiannelides. *Archives de Biologie* 5: 435–516.

Führ, I.M. (1971): A new histriobdellid on a marine isopod from South Africa. *South African Journal of Science* 67: 325–326.

Gelder, S.R. & Jennings, J.B. (1975): The nervous system of the aberrant symbiotic polychaete *Histriobdella homari* and its implications for the taxonomic position of the Histriobdellidae. *Zoologischer Anzeiger* 194: 293–304.

Gelder, S.R. & Tyler, S. (1986): Anatomical and cytochemical studies on the adhesive organs of the ectosymbiont *Histriobdella homari* (Annelida: Polychaeta). *Transactions of the American Microscopical Society* 105: 348–356.

Harrison, L. (1928): On the genus *Stratiodrilus* (Archiannelida: Histriobdellidae), with a description of a new species from Madagascar. *Records of the Australian Museum* 16: 116–122.

Haswell, W.A. (1900): On a new Histriobdellid. *Quarterly Journal of Microscopical Science* 43: 299–335.

Haswell, W.A. (1916): On the embryology of *Stratiodrilus* (Histriobdellidae). *Journal of Cell Science* 2: 301–312.

Hatschek, B. (1888): *Lehrbuch der Zoologie*. G. Fischer, Jena.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Jamieson, B.G.M., Afzelius, B.A. & Franzen, A. (1985): Ultrastructure of the acentriolar, aflagellate spermatozoa and the eggs of *Histriobdella homari* and *Stratiodrilus novaehollandiae* (Histriobdellidae, Polychaeta). *Journal of submicroscopic Cytology* 17: 363–380.

Jennings, J.B. & Gelder, S.R. (1976): Observations on the feeding mechanism, diet and digestive physiology of *Histriobdella homari* Van Beneden 1858: An aberrant polychaete symbiotic with North American and European lobsters. *Biological Bulletin* 151: 487–517.

Lang, K. (1949): Morphology of *Stratiodrilus platensis*. *Arkiv för Zoologi* 42: 43–47.

Lerch, F. & Uglem, I. (1996): High density of *Histriobdella homari* Van Beneden, 1858 (Annelida, Polychaeta) on ovigerous female European lobsters (Decapoda, Nephropidae). *Crustaceana* 69: 916–920.

Mesnil, F. & Caullery, M. (1922): L'appareil maxillaire *d'Histriobdella homari*; affinités des Hitriobdellides avec les Euniciens. *Comptes Rendues de l'Academie des Sciences de Paris* 174: 913–917.

Øresland, V. (2019): The polychaete *Histriobdella homari* and major groups of epibionts on the European lobster, *Homarus gammarus* and other decapods. *Crustaceana* 92: 189–203.

Paxton, H. (2009): Phylogeny of Eunicida (Annelida) based on morphology of jaws. *Zoosymposia* 2: 241–264.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press.

Simon, J.L. (1968): Incidence and behavior of *Histriobdella homari* (Annelida: Polychaeta), a commensal of the American lobster, *Homarus americanus*. *Bioscience* 18: 35–36.

Shearer, C. (1910): Memoirs: On the anatomy of *Histriobdella homari*. *Journal of Cell Science* s2-55: 287–359.

Steiner, T.M. & Amaral, A.C.Z. (1999): The family Histriobdellidae (Annelida, Polychaeta) including descriptions of two new species from Brazil and a new genus. *Contributions to Zooology* 68: 95–108.

Tzetlin, A.B. (1980): *Ophryotrocha schubravyi* sp. n. and the problem of evolution of the mouth parts in the Eunicemorpha (Polychaeta). *Zoologiceskij Zhurnal Akademii NAUK SSSR* 59: 666–676. [in Russian]

Tzetlin, A.B. & Filippova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologie* 535: 113–126.

Uzmann, J.R. (1967): *Histriobdella homari* (Annelida: Polychaeta) in the American lobster *Homarus americanus*. *Journal of Parasitology* 53: 210–211.

Van Beneden, P.J. (1853): Note sur une larve d'annélide d'une forme tout particuliere, rapportée avec doute aux serpules. *Bulletins de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique* 10: 69–72.

Van Beneden, P.J. (1858): Histoire naturelle d'un animal nouveau, designe sous le nom A'Histriobdella. *Bulletins de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique* 2: 270–303.

Vaillant, L. (1890): *Histoire naturelle des annelés marins et d'eau douce: lombricieus, hirudiniens, bdellomorphes, teretulariens et planariens*. Vol. 3. Roret, Paris.

Vila, I. & Bahamonde, N. (1985): Two new species of *Stratiodrilus*, *S. aeglaphilus* and *S. pugnaxi* (Annelida: Histriobdellidae) from Chile. *Proceedings of the Biological Society of Washington* 98: 347–350.

Vila, I. & Véliz, D. (2014): Life cycle of a freshwater gondwanic remnant polychaete *Stratiodrilus aeglaphilus* (Annelida: Eunicida: Histriobdellidae), commensal with *Aegla laevis* (Crustacea: Anomura). *Gayana* 78: 120–126.

Zhang, Y.-T. (2014): New substitute name for the genus *Dayus* Steiner & Amaral, 1999 (Annelida: Polychaeta: Histriobdellidae). *Zootaxa* 3802: 400.

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