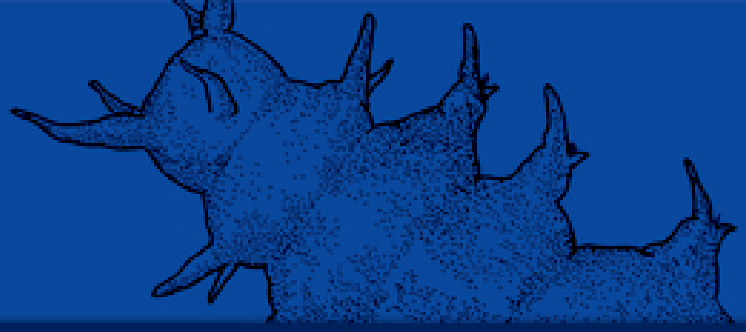
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HANDBOOK OF ZOOLOGY

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

ANNELIDA

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

PLEISTOANNELIDA, ERRANTIA II, PHYLLODOCIDA

VOLUME 4



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AN: 27964 ; Gnter Purschke, Markus Bggemann, Wilfried Westheide.; Pleistoannelida,
Errantia II
Account: ns335141

Handbook of Zoology
Annelida

Volume 4:
Pleistoannelida, Errantia II

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Handbook of Zoology

Founded by Willy Kükenthal
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Annelida

Edited by Günter Purschke, Markus Böggemann,
and Wilfried Westheide

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ISBN 978-3-11-064531-6
e-ISBN (PDF) 978-3-11-064716-7
e-ISBN (EPUB) 978-3-11-064533-0
ISSN 2193-4231

Library of Congress Control Number: 2021943075

Bibliographic information published by the Deutsche Nationalbibliothek
The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available on the Internet at http://dnb.dnb.de.

© 2022 Walter de Gruyter GmbH, Berlin/Boston
Typesetting: Compuscript Ltd. Shannon, Ireland
Printing and Binding: CPI books GmbH, Leck

www.degruyter.com

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Preface

"It is finished!" Said a famous person before us, and the significance of these words was certainly somewhat greater than today, or perhaps not.

In four volumes, we have dealt intensively with "worms," a collective name for various groups of squirming, wriggling, or writhing creatures that most people regard with displeasure or even disgust if they regard them at all. However, if you study Annelida, or segmented worms, more closely, they are not wretched or scary but highly interesting and sometimes even very beautiful organisms. Furthermore, they comprise one of the most important taxon of invertebrates occurring in marine, freshwater, and terrestrial environments. In particular, the marine forms, commonly called polychaetes, are one of the most widespread, abundant, and diverse elements of global marine fauna. With global human activities and climate change, distribution patterns of many taxa are subjected to dramatic changes. As a consequence, certain introduced species become pests with often fatal consequences for the original ecosystems.

Although only comprising approximately 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 multiple primarily identical segments, usually with lateral appendages, and the pygidium. Species are usually of median size and do not exceed a few centimeters in length. However, their range is much wider; some interstitial annelids belong to the smallest adult metazoans known, whereas others reach body lengths of more than 3 m. Some morphologically highly derived taxa have lost their segmentation, whereas others have several hundred segments with parapodia and/or chaetae. The marine forms are often broadcast spawners, and their life cycle primarily comprises an acoelomate planktonic larva, a trochophore, and a coelomate benthic adult. Others practice internal fertilization and direct development. However, they are among the most important groups of invertebrates in the marine food webs, where they can be found in almost every habitat, often in high abundances. They use a wide range of food sources, and their feeding habits include microphagous suspension, predation, occasional mutualism with endosymbiotic bacteria, parasitism, or parenteral nourishment. Besides their segmentation plasticity, their reproductive and feeding biology is likely the main reason for the diversity of annelids. Consequently, several annelid groups have not been recognized as members of this clade and were previously treated as separate phyla: Echiura (today Thalassematidae), Myzostomida, Orthonectida, Pogonophora (today Siboglinidae), and Sipuncula.

Annelida appeared before the Cambrian period and will certainly still be here long after we are gone (into the *paradise*?), and they will continue to complicate our efforts to clarify their phylogenetic relationships and evolutionary history. Although this is certainly not the last word, we present the most current hypotheses of their phylogenetic systematization in these volumes.

Ninety years after the first edition of the *Handbook of Zoology* edited by W. Kükenthal and T. Krumbach, we aimed to absorb knowledge about the morphology, anatomy, reproduction and development, biology and ecology, phylogeny, and taxonomy of the different groups of Annelida like a sponge to secure it for the thirsty posterity.

The first volume details the Palaeoannelida and other basal groups and the initial portion of the Pleistoannelida, the Sedentaria, including Cirratulida and Orbiniida. It was supplemented by chapters on the history of research, fossil records, and an introduction to the phylogeny of annelids and their position in the tree of life.

The second volume continues the Sedentaria and predominantly comprises the clades Sabellida/Spionida and Opheliida/Capitellida.

The third volume is devoted to the remaining Sedentaria, completing the Sabellida/Spionida clade, and continues with Terebellida/Arenicolida. These are followed by two taxa under discussion and here classified as *incertae sedis*: Diurodrilidae and Nerillidae. The volume ends with the first part of Errantia: Myzostomida, Protodriliformia, and some Eunicida.

This fourth and final volume describes members of the clade Errantia with the remaining Eunicida, treating the large group of Phyllodocida, and concludes with a chapter about the Aphanoneura (Aeolosomatidae and Potamodrildae), a group of Sedentaria *incertae sedis*.

Unfortunately, we had to learn that for many annelid groups, specialists did not exist in the contemporary scientific zoological community, were not available for various reasons, or have forsaken us. Therefore, it took much longer than originally planned to compile the manuscripts, and despite our efforts, there will remain a few missing chapters: Amphinomida (Amphinomidae and Euphrosinidae; basal groups), Clitellata (Oligochaeta and Hirudinea; Sedentaria), Siboglinidae (Sedentaria), Hartmaniellidae (Errantia), Phyllodocida (Aphroditidae,

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Eulepethidae, Hesionidae, Phyllodocidae; Errantia), and most of the holopelagic groups (Alciopidae, Iospilidae, Lopadorrhnychidae, Pontodoridae, Typhloscolecidae, Yndolaciidae; Errantia). We still hope that it will be possible to supplement this missing information sometime in the future. Nevertheless, these volumes prove to be a useful resource for those also interested in the curious and fascinating spirit of the "wormland."

It was a great advantage that each chapter ready for publication was published electronically as *Zoology Online*, making the chapters available to the scientific community quite soon after acceptance. All contributions were peer-reviewed and revised before publication.

Although the current COVID-19 pandemic casts a heavy cloud over scientific life and workflow, all people involved managed to publish this volume with only slight delays from the originally established deadline. Again, we would like to thank all authors and reviewers who have contributed to the volumes of the *Handbook of Zoology*; they have done an excellent job. Last but not least, we thank the lectors and employees of our publisher for their endless help and fruitful discussions during the publishing process, especially De Gruyter, who provided this forum for the worms, which, according to Nietzsche, are much within us.

Normally, you always end up thanking your parents or, particularly, your mother, but unfortunately, they are no longer with us and were just puzzled about adults working with worms. Therefore, you can still thank your family and especially your children, but even here, the response does not improve (Ugh! a worm, Dad, your job is so uncool), so taxonomy will probably die out soon. Too bad!

We have to forgive them, for they know not what we do.

Markus Böggemann, Günter Purschke,
and Wilfried Westheide
Vechta, Osnabrück, and Wallenhorst,
Germany, May 2021

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Volume 2: Pleistoannelida, Sedentaria II, 9783110291476
Volume 3: Annelida, Sedentaria III and Errantia I, ISBN 978-3-11-029148-3

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7.12 Errantia: Eunicida

Eivind Oug, Polina Borisova, and Nataliya Budaeva

7.12.6 Lumbrineridae Schmarda, 1861

Introduction

The family Lumbrineridae Schmarda, 1861 belongs to the order Eunicida and consists presently of about 280 recognized species in 19 genera (Zanol et al. 2021). Lumbrinerids are generally long cylindrical worms of small to medium size with rather simple external morphology. Superficially, many species resemble earthworms. As in other Eunicida, Lumbrineridae possess a complicated jaw apparatus in a muscular pharynx (Budaeva and Zanol 2021). The lumbrinerids are mostly free living, and most species are found in soft-sediment environments where they burrow in the substrate. Lumbrinerids are found in all seas around the world and at all depths.

A remarkably large number of species have been described from the early natural history studies and on a worldwide basis (cf. Hartman 1944, 1959, Fauchald 1970). Because of the apparent morphological homogeneity, a rather simplified system for the definition of genera was traditionally used with the majority of species placed in the type genus *Lumbrineris* Blainville, 1828 (variant spelling *Lumbriconereis*) (see Fauchald 1977). Various attempts have been made to subdivide *Lumbrineris* over the years (Hartman 1944, Fauchald 1970), but more stable solutions were not reached until the late twentieth century when phylogenetic principles were taken into account and the definition of genera was based on evaluations of ancestral and derived characters (Orensanz 1990). In recent years, jaw characters have been extensively used for generic diagnoses. This has led to the erection of several new genera, whereas extant genera have been redefined and previously synonymized genera have been resurrected (Orensanz 1973, 1990, Levenstein 1977, Hartmann-Schröder 1979, Frame 1992, Carrera-Parra 2006a).

At present, the most important characters for classification and identification of species are found in jaw structures, types and shapes of chaetae, and parapodial structures. Many species descriptions, however, especially in the older literature, are rather general and do not mention characters that presently are known to be vital for species discrimination. This has led to much confusion about species identities and synonymies. Although several species problems have been clarified in recent taxonomic accounts or studies of regional fauna, many species are still insufficiently characterized and of uncertain status.

Morphology

External Morphology

Body shape. Lumbrinerids have a long cylindrical body with generally similar segments (Fig. 7.12.6.1A). The largest species may reach a length of about 40 cm (Fauvel 1923, Uschakov and Bao-Ling 1979, Gambi et al. 1994 for *Scoletoma impatiens* (Claparède, 1868)), but most species are only 2–10 cm in length and 0.3–2 mm in width. In most species, the width gradually decreases toward the pygidium. The number of segments is high, usually 100–200, but may reach 500 (Fauvel 1923, Uschakov and Bao-Ling 1979). The segments are generally short compared to the length, rounded or somewhat flattened ventrally in cross section, and largely similar throughout. There is no marked regionalization of the body, but development of parapodia and distribution of chaetae usually change from anterior to posterior. Most species are of reddish or brownish color without particular color patterns. Some species, especially among larger forms, are iridescent (Fig. 7.12.6.1A).

Prostomium. The prostomium is well developed and is usually without eyes or appendages (Fig. 7.12.6.1B, C). In most species, it is gently rounded to broadly conical and about as long as wide. In some species or genera, more distinctive shapes may occur, e.g., spherical, triangular, or prolonged. A pair of nuchal organs in the form of pits or short furrows is located dorsally at the posterior margin, sometimes concealed by a fold from the anterior rim of the peristomium. In some genera, a small papilla (nuchal papilla) or short digitiform antennae may be present in a middorsal pouch at the anterior rim of the peristomium. In *Lysarete*, there is an invagination dorsally in the peristomium for antennae. Eyes are present in few cases (*Arabelloneris*, *Lysarete*). In *Cenogenus* and *Ninoe*, a pair of longitudinal posteriorly diverging furrows may run most of the length of the prostomium (dorsal slit-like organs *sensu* Orensanz 1990). Ventrally, the mouth opening is delineated by a pair of low globular structures traditionally referred to as ventral pads or buccal lips (Carrera-Parra 2006a) but which are extensions of eversible folds present on the dorsal side of the pharynx (transverse anterior peristomial extensions *sensu* Zanol 2010) (Fig. 7.12.6.1C).

Peristomium. The peristomium consists of two rings lacking parapodia, chaetae and tentacular cirri (Fig. 7.12.6.1B, C). The two rings represent a subdivision of the peristomium and may be an adaptation to augment the operation of the maxillary apparatus (Eibye-Jacobsen 1994).

https://doi.org/10.1515/9783110647167-001

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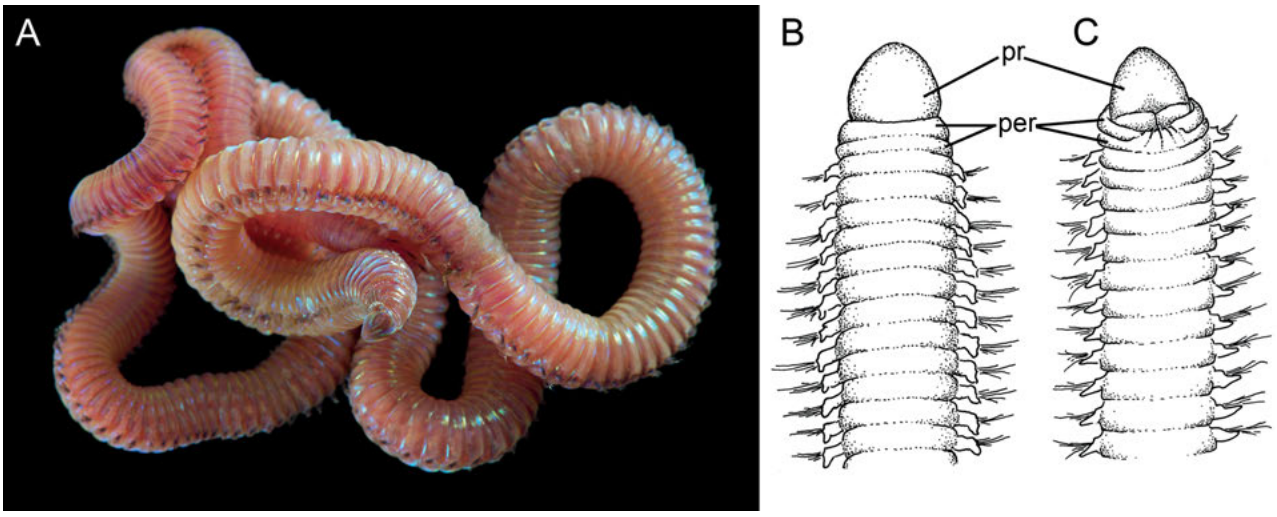


Fig. 7.12.6.1: A, *Scoletoma fragilis* (O.F. Müller, 1776) (photo Alexander Semenov). B, C, Anterior part of *Lumbrineris aniara* Fauchald, 1974: dorsal view (B); ventral view (C). per, peristomium; pr, prostomium.

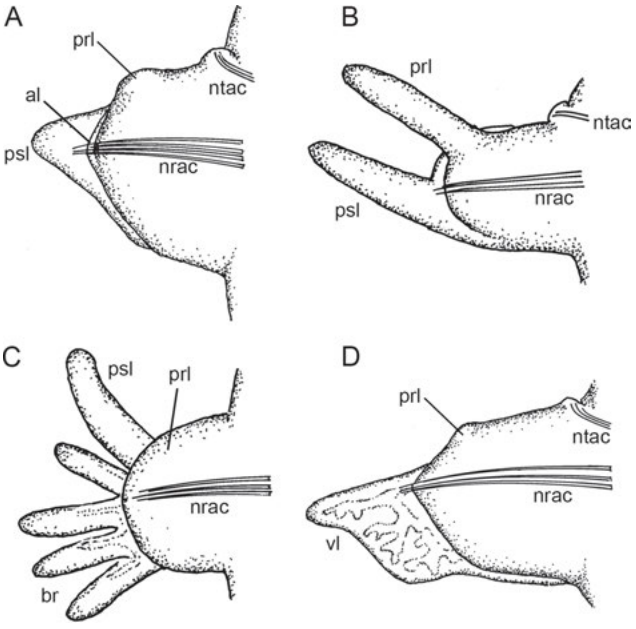


Fig. 7.12.6.2: Parapodial structures in *Lumbrineris* sp. (A, B, D), *Ninoe* sp. (C). A, Anterior parapodium. B, Posterior parapodium. C, Parapodium from branchiated region. D, Posterior parapodium with vascularized postchaetal lobe. al, acicular lobe; br, branchiae; nrac, neuropodial aciculae; ntac, notopodial aciculae; prl, prechaetal lobe; psl, postchaetal lobe; vl, vascularized lobe. Chaetae omitted.

The anterior ring is ventrally incomplete, whereas the second ring is broadened and projected forward at the ventral part of the mouth opening.

Parapodia. The segments following the peristomium carry parapodia that are mostly simple in structure with a well-developed neuropodium and a more or less reduced notopodium. Ventral cirri are lacking. The neuropodium is supported by 1 to 4–5 embedded aciculae that may be light yellow, golden brown, or black in color (Fig. 7.12.6.2A). The number of aciculae generally decreases from anterior to posterior. The notopodium is usually reduced to a small insignificant knob supported by a few needle-thin embedded aciculae but is moderately well developed in the form of a short knob-like cirrus in *Kuwaita* and *Lysarete*.

The neuropodia typically carry pre- and postchaetal lobes of varying development. Prechaetal lobes are usually low and rounded, in some cases almost insignificant and difficult to discern. Postchaetal lobes are more developed, leaf-shaped rounded or conical, and often with a dorsally protruded extension (Fig. 7.12.6.2A). Between the pre- and the postchaetal lobes, there is a low and often faintly visible acicular lobe. Often needle-thin distal parts of the aciculae emerge from the acicular lobe. Generally, parapodial lobes are best developed in anterior body and gradually change in shape along the body. In posterior body, parapodial lobes may be variously developed. In some species, they are largely reduced, whereas in other species, they develop into extended digitiform lobes (Fig. 7.12.6.2B).

In *Ninoe* and *Cenogenus*, branchiae are attached to the neuropodia in anterior body. *Ninoe* has a branched branchia with several filaments located distally on the posterior side of the parapodium and associated to the postchaetal lobe (Fig. 7.12.6.2C). *Cenogenus* has a simple knob-like to digitiform branchia posterodorsal on the parapodium. In other genera, vascularized lobes that obviously have respiratory functions may be found in various positions. Vascularized postchaetal lobes in anterior body are known from tropical *Lumbrineris* (Fig. 7.12.6.2D), whereas vascularized lobes in posterior body

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are known for *Abyssoninoe* and *Lysarete* (see Gilbert 1984, Carrera-Parra 2001b). *Kuwaita* is unique among lumbrinerids in having branchiae located dorsally on the body not associated with the parapodia but may have vascularized parapodial lobes as well.

Nephridial papillae are found ventral to the parapodia in posterior body of *Kuwaita* (see Carrera-Parra and Orensanz 2002, Oug 2002 [as *Eranno papillifera* (Fauvel, 1918)], Arias and Carrera-Parra 2014). Nephridial papillae are absent in other lumbrinerids, but a slight swelling may be found in the same position in ovigerous females releasing eggs through them (Carrera-Parra and Orensanz 2002).

Pygidium. The pygidium is rounded or conical and of simple structure. In most genera, the pygidium carries one or two pairs of long or short gradually tapering cirri. Cirri are lacking in *Lumbrinerides* and *Lumbrineriopsis*. In species with cirri, it may be that they appear rather late in ontogeny, but information is poor. Okuda (1946) described for *Lumbrineris latreilli* Audouin & Milne Edwards, 1833 that early larvae had a rounded pygidium, whereas later larvae (18-chaetiger stage) with most external characters developed had a cup-shaped pygidium with short posterolateral processes that could be rudiments of cirri.

Sense organs. Not much is known about sense organs in lumbrinerids. Typical tactile sensory structures such as palps and tentacular cirri are lacking. Small antennae and eyes are present in some genera and species, but generally most species appear to miss discrete sensory structures that may provide visual or tactile information from the environment. Nuchal organs on the prostomium are usually assumed to have a chemosensory function. Small sense organs, apparently present among eunicid polychaetes in general, are found dorsal to the parapodium along the body (dorsal cirrus organ *sensu* Hayashi and Yamane 1997, Fauchald and Rouse 1997). Structurally, these organs resemble lateral organs present in many sedentary polychaetes (Purschke and Hausen 2007). These are small depressions pitted with numerous pores in the cuticle and projecting cilia and may have a chemoreceptive function (Hayashi and Yamane 1997; for a different hypothesis, see Purschke and Hausen 2007). Arias and Carrera-Parra (2014) illustrated the organ for *Kuwaita hanneloreae* Arias & Carrera-Parra, 2014 from the Bay of Biscay, but little is known about their occurrence in other species.

Fragmentation and body size. Lumbrinerids have a strong tendency to fragment when disturbed. Actually, the first named lumbrinerid *Lumbricus fragilis* O.F. Müller, 1776 (= *Scoletoma fragilis*) got its name from this characteristic. In present routine sampling, for instance, for monitoring purposes, mostly incomplete specimens are collected. Often also, specimens with regenerating posterior ends are found, probably because of attacks from larger predators. These have practical consequences for size measurements and identification in cases where the shape of posterior parapodial lobes and development of pygidial cirri are of taxonomic importance (e.g., *Abyssoninoe*). In some species, posterior segments and pygidia are unknown. Size is usually being recorded as length of a sequence of segments or width at a specified chaetiger. In recent studies, the length from the tip of the prostomium to the posterior border of the tenth chaetiger or the width at the tenth chaetiger (usually designated w10) has been regularly used (e.g., Orensanz 1990, Carrera-Parra 2006a, Cai and Li 2011, Martins et al. 2012).

Chaetae. The chaetae are of two main types: limbate and hooded hooks. Limbate chaetae are found in all species. Typically, limbate chaetae are rather long gently curved chaetae with a marked thin brim on the convex side and taper gradually to a minute tip (Fig. 7.12.6.3A). In some small species, and generally in juveniles, shorter more strongly bent limbate chaetae occur (Fig. 7.12.6.3B). In *Lumbricalus*, articulated limbate chaetae (compound spinigers) are found.

Hooded hooks occur in most species except for *Arabelloneris* and *Lysarete*. Hooded hooks may be bidentate (in *Lumbrinerides* and *Lumbrineriopsis*) or multidentate (in other genera). Bidentate hooks have distally two about equal teeth (Fig. 7.12.6.3E, F). In *Lumbrineriopsis*, and occasionally in *Lumbrinerides*, there is a subdistal spur or knob in the continuation of the shaft giving the impression of a third tooth. Multidentate hooks distally have a series of small teeth, usually consisting of one primary obtuse or squarish tooth followed by a number of gradually diminishing apical teeth. Multidentate hooks may be simple, compound, or less commonly pseudocompound. Compound hooks have a joint or hinge separating a proximal shaft and a distal appendage (also denoted article, blade) (Fig. 7.12.6.3H, I). The appendage is held in place with double ligaments, in contrast to compound hooks in glycerids, syllids, and nereids where the appendage fits into a socket and is supported by one ligament (Fauchald and Rouse 1997, Tilic et al. 2016). Pseudocompound hooks have a slit running partly through the shaft with connection between shaft and appendage at one or both sides (Fig. 7.12.6.3J, K). The hoods of both bidentate and multidentate hooks enclose the outer dental area and distal part of the shaft. In compound and pseudocompound hooks, there is a constriction at the level of the joint or slit with the proximal part of the hood being more or less bulbous.

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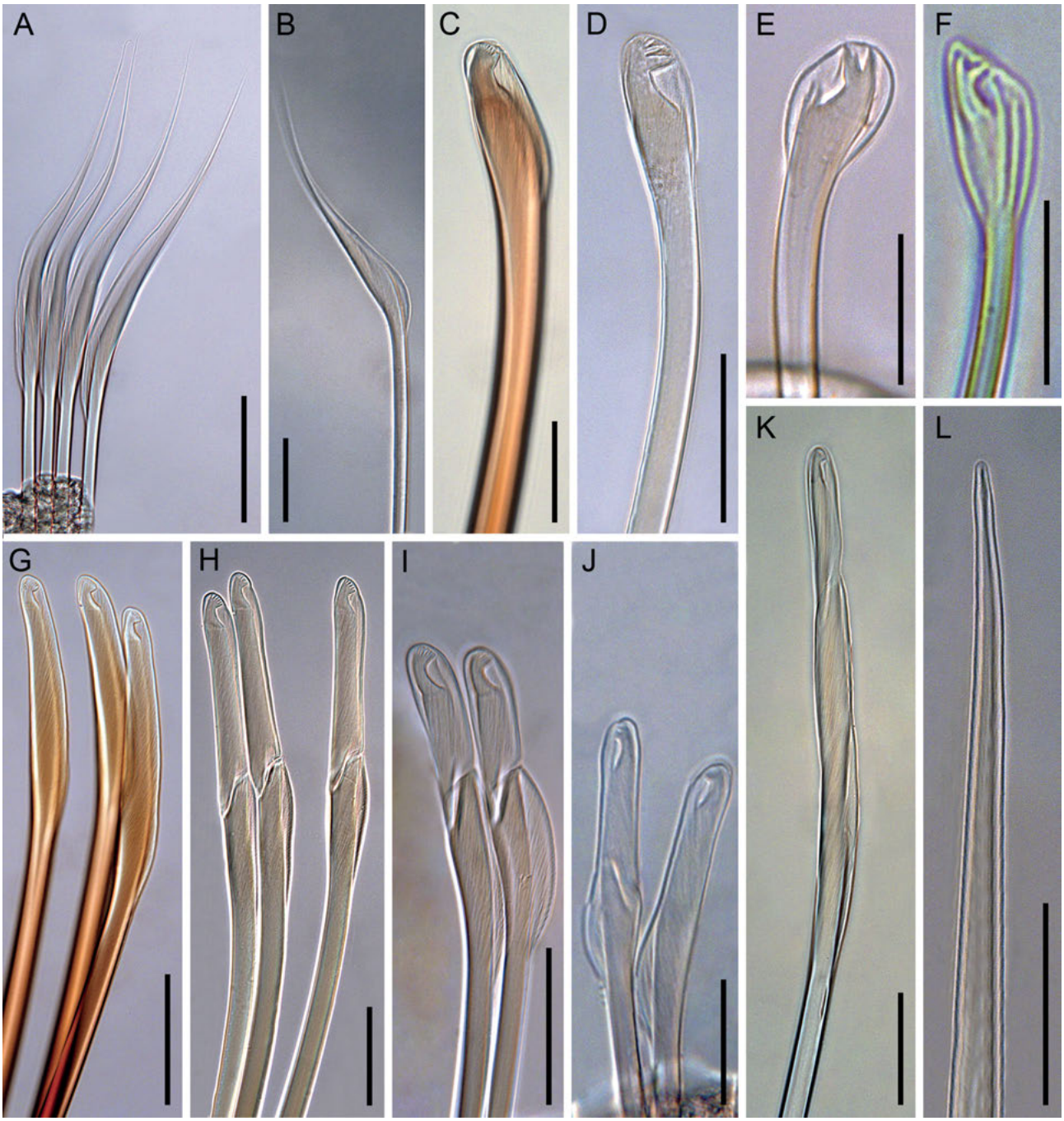


Fig. 7.12.6.3: Types of chaetae. A, limbate chaetae (*Augeneria tentaculata* Monro, 1930). B, Juvenile limbate chaeta (*Lumbrineris aniara* Fauchald, 1974). C, Multidentate simple hooded hook, posterior body, short blade (*Scoletoma fragilis*). D, The same (*Kuwaita* sp.). E, Bidentate hooded hook (*Lumbrineriopsis* sp.). F, The same (*Lumbrinerides* sp.). G, Multidentate simple hooded hooks, anterior body, long blade (*Scoletoma fragilis*). H, Compound hooded hooks, long blade (*Lumbrineris futilis* Kinberg, 1865). I, Compound hooded hooks, short blade (*Augeneria tentaculata*). J, Pseudocompound straight hooded hook and simple hooded hook (*Lumbrineris mixochaeta* Oug, 1998). K, Pseudocompound twisted hooded hook (*Augeneria algida* (Wirén, 1901)). L, Transitional hooded hook (*Cenogenus brevipes* (McIntosh, 1903)). Scale bars: A, G: 100 µm; C, D, H, I, K, L: 50 µm; B, E, J: 25 µm; F, 20 µm.

Simple multidentate hooks vary in shape from nearly straight hooks with a rather long widened outer part ("blade") to gently curved hooks with a short outer part (Fig. 7.12.6.3G, C, D). A rather specialized condition is shown in *Abyssoninoe* and some species of *Cenogenus* where the most anterior hooks may be extremely long

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and tapering to a minute tip with microscopically visible teeth, superficially looking like limbate chaetae (transitional hooded hooks *sensu* Orensanz 1990, truncate bilimbate chaetae *sensu* Parapar et al. 1994, and simple multidentate hooded hooks *sensu* Carrera-Parra 2006a) (Fig. 7.12.6.3L). Short multidentate simple hooded hooks are superficially similar to hooded hooks in Spionidae and Capitellidae. Studies by Tilic et al. (2014) have shown that the lumbrinerid hooded hooks are formed from cellular structures that differ from the structures of spionid and capitellid hooks and, therefore, are not homologous to hooded hooks in these groups.

The distribution and shape of chaetae changes from anterior to posterior along the body. Most types of chaetae of taxonomic importance are best developed in the anterior body, for small and medium-sized species in the first 15 to 30 chaetigers. Limbate chaetae become gradually thinner backward until ending as very thin, often straight capillary chaetae in midbody. Simple multidentate hooded hooks become gradually stouter and more curved with a very short blade posteriorly. The first appearance of simple hooded hooks varies among species, usually within the range of the 1st to the 15th chaetiger. In a few cases, the first hooks do not appear until midbody (in *Sergioneris*, some species of *Scoletoma*). In these cases, anterior chaetigers have limbate chaetae only. In species with compound hooded hooks, the hooks are present in anterior body only and are substituted by simple hooks in mid and posterior body. Likewise, compound spinigers (in *Lumbricalus*) are present in anterior body only.

Within parapodia, the most typical arrangement in the anterior body is a group of limbate chaetae placed dorsal to the aciculae, then followed by a group of hooks (simple or compound) ventral to the aciculae and one or a few ventral limbate chaetae (Fig. 7.12.6.4A). In species with rather late occurrence of the most anterior hooks, there is usually a fan of limbate chaetae also below the aciculae. Progressing backward, the number of dorsal limbate chaetae decreases and the ventral limbate chaetae disappear (often about the 20th chaetiger). In some genera, the dorsal limbate chaetae may extend over the full body length, but more frequently they disappear in posterior body where they are replaced by one or two simple hooded hooks. Further back, simple hooded hooks with short blade are then the only type of chaetae present both above and below the aciculae. The dorsal simple hooks appear before the disappearance of limbate chaetae and are placed above the limbate chaetae, which then are situated between dorsal and ventral hooks (subdorsal position *sensu* Orensanz 1990) (Fig. 7.12.6.4B). Dorsal hooks are often more robust than ventral hooks and have teeth facing downward, in contrast to ventral hooks having teeth facing upward. In *Lumbrinerides* and *Lumbrineriopsis*, short limbate chaetae and bidentate hooded hooks are present with mostly little variation along body (Fig. 7.12.6.4C). In *Abyssoninoe*, the anterior extended hooks with minute tips (transitional chaetae) are found in the same position in the parapodium as ordinary hooded hooks (Fig. 7.12.6.4D). In the following chaetigers, the hooks become gradually shorter in a chaetiger by chaetiger transitional series and change into ordinary short hooks (Fig. 7.12.6.4E–G).

In *Cenogenus* and *Ninoe*, the branchiae are situated posterior to the chaetae (Fig. 7.12.6.5A, B). In *Cenogenus*, the transitional chaetae in anterior body are placed below the aciculae in the same position as transitional chaetae in *Abyssoninoe* (Fig. 7.12.6.5A). In *Ninoe*, there are several dorsal and ventral limbate chaetae in anterior body with one or a few hooded hooks starting from the first chaetiger or further back among the limbate chaetae (Fig. 7.12.6.5B). Vascularized lobes with respiratory function are thin-walled, more or less transparent structures with distinct blood vessels. In *Abyssoninoe*, vascularized pre- and postchaetal lobes may be found in the posterior body (Fig. 7.12.6.5C).

Chaetae of juvenile lumbrinerids differ from those of adults. Juvenile limbate chaetae are short with a marked bend. Also, hooded hooks are short with a short hood (Orensanz 1990). Types and position of chaetae change during ontogeny. Larval stages of *Lumbrineris* initially possess limbate or capillary chaetae only (Okuda 1946, Cazaux 1972, Tilic et al. 2016). In a detailed study of distribution of chaetae in sub-Antarctic *Lumbrineris*, Orensanz (1990) demonstrated that the range of chaetigers with compound hooded hooks and ventral limbate chaetae progressively extends backward with increasing size. In juvenile *Lumbrineris magalhaensis* Kinberg, 1865, compound hooded hooks first appear on two anterior chaetigers and then develop on succeeding chaetigers. In the smallest specimens, all hooks are simple before the appearance of compound hooks. Okuda (1946) recorded for *Lumbrineris latreilli* that simple hooded hooks appeared in eight-chaetiger stage larvae, a species with compound hooded hooks in adults. In juvenile *Scoletoma fragilis*, hooded hooks with very short hood appear in the most anterior chaetigers but disappear with increasing size when hooks with longer blade develop further back (Frame 1992, Oug 1998). In *Abyssoninoe*, recent studies indicate that the body section with transitional hooded hooks is displaced backward with increasing size (Oug, unpublished observations).

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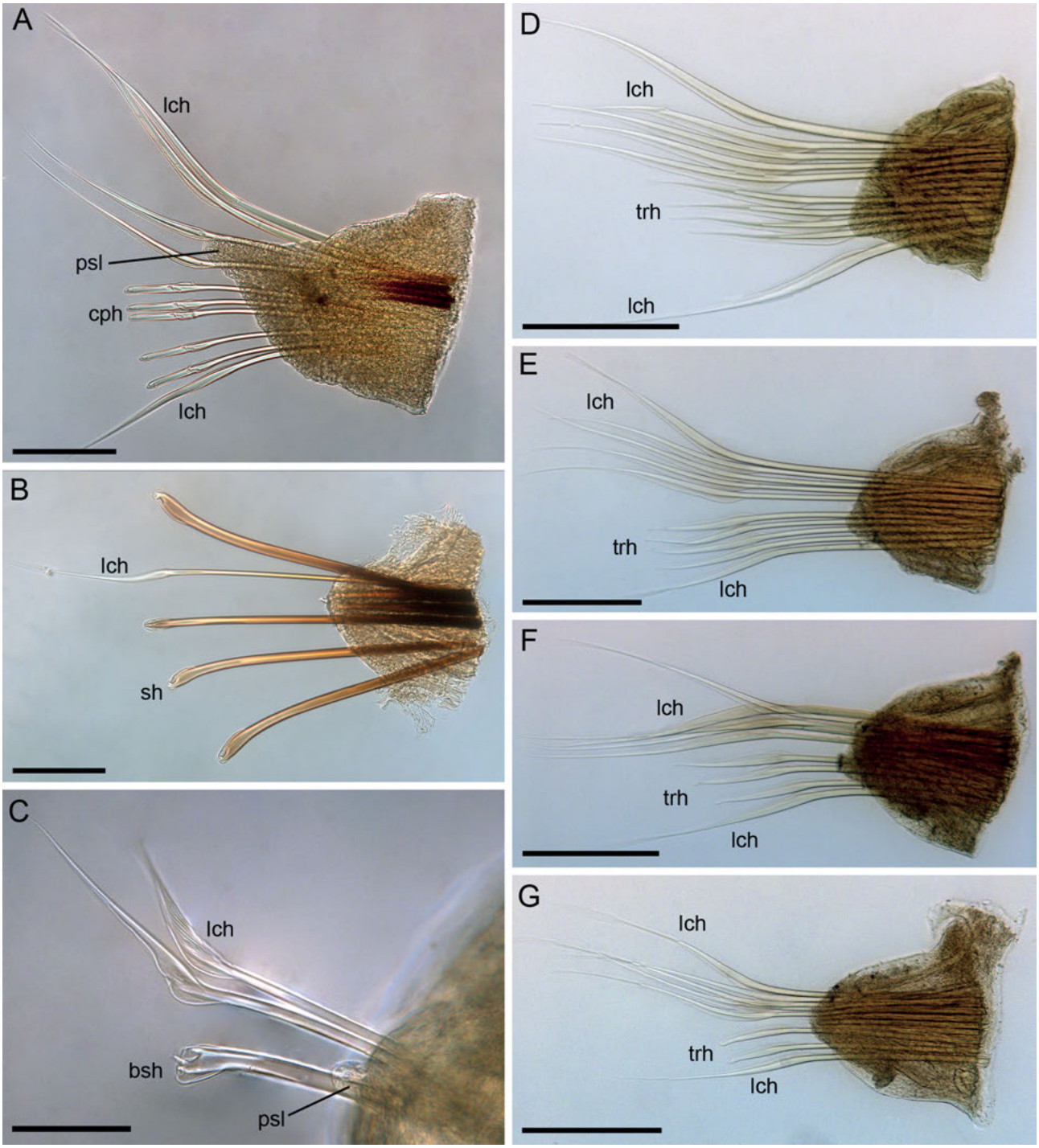


Fig. 7.12.6.4: Parapodial arrangement of chaetae. A, *Lumbrineris futilis*, anterior parapodium. B, *Scoletoma fragilis*, posterior parapodium. C, *Lumbrineriopsis* sp., median parapodium. D–G, *Abyssoninoe hibernica* (McIntosh, 1903), parapodia 7 (D), 12 (E), 14 (F), and 17 (G) showing the change in transitional hooded hooks from limbate-like to normal hooded hooks. bsh, bidentate simple hook; cph, compound hooks; lch, limbate chaetae; psl, postchaetal lobe; sh, simple hooks; trh, transitional hooks. Scale bars: A, B, D–G: 200 µm; C: 50 µm.

Jaw apparatus. The jaw apparatus is comprised of dorsal maxillae and ventral mandibles (Figs. 7.12.6.6 and 7.12.6.7) that are hard cuticular structures formed of scleroproteins and mineralized with calcium carbonate (calcite) (Colbath 1986). The apparatus is mounted in a muscular pharynx running from the mouth opening through the peristomium and into six to eight anterior chaetigers. The whole structure can be protruded so that maxillae and

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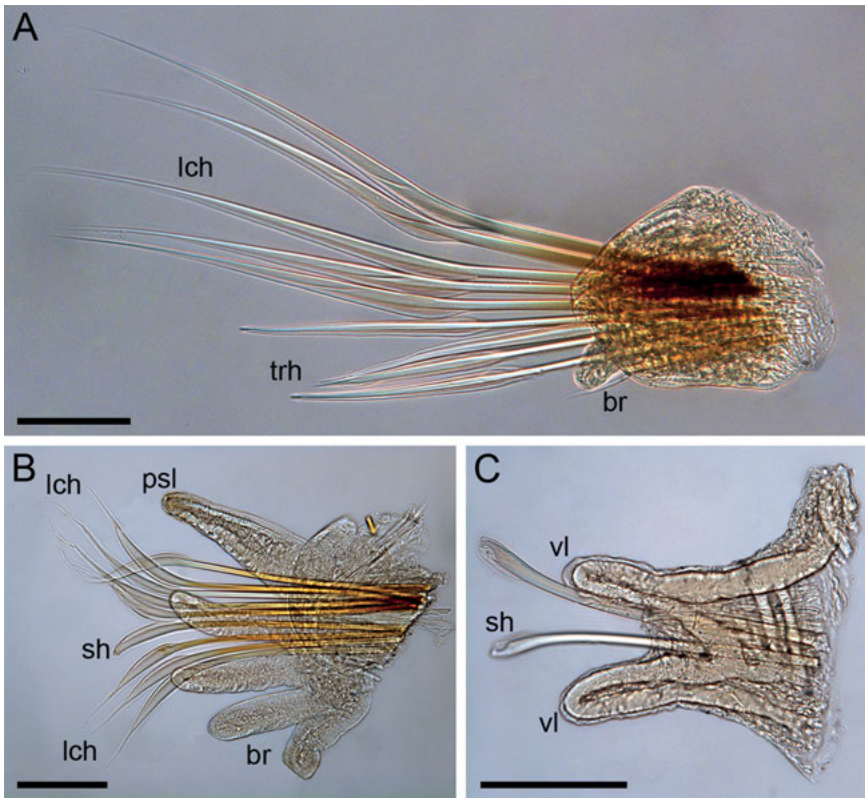


Fig. 7.12.6.5: Parapodial structures. A, *Cenogenus brevipes*, sixth parapodium with single branchia. B, *Ninoe* sp., 16th parapodium with branched branchia. C, *Abyssoninoe hibernica*, posterior parapodium with vascularized parapodial lobes. br, branchia; lch, limbate chaetae; psl, postchaetal lobe; trh, transitional hooks; sh, simple hook; vl, vascularized lobe with blood vessel. Scale bars: 100 µm.

anterior parts of mandibles appear in the mouth opening (Clemo and Dorgan 2017). The maxillae consist of paired elements that are arranged in two rows with a pair of posterior elements termed maxillary carriers and four or five pairs of dental plates. The mandibles are represented by paired more or less fused elements widening distally into cutting plates. The maxillary arrangement has for long been referred to as "labidognath" (pincer-jaw) type, a denotation dating back from Ehlers (1868), that also included the maxillae of Eunicidae and Onuphidae (see, e.g., Orensanz 1990, Carrera-Parra 2006a, Struck et al. 2006, Budaeva and Zanol 2021). Eunicidae and Onuphidae have, however, an asymmetric arrangement of maxillae with respect to both the number of elements and their shape, in left and right rows. In a recent study, Paxton (2009) reevaluated the jaw types of Eunicida and denoted the lumbrinerid maxillary arrangement as "symmetrognath" (symmetric-jaw) type to distinguish it from other Eunicida with asymmetric maxillae. Maxillae of Eunicida have an extensive fossil record comprising both extinct and recent main types. The fossil types have been used in evaluating theories of phylogenetic relationships among the recent families (Orensanz 1990, Paxton 2009, see also Budaeva and Zanol 2021).

The maxillary elements are referred to by roman numerals from I to V (VI) from posterior to anterior (Fig. 7.12.6.7A–B). The carriers are mostly triangular elements, somewhat longer than broad, and loosely joined to maxillae I by their outer parts (Paxton 2009). Maxillae I are relatively large falcate elements with gently curved anterior prongs and broad bases. The left and the right maxillae I are connected posteriorly with a locking system composed of ridges and furrows (Colbath 1986, Paxton 2009). In *Lumbrinerides* and *Lysarete*, there are additional teeth at inner border of the prongs. Maxillae II are placed inside and partly below maxillae I and have several inward or upward pointing teeth (3–6). Maxillae III and IV are vertically oriented elements in the anterior part of the pharynx with or without denticulate inner borders, and maxillae IV are hemispherical elements over a muscular ridge. Maxillae V are generally rounded elements placed outward of maxillae III and IV. Shape and occurrence of maxillae V may vary; however, they may be completely missing (e.g., *Augeneria*, *Cenogenus*), be partly fused to maxillae IV (*Eranno*, some species of *Abyssonine* and *Lumbrineris*), or completely fused with maxillae IV (most *Abyssoninoe*). *Lysarete* is unique in having an additional pair of maxillae (VI) anterior to maxillae IV.

In the maxillary apparatus, there are several additional elements connected to or placed aside of the maxillae. In many genera, there is a pair of narrow or wide

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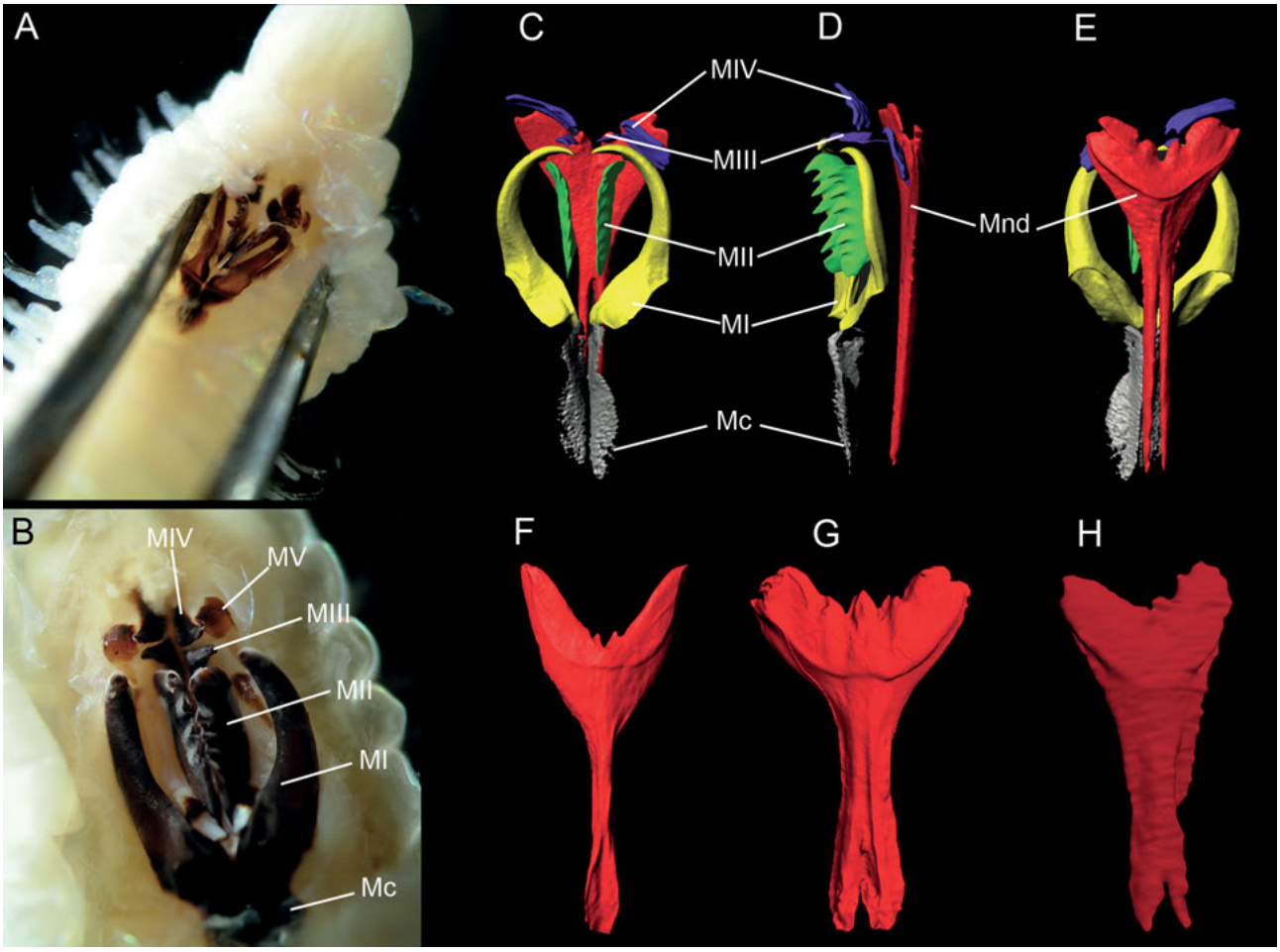


Fig. 7.12.6.6: Arrangement of jaw apparatus. A, Dorsal incision of anterior body (chaetigers 1–6) to expose maxillae (*Lumbrineris* cf. *coccinea* (Renier in Meneghini, 1847)). B, Maxillae in contracted state with maxillae II raised (*Lumbrineris latreilli*). C–E, 3D reconstruction of maxillae and mandibles based on micro-CT scans in *Hilbigneris* sp.: maxillae and mandibles, dorsal view (C); the same, lateral view (D); the same, ventral view (E). F–H, 3D reconstruction of mandibles based on micro-CT scans, ventral view: *Gallardoneris* sp. (F); *Lumbrineris* sp. (G); *Augeneria* sp (H). Mc, maxillary carriers; MI–V, maxillae I–V; Mnd, mandibles.

plates between the basal part of maxillae I and the posterolateral border of maxillae II, in recent literature termed connecting plates (Fig. 7.12.6.7A). In addition, there is a pair of thin strap-like ligaments connecting the base of maxillae I to the posterior tip of maxillae II. Outside of or beneath the maxillae, there may be several rod-shaped, aliform, or rounded elements with a punctured structure that in recent literature are referred to as attachment lamellae (Carrera-Parra 2006a, Paxton 2009). The attachment lamellae of maxillae I are rod-shaped and usually free (Fig. 7.12.6.7A), whereas the attachment lamellae of maxillae II–IV are fused with the maxillary elements (Fig. 7.12.6.7B). Maxillae V, when present, are essentially reduced to the attachment lamellae only. Fused attachment lamellae may be discerned by the punctured structure but are generally considered as part of the maxillae they belong to and often not perceived as separate structures. The presence and the shape of maxillae and additional elements are of great importance for the definition of genera in recent taxonomy. The diversity of maxillary parts is illustrated in Figure 7.12.6.8A–I.

The mandibles are generally of simple structure and formed as two more or less fused rods with flared anterior ends (Fig. 7.12.6.7C). The flared parts have sclerotized arcuate lines that are interpreted as growth lines (Paxton 2009). Valderhaug (1985) demonstrated high correlations ($r > 0.9$) between the number of lines and number of segments, weight, and width of prostomium for *Scoletoma fragilis* and interpreted the lines as annual structures with dark lines being formed during winter. The mandibles may be reinforced by calcium carbonate (calcite) (Valderhaug 1985, Colbath 1986).

The naming of maxillary elements has varied rather much through taxonomic history and has become

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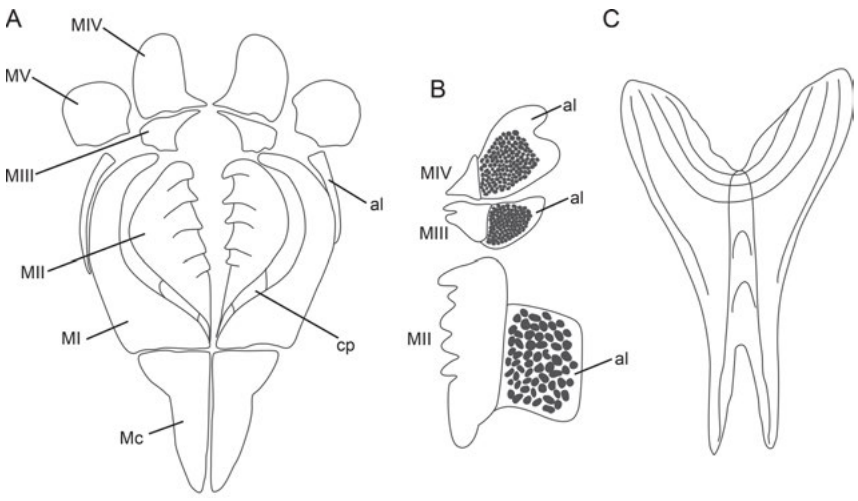


Fig. 7.12.6.7: Maxillae and mandibles. A, General arrangement and shape of maxillae. Note that maxillae III and IV for purpose of illustration usually are drawn flat though being vertically oriented in pharynx region (*Lumbrineris*). B, Maxillae II–IV showing fused attachment lamellae. C, Mandibles (*Lumbrineris*). al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–V, maxillae I–V. B, modified from Carrera-Parra (2006a).

stabilized only in recent years following studies of Orensanz (1973, 1990), Orensanz and Carrera-Parra (2002), and Carrera-Parra (2006a). The system for numbering of maxillae with roman numerals was already used by Kinberg (1865). Many of the contemporary and later scientist used different notations; however, early German researchers (e.g., Ehlers 1868, 1901) referred to maxillae I–II as "Zangen" and "Zähne" respectively, whereas maxillae III–IV were denoted as "Sägeplatten," "Zahnplatten," or only "Platten." McIntosh (1885, 1910) denoted only maxillae I as "maxillae," whereas maxillae II were denoted "great dental plates" and maxillae III–IV "lateral plates." Pruvot and Racovitza (1895) and Crossland (1924) used "pincer" for maxillae I and then "maxillae I–III" for maxillae II–IV. In several French works, maxillae III and IV are referred to as "dents," D1 and D2, respectively (e.g., Ramos 1976). All treatises of lumbrinerids up to about 1970 considered only four pairs of maxillae (e.g., Hartman 1944, Fauchald 1970). The denotation of maxillae V is of more recent use and seems to appear in the 1970s (see e.g., Orensanz 1973). Orensanz (1990) suggested that this element is homologous with maxilla V in other Eunicida, but this view has been disputed by Paxton (2009), who did not consider the element as a maxilla.

Added elements such as connecting plates and attachment lamellae have been variously described but often neglected in species descriptions. When mentioned, attachment lamellae have been designated as "Reibplatten" (e.g., Ehlers 1868, 1901), horny patches (McIntosh 1910), lateral supports (e.g., Uebelacker 1984), lateral lamellae, or bridles (attachment lamellae to maxillae I: Orensanz 1990). In recent taxonomy, several of the added elements were considered of high taxonomic importance for discrimination of genera, for instance, presence and shape of connecting plates (*Eranno*, *Hilbigneris*) or absence of attachment lamellae to maxillae I (*Gallardoneris*). Maxillae V often have been interpreted as added elements and omitted from species descriptions. Species with maxillae V are in such cases reported to have four pairs of maxillae, whereas recent numbering, including maxillae V as integrated elements, would count five pairs of maxillae.

For taxonomic purposes, the number of teeth on the first four pairs of maxillae is of importance. In many cases, this is shown by a maxillary formula, for instance, 1 + 4/5 + 2 + 1, denoting one tooth on maxilla I, four or five on maxilla II (may differ between left and right maxilla), two on maxilla III, and one on maxilla IV. In recent literature, the term "tooth" may be restricted to evaginated structures with an internal pulp cavity (e.g., Carrera-Parra 2004, 2006b), whereas in older literature any more or less acute evaginated structure was referred to as tooth. Recent literature may evade the possible confusion on the number of teeth by referring to "false" teeth as protuberances or bulbous structures.

The examination of maxillae is conventionally performed by dissection from the dorsal side in the region of chaetigers 1–2 to 6–8 (Fig. 7.12.6.6A). Maxillae III and IV are oriented more or less vertically with teeth projecting upward just in front of the tip of maxillae I (e.g., Fig. 7.12.6.8C, E) and may need to be separated for the examination of their shape. In cases when the pharynx is partly protruded and the maxillae appear in the mouth opening, a ventral incision at the side of the midline may be made instead of a dorsal incision.

Biology and ecology

Distribution

Lumbrinerids are found in all seas and at all depths around the world. Some genera, as for instance *Lumbrineris*, *Scoletoma*, *Abyssoninoe*, and *Augeneria*, have a

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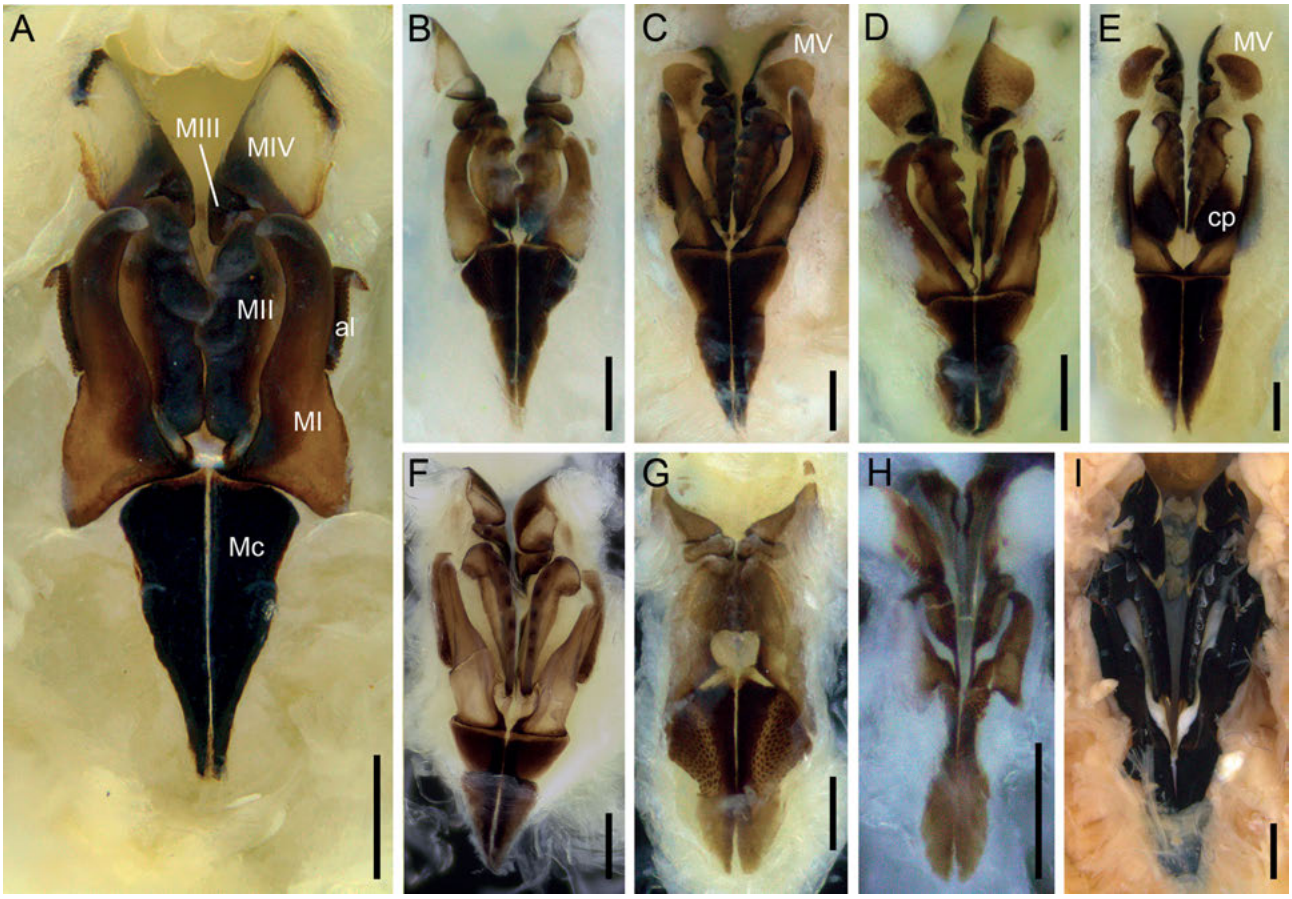


Fig. 7.12.6.8: Diversity of maxillae. A, *Augeneria* sp. B, *Gallardoneris* sp. C, *Lumbrineris* sp. D, *Abyssoninoe* sp. E, *Hilbigneris* sp. F, *Helmutneris vadum* Borisova & Budaeva, 2020. G, *Lumbrinerides* sp. H, *Lumbrineriopsis* sp. I, *Lysarete* sp. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–V, Maxillae I–V. Scale bars: A, 250 µm; B–I, 100 µm.

worldwide distribution, whereas other genera are more limited, for instance, *Ninoe*, *Lysarete*, and *Kuwaita* that appear to be restricted to tropical or warm-temperate seas. In general, it seems that generic diversity is highest in tropical or subtropical waters with particularly many genera represented in the Pacific Ocean. Gil (2011) and Zanol et al. (2021) have presented overviews of contributions to regional faunas for a number of areas of the world. With regard to distribution of species, however, knowledge is imprecise and uncertain in many cases. Several of the early described species have been reported from worldwide areas, for instance, *Lumbrineris latreilli* and *Scoletoma tetraura* (Schmarda, 1861) (*Scoletoma impatiens*). Apparently, many reports of wide distributions are due to confusion with morphologically similar species, especially among early described and imperfectly diagnosed species. Wide distributions might, however, be expected among species living in extensive homogeneous environments such as oceanic deepwater areas.

Species ranges may also be extended by translocation due to human activities. Translocated species are most commonly found in harbor areas and naturally stressed environments where competition from native species is reduced. There are not many verified reports of translocated lumbrinerids. Recent assessments of reported nonindigenous lumbrinerids in the Mediterranean Sea have shown most of them to be either recently described native species or questionable introductions because of uncertain taxonomic status (Langeneck et al. 2020). One species, *Lumbrineris* cf. *perkinsi* Carrera-Parra, 2001, is accepted as nonindigenous having probably migrated from the Red Sea through the Suez Canal, but the species identity and consequently the place of origin is not fully clear.

Habitat preferences and behavior

Lumbrinerids are generally free-living species that burrow into muddy and sandy substrates. A few species have been reported to construct a semipermanent burrow

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system with some reinforcement of the walls (Petch 1986), but most species probably move their way through the sediment without occupying permanent positions. Burrows have been observed to a sediment depth of 11–14 cm (Petch 1986, Casado-Coy et al. 2020), but presumably most species inhabit more shallow sediment levels (see Fauchald and Jumars 1979). Aquarium observations of *Lumbrineris* show that burrowing is an advance and retreat activity where the prostomium is used actively to penetrate the sediment (Jumars et al. 2015). As borrowers, the lumbrinerids play an important role for sediment biogeochemistry by contributing to bioturbation, i.e., the activity of macroinfauna that leads to displacement of sediment particles and enhances water irrigation, processes that in turn promotes oxygen supply into the sediments and enhances metabolic capacity (Kristensen et al. 2012). In a classification of macrofauna with regard to bioturbation, Queirós et al. (2013) categorize lumbrinerids (species of *Abyssoninoe*, *Lumbrineriopsis*, *Lumbrineris*, *Ninoe*, and *Scoletoma*) as biodiffusors, i.e., species that cause diffusive random particle transport over short distances. This activity is important for water irrigation and contributes to the exchange of oxygen and solutes from the mineralization of organic matter between the sediments and the overlying water. Pictures provided by Casado-Coy et al. (2020) show burrows of *Lumbrineris latreilli* with light-colored sediments close to the burrows, indicating oxic conditions. The worm movements with rapid retreats likely cause fresh water to be pulled into the burrows and percolate into the surroundings.

Several species are reported to live in hard-bottom environments and among algal holdfasts, e.g., *Eranno bifrons* Kinberg, 1865, *Lumbrineris magalhaensis* and *Lumbricalus harrisae* Carrera-Parra, 2004 (Kinberg 1865, Orensanz 1990, Carrera-Parra 2004). Averincev (1989) reported *Lumbrineris zatsepini* Averincev, 1989 to live in mucus tubes among algal hapters, hydroids, and red algae on stony bottoms at Franz Joseph Land. A few examples of symbiosis have also been reported. Species of the genus *Helmutneris* are associated with corals (Zibrowius et al. 1975, Carrera-Parra 2006a, Borisova and Budaeva 2020). Ayyagari and Kondamudi (2014) reported an association between *Lumbrineris latreilli* (probably a related species) and the rock boring sea urchin *Stomopneustes variolaris* (Lamarck, 1816) in intertidal areas of the Bay of Bengal. The worm is found between the spines at the aboral side of the sea urchin test. Stabili et al. (2014) found mucus tubes of the sabellid *Myxicola infundibulum* (Montagu, 1808) to be colonized by several specimens of *Lumbrineris* cf. *latreilli* in the Mediterranean Sea.

Feeding modes. Lumbrinerids are largely considered to be carnivores or scavengers, but several studies have indicated detritus and also herbivorous feeding (Fauchald and Jumars 1979, Jumars et al. 2015). Blegvad (1914) found a variety of polychaetes, mollusks, crustaceans, and echinoderms in the gut of *Scoletoma fragilis*. The predatory behavior of *S. fragilis* was supported by studies of Valderhaug (1985) and Gaston (1987), but Valderhaug (1985) also observed quantities of detritus in the gut. Ockelmann and Muus (1978) observed predation from *S. fragilis* on foraminifera, small bivalves and polychaetes, and newly settled juvenile heart urchins. They also observed that adult *S. fragilis* mainly took bivalves less than three mm long, whereas several larger bivalves had surface scratches from unsuccessful attacks. *Scoletoma fragilis* was the only carnivore that was able to catch prey from a subsurface position, whereas all other studied species had to catch prey on the surface or from a surface position. Gaston (1987) examined several species and concluded that *Augeneria albidentata* (Ehlers, 1908) and *Lumbrinerides acuta* (Verrill, 1875) were carnivores in addition to *S. fragilis* on the basis of empty guts. Carnivorous feeding was also supported by studies of the functioning of jaws by Clemo and Dorgan (2017). During the extrusion of jaws, maxillae I and II were moved forward and opened to a wide gape for grasping mobile prey, whereas the locking system of maxillae I appeared to secure prey organisms during retraction. Detritus feeding was assumed by Gaston (1987) for *Ninoe nigripes* Verrill, 1873, *Scoletoma impatiens*, and *Lumbrineris latreilli* because most examined specimens had detritus in the gut. Sanders (1960) characterized *N. nigripes* and *Scoletoma tenuis* (Verrill, 1873) (as *Lumbrineris tenuis*) as nonselective deposit feeders from gut content analyses. Petch (1986) reported that intertidal *Lumbrineris* cf. *latreilli* in Australia was a subsurface selective deposit feeder but supplemented the diet with animal and plant matter.

Other more specialized feeding behavior has been reported for symbiotic living species. *Helmutneris flabellicola* (Fage, 1936) appears to steel prey organisms from its coral host (Zibrowius et al. 1975). In the association of *Lumbrineris* cf. *latreilli* and *Myxicola*, the lumbrinerid presumably obtain defense from the mucus envelope and may feed on envelope material and associated bacteria (Stabili et al. 2014). Ayyagari and Kondamudi (2014) assumed that *L. latreilli* in association with rock boring sea urchins obtains protection from predators but may also feed on released undigested organic matter.

More recent studies using stable isotope ratios to assess trophic networks in benthic ecosystems have largely corroborated previous findings on feeding for

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lumbrinerids. Jumars et al. (2015) list close to 20 studies from the period 2002–2014 where results for $\delta^{15}N$ indicate carnivory in species of *Lumbrineris*, *Scoletoma*, and *Hilbigneris*. Some other studies have indicated stable isotope values that are comparable to values for detrivorous polychaetes (McLeod et al. 2010). Field experiments with $\delta^{13}C$-labeled fresh detritus have shown rapid uptake in lumbrinerids in deep fjord environments (Sweetman and Witte 2008) and deep continental slope areas (Levin et al. 1999). In the latter study, lumbrinerids were found at 5–10 cm sediment depth, suggesting that even deep-dwelling individuals were able to access fresh surficial organic matter rapidly.

Some species, especially *Lumbrineris latreilli*, have been reported to show different living modes and different feeding behavior. *Lumbrineris latreilli* is one of the early described species that has been reported from worldwide areas and most probably represents a complex of morphologically similar species that may have different living habits and functional performances. Fauchald and Jumars (1979) postulated that each lumbrinerid species would use only one feeding mode. However, the possibility that several modes can be utilized, for instance, facultative deposit feeding among carnivores, cannot be ruled out. The frequent observation of detritus in the guts of carnivorous species has often been interpreted as having been accidentally swallowed with the prey. It remains to be clarified if the detritus can be digested and be of nutritional value, and further, if carnivory can be important also for species that appear to rely on detritus (Jumars et al. 2015).

Population structure and role in ecosystems

There is little information on population structure and longevity of lumbrinerids. Most species of *Lumbrineris* are expected to live for 3–5 years (Marlin database 2021), but larger species may be several years old. Valderhaug (1985) recorded up to 10 size classes for *Scoletoma fragilis* in the Oslofjord based on growth lines in the mandibles and width of prostomium and argued that these represented year classes. The first six classes were the most commonly represented. The smallest specimens were recruited into the population (specimens retained on 1 mm sieves) in late autumn each year.

Lumbrinerids are generally common and consistent representatives in soft-bottom macrofaunal communities. Not uncommonly they are among top 5 or top 10 abundance dominants, for instance, in Arctic waters (Kedra et al. 2010), the Mediterranean (Labrune et al. 2008), and temperate and tropical Atlantic (Sanders 1960, Bone and Klein 2000). Oug (1998, 2000) found that *Lumbrineris mixochaeta* Oug, 1998 was among the top 5 macrofaunal dominants during a 20-year monitoring series in northern Norway. Local densities of species of *Lumbrineris* of more than 500–1000 individuals per m^2 have been reported from eastern Russia (Belan 2003); coastal waters of Alicante, Spain (Casado-Coy et al. 2020); coastal waters of Crete (Papadopoulou et al. 1994); Venezuela (Bone and Klein 2000); and fallowed aquaculture sites in southern Australia (Putro 2007).

Sensitivity and tolerance to pollution

Lumbrinerids appear generally to be sensitive to pollution. Rygg (1985a, b) classified a suite of lumbrinerids as nontolerant to sediment contaminants, in particular copper, by being absent from sampling stations with very low species diversity in Norwegian fjords polluted from industrial effluents. However, Burd (2002) found that the Pacific *Lumbrineris luti* Berkeley & Berkeley, 1945 was one of the most common species in areas subject to tailings from a copper mine in British Columbia. With regard to organic enrichment, the European AMBI index classifies lumbrinerids as indifferent (AMBI group II) generally showing nonsignificant variation along spatial or temporal enrichment gradients (Borja et al. 2000). Several recently described species from Portuguese coastal waters and the western Mediterranean have been reported from sediments enriched from municipal effluent discharges (Gomez et al. 2016).

Exploitation

Lumbrinerids are collected for bait fishery in several areas of the world. In the Mediterranean Sea, *Scoletoma impatiens* individuals are harvested by scuba divers from shallow sandy areas in the Gulf of Naples (Gambi et al. 1994). In Spain, local fishermen collect *Kuwaita hanneloreae* Arias & Carrera-Parrara, 2014 and *S. impatiens* from intertidal sandy flats at the Bay of Biscay (Arias and Carrera-Parra 2014) and *Lumbrineris latreilli* at the east coast (Casado-Coy et al. 2020). In the Suez Canal, *Lumbrineris funchalensis* (Kinberg, 1865) is collected by snorkeling at shallow depth (Osman et al. 2010).

Reproduction and development

As far is known, all lumbrinerids have separate sexes (gonochoristic), and the sexes look similar. Sexually mature specimens are indicated by the presence of eggs or sperm in the coelom. Developing gametes are located in midbody segments, often starting about chaetigers 20–40. There are no particular morphological changes

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involved with maturation, but ovigerous females may be recognized by a slight swelling of egg-filled segments and minor color changes. Not much is known about regularity in breeding. Seasonal breeding has been reported for northern and temperate species, respectively, during late winter and spring and during summer or autumn (Okuda 1946, Pettibone 1963, Buchanan and Warwick 1974, Martins et al. 2012, see also summary in Richards 1967). Osman et al. (2010) did not find any particular breeding season for *Lumbrineris funchalensis* in the Suez Canal. In the northern *Lumbrineris mixochaeta*, females with developing eggs were found all year round, whereas males with sperm were restricted to the spawning period (Oug 1998).

Shape and structure of sperm has been examined for a few species of *Lumbrineris* and *Scoletoma* (Rouse 1988, Conti et al. 2011). The sperm is subspherical in shape, has an apical cap-like acrosome with crenulated edges and a long flagellum with 9+2 microtubules. This morphology is generally seen in animals where gametes are released into the surrounding water for external fertilization, a functional condition that is indicated by denoting the sperm type as ect-aquasperm (Rouse 1988).

Most species appear to have yolk-rich eggs that pass through cleavage and initial development stages before hatching. Initial development has been described for *Lumbrineris funchalensis* by Osman et al. (2010), who identified three maturity stages with regard to yolk deposition. Mature eggs vary in size among species from 90 to 500 µm. Most species of *Lumbrineris* appear to have eggs of 150–300 µm (Hartman 1944, Okuda 1964, Richards 1967, Cazaux 1972, Curtis 1977, Oug 1998, Osman et al. 2010, Martins et al. 2012), whereas smaller eggs (110–190 µm) have been reported for *Ninoe* (Pettibone 1963). Large eggs (500 µm) were recorded by Hartman (1939) for *Scoletoma zonata* (Johnston, 1901) (originally reported as *Lumbrineris brevicirra* (Schmarda, 1861); fide Hartman 1944). Fertilization appears to be external for all species. Messina et al. (2005) observed fertilization *in vitro* in experiments with *Scoletoma impatiens*. Sato and Osanai (1996) described the fertilization in *Lumbrineris latreilli* where females spawn eggs into a jelly matrix that are subsequently fertilized. The jelly is important for the fertilization as eggs that were separated from the matrix lost the capacity for sperm binding and became unfertilized.

Further development is either through relatively short pelagic stages or through protected benthic stages with larvae released directly onto the bottom. Pelagic development has been described in detail by Cazaux (1972) and Messina et al. (2005) for *Scoletoma impatiens*. Cazaux (1972) observed that the eggs hatch after a few hours into spherical densely ciliated larvae (protrochophores) that after one day show eye patches and after five days have become more elongated with distinct eyes, pigment patterns, and new ciliary bands. The next stage (metatrochophore) with the appearance of two larval segments and thin larval chaetae appeared after nine days, and the first benthic stage (erpochaete) with four segments after 16 days. The erpochaete larva has lost the ciliation, the prostomium is large and about as long as the following segments, and developing jaws are discernible. Messina et al. (2005) observed a similar pattern, but the metatrochophore stage was reached in three days and the benthic postlarval stage in eight days. Messina et al. (2005) observed from *in vitro* cultures that the larvae were feeding on planktonic microalgae, despite the general apprehension that all lumbrinerids have nonfeeding lecithotroph larvae (cf. Rouse and Pleijel 2006). The postlarvae construct tubes among sand grains from mucoid secretions (Cazaux 1972). Further development proceeds with the addition of new segments and the development of parapodia. Eight-chaetiger juveniles dig into the sediments and will presumably start feeding as carnivores. Summaries of larval development have been presented by Richards (1967), Bhaud and Cazaux (1987), and Wilson (1991).

Larval development within jelly masses attached to objects on the bottom is known for a few species. Japanese populations of *Lumbrineris latreilli* spawn in *Zostera* habitats attaching eggs in jelly masses to the seaweeds. Development goes through ciliated stages (metatrochophore) and early development of chaetigers and segments within the jelly mass until the juveniles are released into the environment at four to seven chaetiger stage (Okuda 1946, Nishihira et al. 1983). At the early bottom stages, jaw apparatus, digestive tract, and new segments are formed. The larvae start creeping around with functional jaw apparatus at eight to ten chaetiger stage (Okuda 1946). At the northern US Pacific coast, *Lumbrineris inflata* Moore, 1911 lays yolky eggs in single layers in flat gelatinous masses under rocks, shells, wood, and algae (Woodin 1974, Strathmann 1987).

Development in parental burrows was described by Hartman (1939) for *Scoletoma zonata* (originally reported as *Lumbrineris brevicirra*) from intertidal waters of California. Early larvae are nearly filled with yolky material. There is no gelatinous sheath or other kind of protection within the burrow where the embryos develop. At the three-chaetiger stage, juvenile limbate chaetae occur, and at the eight-chaetiger stage, both limbate chaetae and

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hooded hooks are present as well as jaw elements and intestine. When isolated, the larvae will feed and secrete a mucus tube where they keep themselves (Hartman 1939). Also North Pacific *Scoletoma zonata* has been reported with three-chaetiger juveniles developing in parental burrows (Strathmann 1987). Additional but scarce records of various aspects of reproductive biology in lumbrinerids are summarized in Richards (1967).

It seems that at least long-lived lumbrinerids do not reproduce each year. Valderhaug (1985) observed for *Lumbrineris fragilis* (= *Scoletoma fragilis*) in the Oslofjord that the number of specimens with gonadal products comprised only a small fraction of the population and involved only the larger specimens, whereas Buchanan and Warwick (1974) recorded that *L. fragilis* at Northumberland reproduced only once at the age of 3 years. Curtis (1977) observed for the same species in Greenland that only one fifth of the specimens were involved in gametogenesis. Oug (1998) observed for *Lumbrineris mixochaeta* that fully grown specimens without gonadal products were found in all seasons.

In a study of life diagram patterns, Fauchald (1983) classified lumbrinerids as perennial motile forms with nonfeeding larvae using the Pacific *Lumbrineris luti* as a representative species. This group of species is characterized by low lifetime reproductive investments (< 10 % of female volume), sexual reproduction, moderately large to large eggs, and limited dispersal ability of larvae and adults. Fauchald (1983) suggested that this life strategy might be an adaptation to maintain high genetic variability (genome fit) within small successful interbreeding populations while also retaining high evolutionary flexibility in a long-term perspective.

Taxonomy and phylogeny

Classification and definition of genera

The family Lumbrineridae has undergone rather many changes since its erection in the mid nineteenth century with regard to taxonomic status and rank, the inclusion of genera and species, and the type of characters used for definition and discrimination of genera. Schmarda (1861) is now generally credited the authorship of the family (erected as Lumbrinereida within order Dorsibranchiata), but Malmgren (1867) and Grube (1878) have also been cited as authors (e.g., Hartman 1959, Fauchald 1970, 1977, Orensanz 1973, 1990, Uebelacker 1984, Frame 1992). Schmarda (1861) erected the family for a range of species with or without antennae and branchiae and with symmetric or asymmetric maxillae within the frame of an early system that divided Eunicida into branchiate and abranchiate forms (Audouin and Milne Edwards 1834).

The first more stringent classification systems were developed by Kinberg (1865) and Ehlers (1868). Kinberg (1865) established 10 families for Eunicida based on maxillary characters and presence or absence of branchiae. Lumbrineridae, as presently defined, was represented by three families comprising the genera *Ninoe*, *Eranno*, *Lumbrineris*, and *Lysarete*. Species of *Lumbrineris* were further divided in two groups based on the presence of one or two teeth on maxillae III. Ehlers (1868) ranked the eunicidans as a family and subdivided this into Eunice Labidognatha and Eunice Prionognatha from the basic structure of maxillae and made further subdivisions based on antennae and branchiae. The lumbrinerids (as Labidognatha nuda: "nude" for no antennae) comprised the genera *Ninoe* (with branchiae) and *Lumbrineris* (without branchiae). Grube (1878, 1879) merged the two systems and extended lumbrinerids to include genera that are presently referred to Oenonidae and were placed in separate families by Kinberg (1865). Contemporary and later authors hence came to use different systems for classification (e.g., Malmgren 1867, McIntosh 1885, 1910), in some cases also with further modification. The broad conception of lumbrinerids, however, was generally accepted for a longer period into the twentieth century with the consequence that genera such as *Drilonereis*, *Notocirrus*, and *Arabella* were included (e.g., Fauvel 1923, Monro 1930). McIntosh (1910) and Hartman (1944) have given detailed accounts of the early history of the classification schemes.

A step toward a unified and more modern system with families defined with emphasis on maxillary architecture was taken by Hartman (1944). She revived partly Kinberg's (1865) system and raised the Eunicea to the rank of superfamily. Lumbrineridae was restricted and defined distinct from Arabellidae that was erected as a new family to encompass, e.g., *Drilonereis* and *Arabella* that had previously been included in Lumbrineridae. Within Lumbrineridae, she recognized four genera. In accordance with tradition, the majority of species was referred to *Lumbrineris*. The other genera were *Ninoe* with several species and *Augeneria* and *Cenogenus* with one species each. In her later catalogue of world polychaetes, she (Hartman 1959) recognized the same genera but added the symbiotic *Haematocleptes* (now Oenonidae) and *Ophiuroicola*. Hartman (1944) also attempted to subdivide *Lumbrineris* in groups for identification purposes based on morphological characters such as chaetae, parapodial lobes, and aciculae. She considered maxillary structures to be of generally little value for species discrimination, although admitting that the examination of maxillae might be

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necessary because of the rather few external characters of species-specific value.

Fauchald (1970, 1977) followed up Hartman's work but placed *Augeneria* and *Cenogenus* in synonymy with *Lumbrineris* and recognized only *Ophiuroicola*, *Ninoe*, and *Lumbrineris* (in Fauchald 1977 also *Kuwaita*) as valid genera. All species carrying gill structures were referred to *Ninoe*. Fauchald (1970) further extended Hartman's groups of *Lumbrineris* into a system with four levels addressing hooded hooks (compound/ simple), compound limbate chaetae (presence/ absence), posterior hooks (bidentate/ multidentate), and dentition of maxillae III. The system has been in some use (e.g., Ramos 1976), but its value is mainly limited to identification purposes and has modest relevance for taxonomic accounts.

A new approach for discrimination of genera and species within Lumbrineridae was introduced by Orensanz (1973). He reinstated *Augeneria* and erected *Lumbrinerides* and *Lumbrineriopsis* pointing out that these represented groups of species with several common characteristics that distinguished them from the basic *Lumbrineris* forms. He referred in particular to maxillary structures in addition to shape of parapodia and type of chaetae. In a later work, Orensanz (1990) developed a phylogenetically based system for defining genera that implied a systematic assessment of characters with respect of being derived (apomorphic) or ancestral (plesiomorphic). Maxillary structures were used extensively assuming that different shapes of maxillae are apomorphies within Lumbrineridae. In this study (Orensanz 1990), he resurrected *Eranno* and erected *Abyssoninoe*. Orensanz' principles were followed up by Frame (1992), who erected *Lumbricalus* and resurrected *Scoletoma*, and later by Carrera-Parra (2006a), who erected several new genera as part of a phylogenetic analysis of the Lumbrineridae (see below).

Orensanz (1990) moved *Lysarete* into Lumbrineridae. *Lysarete* was erected for the species *L. brasiliensis* Kinberg, 1865 by Kinberg (1865), who also created the family Lysaretea (Lysaretidae) to encompass it. Later authors redefined Lysaretidae, but some authors (see Colbath 1989) noted that the maxillae of *Lysarete* were structurally similar to those of Lumbrineridae. Colbath (1986, 1989) provided further evidence for the potential relationship by showing that the jaws of *Lysarete* are mineralized with calcite, as is also the case in Lumbrineridae. Based on jaw morphology and mineralization, he suggested to restrict Lysaretidae to *Lysarete* only and reinstate Oenonidae for the other genera. Orensanz (1990) was of similar opinion but took it a step further by transferring *Lysarete* into the Lumbrineridae and merging the related family Arabellidae into Oenonidae. As a consequence, neither Lysaretidae nor Arabellidae were recognized, whereas the definition of Lumbrineridae was extended to include *Lysarete* (Orensanz 1990).

Phylogeny

To date, the phylogeny of Lumbrineridae has been reconstructed based on morphological data only. Carrera-Parra (2006a) utilized 38 morphological characters for 19 genera treated as terminal taxa and suggested the placement of *Lysarete* and *Arabelloneris* at the base of the tree with the rest of the genera forming a polytomy of two large clades and the genus *Ninoe*. The largest clades were defined by details of the maxillary apparatus such as the presence or absence of the connecting plates and the number of maxillae (four or five pairs). Nevertheless, the monophyly of all genera has not been tested in the study, and the proposed phylogenetic hypothesis requires further corroboration. Furthermore, no autapomorphies have been identified for the type and the largest genus of the family, *Lumbrineris*. Our own preliminary and unpublished data on the phylogenetic analysis of Lumbrineridae based on molecular data with two mitochondrial and one nuclear marker suggest a polyphyletic position of *Lumbrineris* and do not support the clades proposed by Carrera-Parra (2006a). Nevertheless, the family awaits thorough phylogenetic analyses based on extensive molecular data and taxon coverage. A morphology-based phylogenetic reconstruction is available for the eight species belonging to the genus *Lumbricalus* (Carrera-Parra 2005).

Lumbrineridae has been included into several phylogenetic reconstructions of the whole taxon Eunicida based on molecular data, however, with only very few representatives of the genera *Lumbrineris*, *Ninoe*, and *Scoletoma*. All these phylogenies placed Lumbrineridae as the most basal family within Eunicida (Struck et al. 2006, Tilic et al. 2016). In the most recent phylogenetic reconstruction based on the genomic data, two species, *Scoletoma zonata* and *Ninoe nigripes* Verrill, 1873, were included resulting in sister group relationships between Lumbrineridae and Oenonidae with Dorvilleidae in the basalmost eunicidan clade (Struck et al. 2015; see Fig. 7.12.1.3 in Budaeva and Zanol 2021).

Status of species taxonomy

Species taxonomy in lumbrinerids is in many ways still underdeveloped. Many named species, particularly among those originally referred to *Lumbrineris*, in the wide sense, are imperfectly known because of insufficient original descriptions. It may be assumed that a number of these will turn out to be synonyms of presently valid species if their identity can be established

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at all, whereas others should be transferred to different genera upon assessment of present generic diagnostic characters. At the same time, several species reported from wide geographic areas may essentially represent groups of morphologically similar species (e.g., *Lumbrineris latreilli*). It has also contributed to uncertain species reports that some species have been differently diagnosed during taxonomic history. An example is *Lumbrineris tetraura* from Cape of Good Hope (South Africa) and coast of Chile that was originally described with asymmetric maxillae and bidentate hooks (Schmarda 1861) as *Notocirrus tetraurus* Schmarda, 1861. Ehlers (1901) gave a new and extended description based on specimens from Chile, indicating the presence of bidentate maxillae III and anterior simple long, slender multidentate hooded hooks, characters that later got Day (1953) to synonymize *Lumbrineris impatiens* (= *Scoletoma impatiens*) from Italy with *L. tetraura*. This synonymy, for which the name *tetraura* has priority, has been accepted in several more recent faunal works and used widely (e.g., Hartmann-Schröder 1996).

It may also be assumed that there still is a number of undescribed species among the lumbrinerids, even in well-investigated areas. In environmental monitoring studies, specimens with characters that deviate from current species descriptions are regularly found (own unpublished observations). Whether such specimens represent intraspecific variation or separate species remains to be clarified. Following new interest in lumbrinerid taxonomy (Gomez et al. 2016), a number of new species from several genera have been described in recent years from the Bay of Biscay, Iberian Peninsula, and Mediterranean waters (Aguirrezabalaga and Carrera-Parra 2006, Martins et al. 2012, Arias and Carrera-Parra 2014, Kurt-Sahin et al. 2016). Similarly, new species have recently been described from the West Pacific (Cai and Li 2011, Miura 2017), East Pacific (Hernandez-Alcantara et al. 2006), and Caribbean waters (Carrera-Parra 2001b). With regard to discrimination of species, the implementation of molecular genetic methods as new tools in taxonomy appears promising, both for assisting morphological assessments and for detecting possible occurrences of cryptic species. A recent study from sub-Antarctic waters clearly supported the presence of several species in a morphologically variable *Lumbrineris* species complex (Brasier et al. 2016). Presently, own ongoing studies of lumbrinerids in the North Atlantic and the Nordic Seas applying DNA sequencing indicate the presence of several undescribed species in the genera *Abyssoninoe*, *Augeneria*, and *Lumbrineris*.

Lumbrineridae Schmarda, 1861

Synonym: Lysaretidae Kinberg, 1865

Type genus: *Lumbrineris* Blainville, 1828

Diagnosis: Body slender, with numerous segments. Prostomium rounded, usually without eyes or appendages, with dorsolateral nuchal organs, some taxa with middorsal nuchal papilla or small antennae at posterior margin. Peristomium with two achaetous rings, first ring ventrally incomplete, second ring ventrally projecting forward. Parapodia subbiramous with notopodia reduced to small knobs or represented by short dorsal cirri, with thin notoaciculae, without chaetae. Neuropodia well developed, with one to several distinct neuroaciculae, with chaetae of one or several kinds. Ventral cirrus lacking. Branchiae absent in most genera, when present situated in anterior neuropodia or at dorsum in posterior body. All taxa with limbate chaetae, other chaetae variously present comprising simple, compound, and pseudocompound multidentate hooded hooks, transitional hooded hooks, simple bidentate hooded hooks, and compound spinigers. Maxillary apparatus symmetric, with short maxillary carriers, with up to six pairs of maxillae. Attachment lamellae and connecting plates variously present. Mandibles more or less fused, with distal calcified plate and concentric growth rings (adapted from Orensanz 1990 and Carrera-Parra 2006a).

Genera

Abyssoninoe Orensanz, 1990 (Fig. 7.12.6.9A–H)

Type species: *Lumbriconereis abyssorum* McIntosh, 1885. Off west coast of South America, south of Valparaiso, 4060 m.

Diagnosis: Prostomium conical, without antennae and eyes. Parapodia with reduced notopodia, with simple limbate chaetae and simple, multidentate hooded hooks. Anterior hooks extremely long, tapering, resembling limbate chaetae, evolving through anterior chaetigers to faintly outlined transitional hooks and further to clearly defined multidentate hooks. Aciculae yellow. Pygidium with one to two pairs of anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament, with or without connecting plates; maxillae III and IV pigmented; maxillae V connected to or completely fused with maxillae IV forming a broad semicircular plate with a tooth protruding from inferior border. All maxillae with attachment lamellae. Mandibles fused up to three fourths of length (adapted from Frame 1992 and Carrera-Parra 2006a).

Composition: Eight species

Distribution: Worldwide.

Remarks: The genus is characterized by the modified hooded hooks in anterior chaetigers and the fusion of

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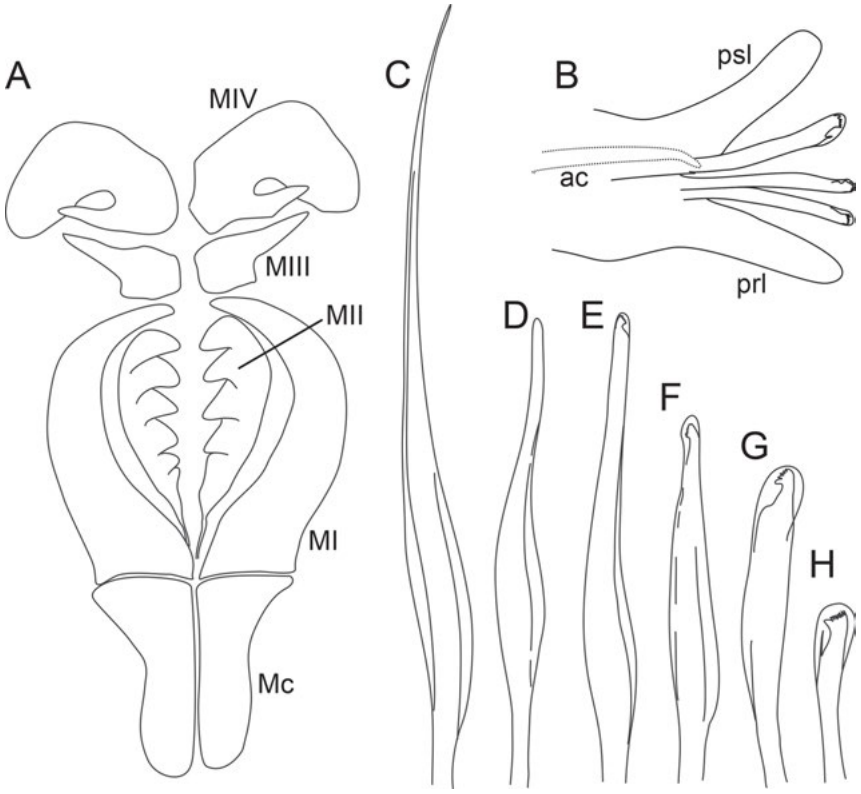


Fig. 7.12.6.9: Morphology of *Abyssoninoe*; *Abyssoninoe hibernica* (A, B) and *Abyssoninoe abyssorum* (McIntosh, 1885) (C–H). A, Maxillary apparatus. B, Posterior parapodium with extended vascularized postchaetal lobes. C, Limbate chaeta. D–H, Progression from anterior prolonged hooded hooks to ordinary hooded hooks: third parapodium (D); seventh parapodium (E); eighth parapodium (F); tenth parapodium (G); median parapodium (H). ac, acicula; Mc, maxillary carriers; MI–MIV, maxillae I–IV; prl, prechaetal lobe; psl, postchaetal lobe. Modified from Orensanz (1990) (C–H).

maxillae IV and V. Species discrimination is problematic, however. Characters which have been used for species separation include the most anterior position of "normal-shaped" hooded hooks and the development of prolonged digitiform vascularized lobes in far posterior chaetigers. Carrera-Parra (2006a) considered *Abyssoninoe* to be a genus with four pairs of maxillae due to complete fusion of maxillae IV and V, but recently new species have been found with partial fusion only (Oug, unpublished observations).

Arabelloneris Hartmann-Schröder, 1979 (Fig. 7.12.6.10A–D)
Type species: *Arabelloneris broomensis* Hartmann-Schröder, 1979. Willies Creek, Broome, Western Australia, intertidal.
Diagnosis: Prostomium without antennae, with or without eyes. Parapodia with notopodia reduced, with limbate chaetae only, with no hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles separate or fused up to three fourths of length (modified from Hartmann-Schröder 1979 and Carrera-Parra 2006a).
Composition: Two species
Distribution: Australia, South Atlantic.
Remarks: Hartmann-Schröder (1979) commented the genus' similarity with arabellid polychaetes (now Oenonidae) in external morphology (presence of eyes, no ventral mouth field) as well as the lack of hooded hooks, but that the structure of the maxillary apparatus clearly places the genus within Lumbrineridae. The presence of maxillae V is not indicated in her description but is reported for *Arabelloneris janeirensis* (Augener, 1934) by Orensanz (1973, as *Lumbrineris janeirensis*).

Augeneria Monro, 1930 (Fig. 7.12.6.11A–F)
Type species: *Augeneria tentaculata* Monro, 1930. South Orkney Islands and Palmer Archipelago, Southern Ocean.
Diagnosis: Prostomium with or without small antennae or nuchal papillae. Parapodia with reduced notopodia, with simple and compound hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III pigmented; maxillae IV shaped like broad plates with whitish central and dark peripheral areas. Maxillae V absent. All maxillae with attachment lamellae, narrow at maxillae III and IV. Mandibles proportionally

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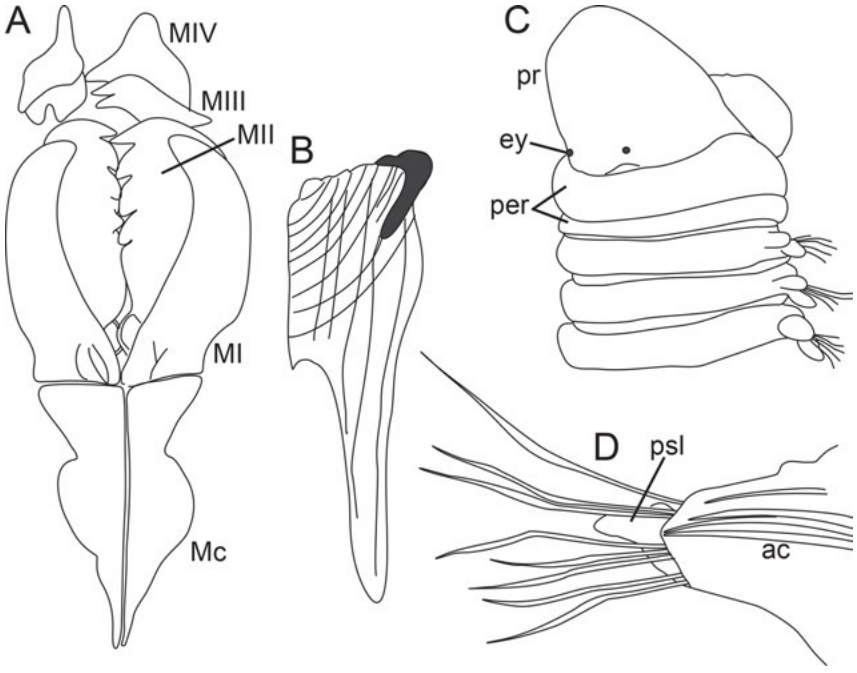


Fig. 7.12.6.10: Morphology of *Arabelloneris broomensis* Hartmann-Schröder, 1979. A, maxillary apparatus, maxillae V not illustrated; B, half of mandibles; C, anterior body, dorsolateral view; D, ninth parapodium, anterior view. ac, acicula; ey, eye; Mc, maxillary carriers; MI–MIV, maxillae I–IV; per, peristomium; pr, prostomium; psl, postchaetal lobe. Modified from Hartmann-Schröder (1979).

short and robust, with short, divergent shafts (adapted from Orensanz 1990 and Carrera-Parra 2006a).
Composition: Nine species
Distribution: Worldwide, shallow water and deep sea.
Remarks: Monro (1930) indicated the presence of three small occipital antennae as diagnostic for the genus. Orensanz (1973) emended and extended the diagnosis based on structure of chaetae, maxillae, and mandibles, also noting that occipital antennae were not always present. Carrera-Parra (2006a) reinstated the presence of three occipital antennae and further indicated the presence of carriers with wide anterior border as diagnostic but these changes will imply that several species presently referred to *Augeneria* will be left without generic affiliation.

Cenogenus Chamberlin, 1919 (Fig. 7.12.6.12A–F)
Paraninoe Levenstein, 1977.
Type species: *Cenogenus descendens* Chamberlin, 1919. Pacific Ocean, NW of Aguja Point, Peru.
Diagnosis: Prostomium with single small antenna (nuchal papilla), sometimes concealed under anterior rim of peristomium. Parapodia with reduced notopodia, anterior parapodia with postchaetal dorsolateral branchial lobe, with simple multidentate hooded hooks. Anterior hooks prolonged, with slender tips, posterior hooks short. Pygidium with anal cirri. Maxillae I forceps-like; MII about as long as MI, with ligament, without connecting plates; MIII and MIV pigmented plates. All maxillae with attachment lamellae. Maxillae V absent. Mandibles fused up to three fourths of length (adapted from Orensanz 1990 (as *Paraninoe*) and Carrera-Parra 2001a).
Composition: Twelve species
Distribution: Deep waters of the Pacific, Atlantic, and Southern Oceans.
Remarks: The genus *Cenogenus* was considered valid by Hartman (1944, 1959) but was regarded as a junior synonym of *Lumbrineris* by Fauchald (1970, 1977), following the traditional perception of *Lumbrineris* as a heterogeneous taxon with wide morphological variation. The genus was reinstated by Carrera-Parra (2001a) after the restriction of *Lumbrineris* by Orensanz (1990) to include species with five pairs of maxillae and compound and simple multidentate hooded hooks. Several species had previously been referred to *Ninoe* because of the presence of branchiae (Fauchald 1970). Levenstein (1977) erected the genus *Paraninoe* for species with simple gills and edentate maxillae III and IV and restricted *Ninoe* to include species with two or more branchial filaments. Carrera-Parra (2001a) redescribed *Cenogenus* and placed *Paraninoe* as a junior synonym of *Cenogenus*.

Eranno Kinberg, 1865 (Fig. 7.12.6.13A–D)
Type species: *Eranno bifrons* Kinberg, 1865. Cape Virgenes, Patagonia, Argentina; rocky bottom, 30 fathoms.
Diagnosis: Prostomium conical, without antennae and eyes. Parapodia with reduced notopodia, with simple

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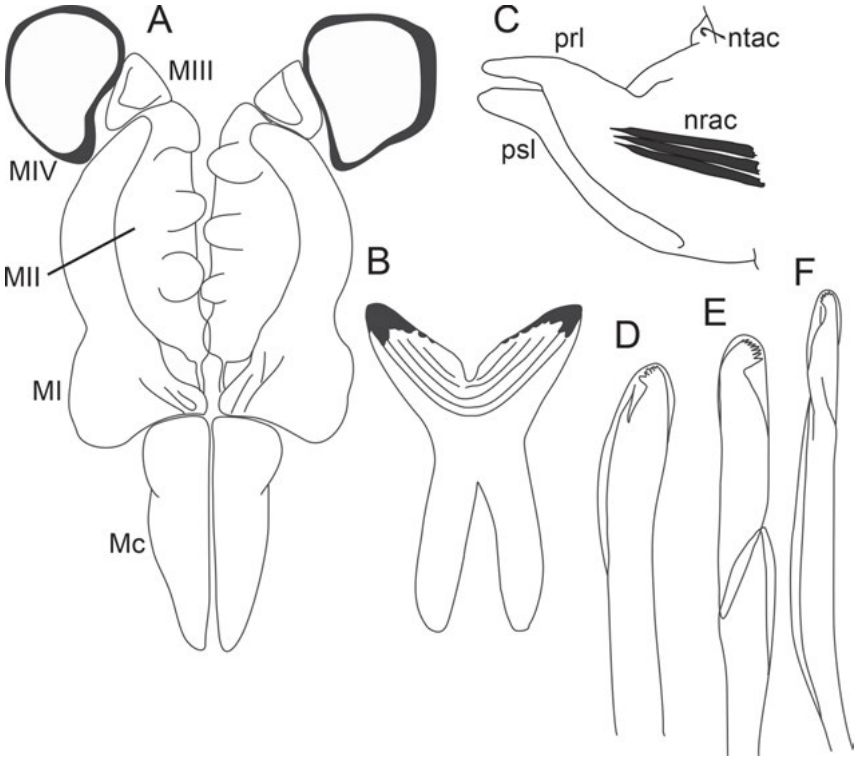


Fig. 7.12.6.11: Morphology of *Augeneria*; *Augeneria polytentaculata* Imajima & Higuchi, 1975 (A), *Augeneria algida* (B, D, F), and *Augeneria riojai* Aguirrezabalaga & Carrera-Parra, 2006 (C, E). A, maxillary apparatus; B, mandibles; C, parapodium 26; D, simple hooded hook, posterior body; E, compound hooded hook; F, pseudocompound twisted hooded hook. Mc, maxillary carriers; MI–MIV, maxillae I–IV; nrac, neuroaciculae; ntac, notoaciculae; prl, prechaetal lobe; psl, postchaetal lobe. Modified from Imajima and Higuchi (1975) (A), Winsnes (1987) (B, D, F), and Aguirrezabalaga and Carrera-Parra (2006) (C, E).

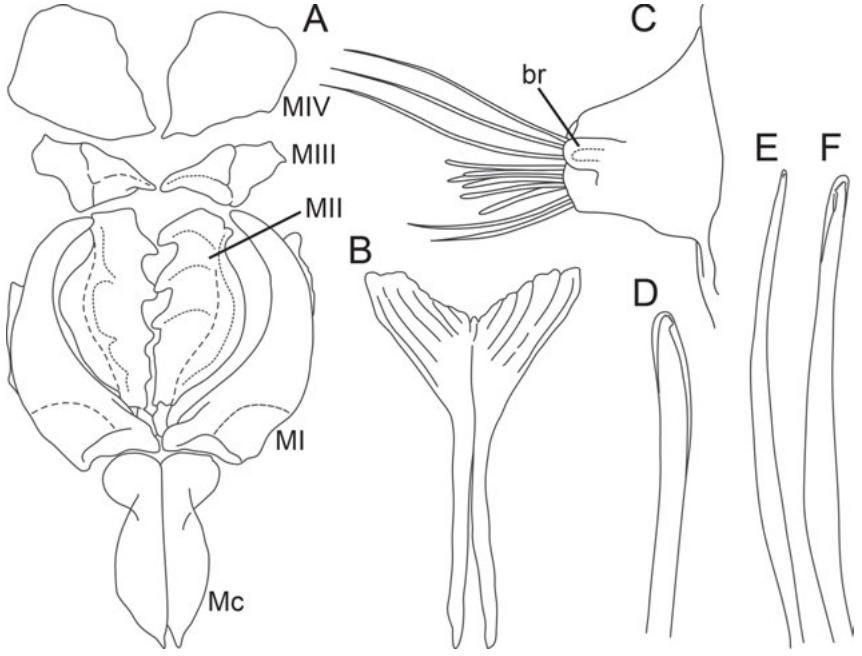


Fig. 7.12.6.12: Morphology of *Cenogenus antarctica* (Monro, 1930). A, maxillary apparatus; B, mandibles; C, 19th parapodium, posterior view; D, posterior hooded hook; E, prolonged simple hooded hook from the first parapodium; F, the same from a median parapodium. br, branchia; Mc, maxillary carriers; MI–MIV, maxillae I–IV. Modified from Orensanz (1990).

multidentate hooded hooks that may be very slender in anterior chaetigers. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II proportionally short, about half length of maxillae I, connected to maxillae I by long narrow sclerotized connecting plates, with ligament; maxillae III and IV pigmented; maxillae V partially fused to maxillae IV or free. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles fused up to three fourths of length, with long narrow shafts (adapted from Frame 1992, Hilbig 1995, and Carrera-Parra 2006a).

Composition: Eleven species

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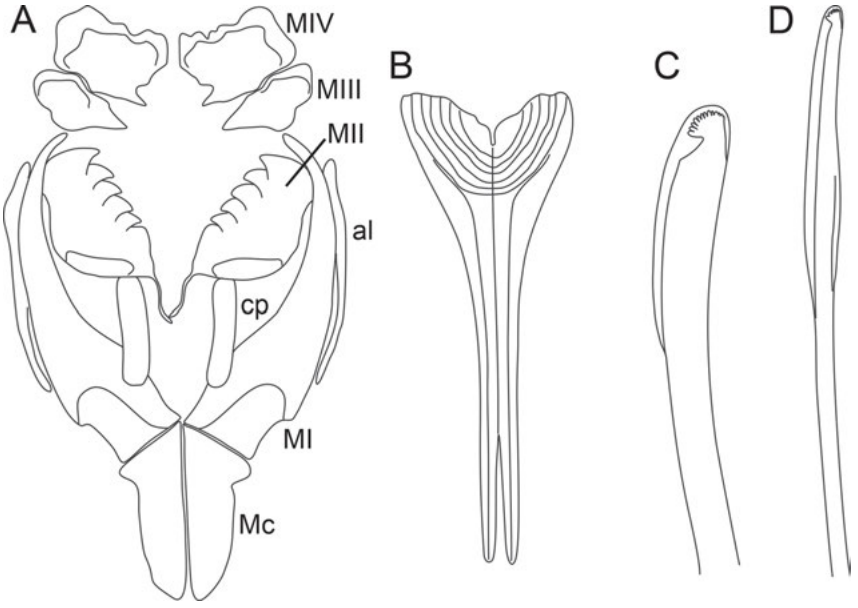


Fig. 7.12.6.13: Morphology of *Eranno*; *Eranno* sp. (A, B) and *Eranno bifrons* Kinberg, 1865 (C, D). A, maxillary apparatus; B, mandibles; C, posterior hooded hook; D, anterior prolonged simple hooded hook. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MIV, maxillae I–IV. Modified from Budaeva (2005) (A, B) and Kongsrud et al. (2013) (C, D).

Distribution: Atlantic, Pacific, and Southern Oceans.
Remarks: The genus *Eranno* was erected by Kinberg (1865) but was for a long period considered a junior synonym of *Lumbrineris* (e.g., Hartman 1944, 1959, Fauchald 1970, 1977). It was reinstated and redefined by Orensanz (1990) based on jaw and chaetal characters. Frame (1992) and Hilbig (1995) partly refined the diagnosis. Degree of fusion of maxillae IV and V appears to vary rather much. Hilbig (1995) illustrated species with free maxillae V. A list of species presently recognized in *Eranno* has been given by Cai and Li (2011).

Gallardoneris Carrera-Parra, 2006 (Fig. 7.12.6.14A–D)
Type species: *Lumbrineris shiinoi* Gallardo, 1968. Nha Trang, South Vietnam.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia, with compound and simple multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like, with wide base; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III completely pigmented; maxillae MIV with whitish central area. Maxillae III and IV with narrow attachment lamellae, at maxillae III short at posterolateral edge. Maxillae V absent. Mandibles fused (adapted from Carrera-Parra 2006a).
Composition: Three species
Distribution: Vietnam, Thailand, Western Europe, the Mediterranean Sea and western Africa.
Remarks: The genus is close to *Augeneria*. It is distinguished by the total absence of antennae, absence of attachment lamellae at maxillae I and II, the short attachment lamellae of maxillae III and mandibles that are completely fused. A new species has recently been described by Martins et al. (2012).

Gesaneris Carrera-Parra, 2006 (Fig. 7.12.6.15A–C)
Type species: *Lumbriconereis malaysiae* Rullier, 1969. Malaysia. (= *Gesaneris malayensis* fide Carrera-Parra 2006a).
Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia, with simple multidentate hooded hooks. Maxillae I forceps-like with wide base; maxillae II shorter than maxillae I, with ligament, without connecting plates; MIII completely pigmented; MIV with whitish central area. Maxillae II–IV with narrow attachment lamellae. Maxillae V absent. Mandibles with shafts partly separated (adapted from Carrera-Parra 2006a).
Composition: Monotypic
Distribution: Malaysia.
Remarks: The genus resembles *Augeneria*, *Gallardoneris*, and *Helmutneris* by the presence of maxillae IV having a whitish central area. It is separated by the absence of compound hooded hooks, the rather short maxillae II and the absence of attachment lamellae at maxillae I.

Helmutneris Carrera-Parra, 2006 (Fig. 7.12.6.16A–D)
Type species: *Lumbriconereis flabellicola* Fage, 1936. West of Safi, Morocco, western Africa, associated with the coral *Flabellum*.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia, with simple

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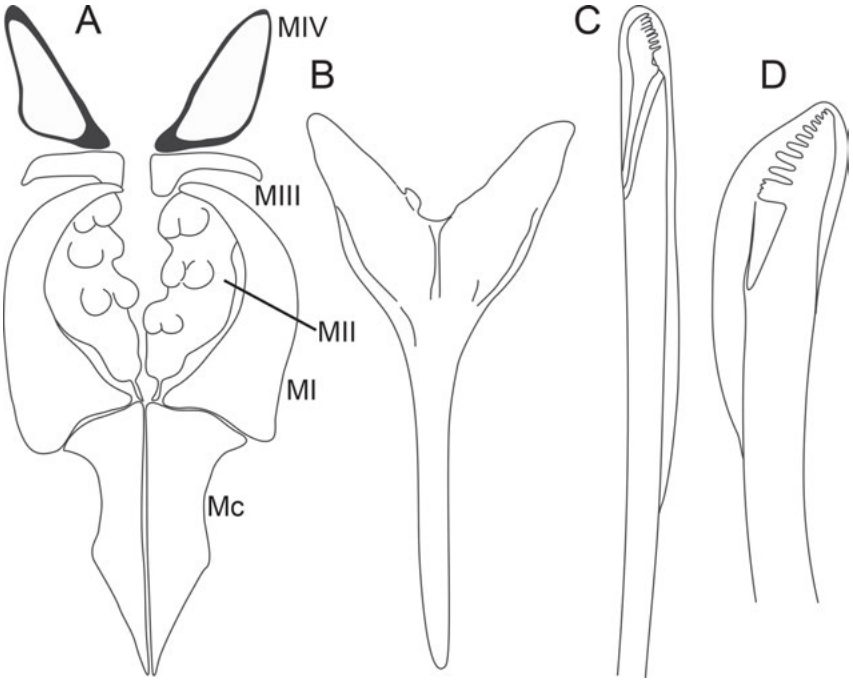


Fig. 7.12.6.14: Morphology of *Gallardoneris shiinoi* (Gallardo, 1968). A, maxillary apparatus; B, mandibles; C, compound hooded hook; D, posterior simple hooded hook. Mc, maxillary carriers; MI–MIV, maxillae I–IV. Modified from Gallardo (1968).

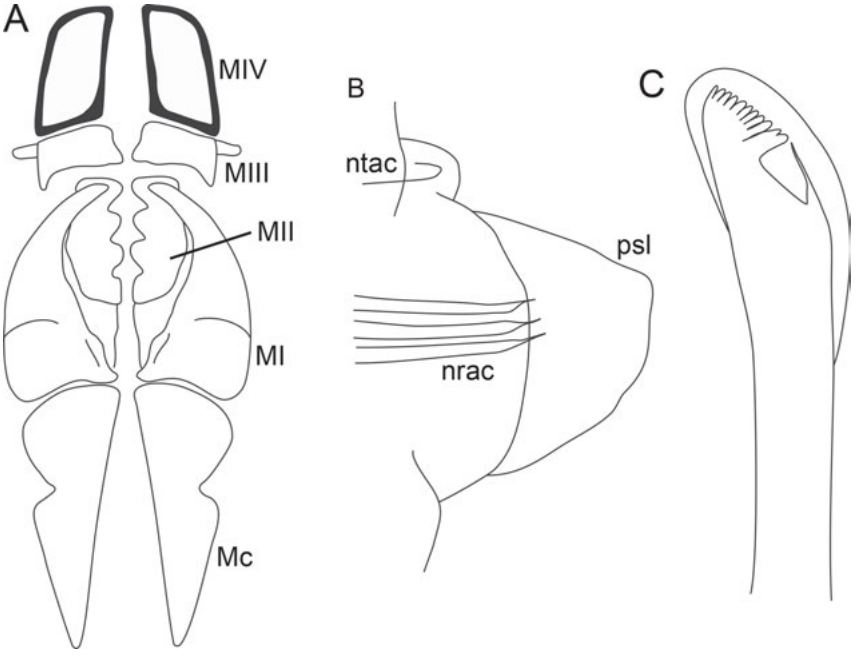


Fig. 7.12.6.15: Morphology of *Gesaneris malaysiae* (Rullier, 1969). A, maxillary apparatus; B, anterior parapodium; C, simple hooded hook. Mc, maxillary carriers; MI–MIV, maxillae I–IV; nrac, neuroaciculae; ntac, nototaciculae; psl, postchaetal lobe. Modified from Carrera-Parra (2006a).

multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like with wide base; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III and IV with whitish central area. All maxillae with attachment lamellae. Maxillae V absent. Mandibles with shafts partly separated (adapted from Carrera-Parra 2006a, and Borisova and Budaeva 2020).

Composition: Three species

Distribution: East Atlantic, Japan, China, Philippine islands, east Australian tropics, associated with stone corals.

Remarks: The genus has recently been established to incorporate species previously included in *Lumbrineris*. It is close to *Gesaneris* but differs by the length of maxillae II, the unpigmented central area of maxillae III,

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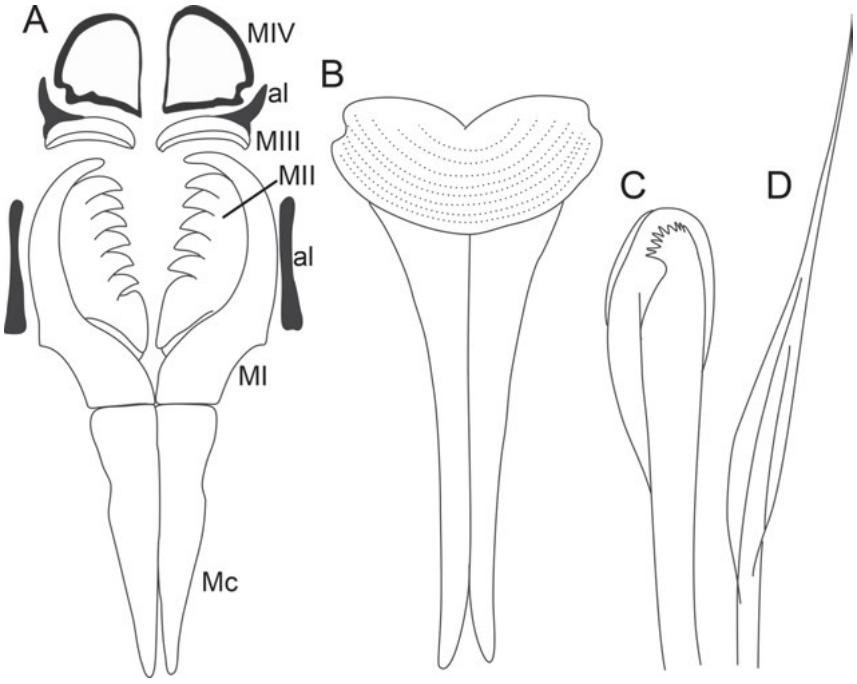


Fig. 7.12.6.16: Morphology of *Helmutneris flabellicola* (Fage, 1936). A, maxillary apparatus; B, mandibles; C, hooded hook; D, limbate chaeta. al, attachment lamella; Mc, maxillary carriers; MI–MIV, maxillae I–IV. Modified from Zibrowius et al. (1975)

and the presence of attachment lamellae at maxillae I. A new species has recently been described by Borisova and Budaeva (2020).

Hilbigneris Carrera-Parra, 2006 (Fig. 7.12.6.17A–D)
Type species: *Hilbigneris pleijeli* Carrera-Parra, 2006. Gulf of St. Malo, Dinard, France.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with notopodia as small knobs, neuropodia with compound and simple multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II shorter than maxillae I, with ligament and wide strongly sclerotized connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles with shafts partly fused (adapted from Carrera-Parra 2006a).
Composition: Three species
Distribution: East Atlantic (English Channel), Mediterranean Sea, Gulf of Mexico.
Remarks: The genus has recently been established to incorporate species previously included in *Lumbrineris*. It is mainly distinguished from *Lumbrineris* by a relatively short maxillae II and wide connecting plates between maxillae I and maxillae II. European specimens have previously been identified as *Lumbrineris latreilli* or *L. gracilis*.

Kuwaita Mohammad, 1973 (Fig. 7.12.6.18A–F)
Type species: *Kuwaita magna* Mohammad, 1973. Sulaibikhair, Kuwait, Persian Gulf, intertidal.
Diagnosis: Prostomium with three small antennae, without eyes. Parapodia subbiramous, notopodia represented by dorsal cirri and notoaciculae. Chaetae include limbate chaetae and simple multidentate hooded hooks. Posterior segments with nephridial papillae emerging from body wall below parapodia. Branchiae in dorsal position on body wall in posterior segments. Pygidium with two pairs of anal cirri. Maxillae I forceps-like; maxillae II shorter than maxillae I, with ligament and wide strongly sclerotized connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles free from each other along most of their length (adapted from Carrera-Parra and Orensanz 2002, and Arias and Carrera-Parra 2014).
Composition: Five species
Distribution: Widely distributed in tropical and warm temperature waters (Carrera-Parra and Orensanz 2002).
Remarks: The position of *Kuwaita* within Lumbrineridae has been somewhat uncertain because of the presence of dorsal cirri (Fauchald 1977). Carrera-Parra and Orensanz (2002) revised the genus and pointed out the affinity to Lumbrineridae with reference to maxillary structures and chaetae. Several external characteristics,

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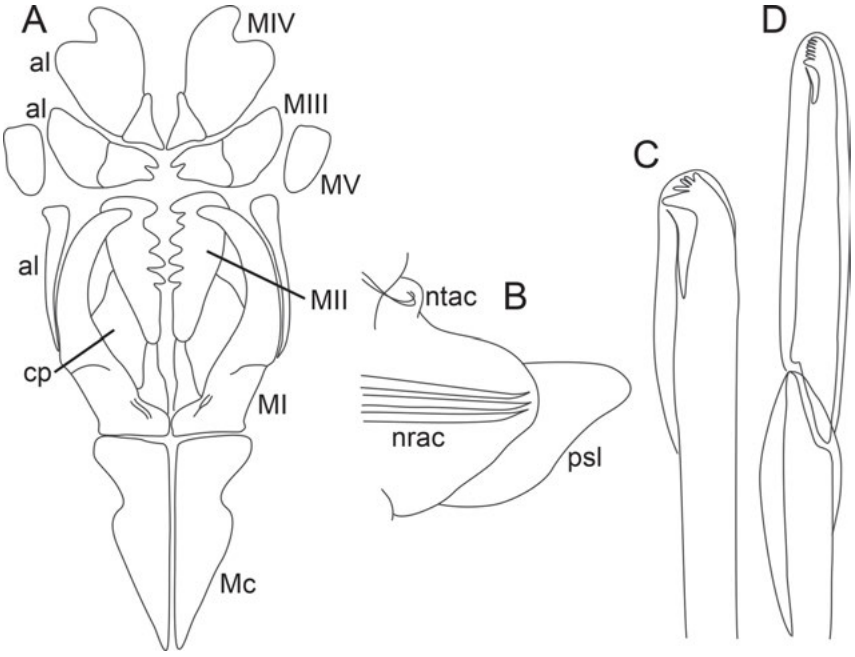


Fig. 7.12.6.17: Morphology of *Hilbigneris pleijeli* Carrera-Parra, 2006. A, maxillary apparatus; B, anterior parapodium, anterior view; C, simple hooded hook; D, compound hooded hook, anterior body. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MV, maxillae I–V; nrac, neuroaciculae; ntac, notoaciculae; psl, postchaetal lobe. Modified from Carrera-Parra (2006a).

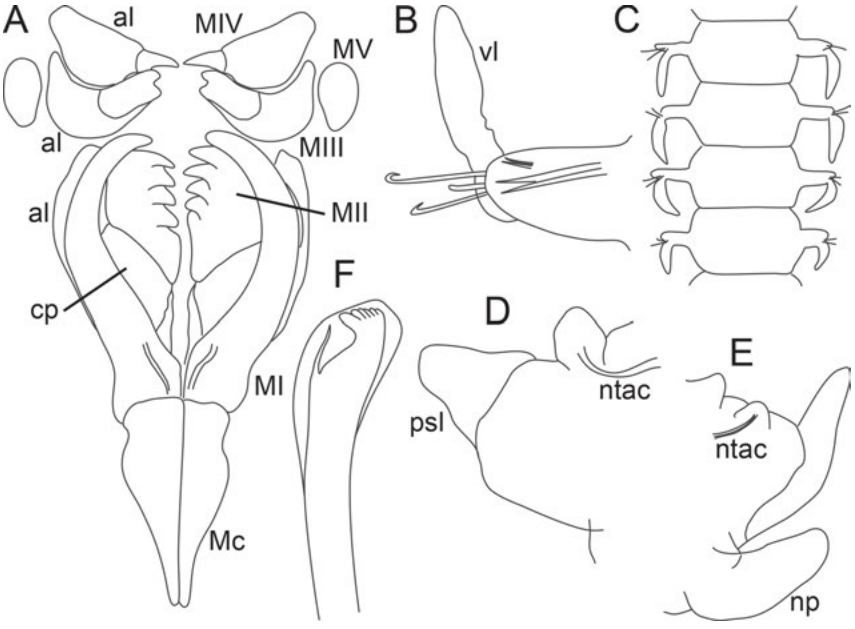


Fig. 7.12.6.18: Morphology of *Kuwaita*; *Kuwaita heteropoda* (Marenzeller, 1879) (A, B, C), *Kuwaita papillifera* (Fauvel, 1918) (E, F), and *Kuwaita* sp. (D). A, maxillary apparatus; B, posterior parapodium with vascularized lobe, anterior view; C, four segments from posterior body; D, midbody parapodium, anterior view; E, posterior parapodium, anterior view; F, simple hooded hook. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MV, maxillae I–V; np, nephridial papilla; ntac, nototaciculae; psl, postchaetal lobe, vl, vascularized lobe. Modified from Carrera-Parra and Orensanz (2002) (A, D–F) and Crossland (1924) (B, C).

however, such as development of notopodia, size and position of branchiae and shape of nephridial papillae appear to vary significantly among species in the genus. Long vascularized parapodial lobes with respiratory function have been described for *Kuwaita heteropoda* (Marenzeller, 1879) by Crossland (1924) and Uschakov and Bao-Ling (1979). Carrera-Parra and Orensanz (2002) transferred a couple of species previously referred to *Lumbrineris* or *Ninoe* to *Kuwaita*. Recently, a new species has been described from European waters (Arias and Carrera-Parra 2014).

Loboneris Carrera-Parra, 2006 (Fig. 7.12.6.19A–D)
Type species: *Lumbrineris pterignatha* Gallardo, 1968. Nha Trang, South Vietnam.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia, with compound and simple multidentate hooded hooks. Pygidium with

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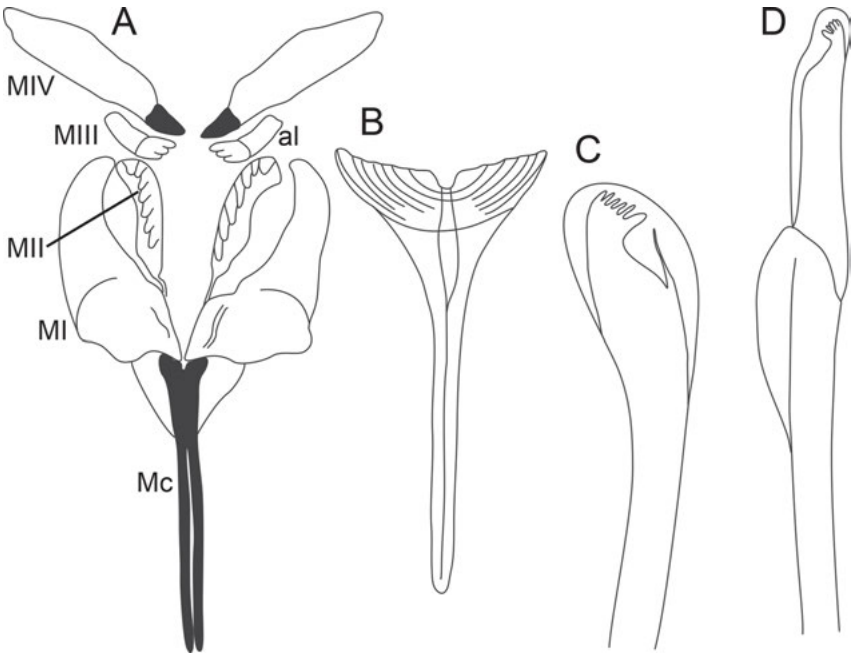


Fig. 7.12.6.19: Morphology of *Loboneris pterignatha* (Gallardo, 1968). A, maxillary apparatus; B, mandibles; C, simple hooded hook; D, compound hooded hook, parapodium 5. al, attachment lamella; Mc, maxillary carriers; MI–MIV, maxillae I–IV. Modified from Carrera-Parra (2006a) (A) and Gallardo (1968) (B–D).

anal cirri. Maxillary carriers long and narrow. Maxillae I forceps-like, with wide base; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III completely pigmented; maxillae MIV wing-shaped, with colorless central area. Maxillae III with wide attachment lamellae. Maxillae V absent. Mandibles with shafts partly separated (adapted from Carrera-Parra 2006a).

Composition: Monotypic

Distribution: Vietnam.

Remarks: The genus *Loboneris* is distinguished from all other lumbrinerid genera by the long and narrow carriers and the wing-formed shape of maxillae IV. The single known species *Loboneris pterignatha* (Gallardo, 1968) is further characterized by numerous teeth (seven) in maxillae II and three teeth in maxillae III. *Loboneris* resembles *Augeneria* and *Gallardoneris* by maxillae IV having a clear or whitish central area and in having compound hooded hooks.

Lumbricalus Frame, 1992 (Fig. 7.12.6.20A–G)

Type species: *Lumbriconereis januarii* Grube, 1879 (replacement name for *Lumbriconereis brasiliensis* Grube *sensu* Kinberg, 1865). Rio de Janeiro, Brazil, harbor.

Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia, with compound spinigers, simple and compound multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II shorter than maxillae I, with ligament and wide strongly sclerotized connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles fused up to three fourths of length (adapted from Frame 1992, and Carrera-Parra 2006a).

Composition: Nine species

Distribution: Shallow water, tropical and warmer seas (Carrera-Parra 2004).

Remarks: The genus *Lumbricalus* was erected by Frame (1992) to encompass species previously included in *Lumbrineris* with compound spiniger chaetae. The genus was revised by Carrera-Parra (2004), who indicated that the fairly short maxillae II and the solid connecting plates between maxillae I and II also are characteristic features. The type species was originally recorded and briefly described by Kinberg (1865) as *L. brasiliensis* Grube. Later Grube (1879) considered Kinberg's species to differ and proposed the new name *L. januarii* for it. The original material (one specimen) was examined and described by Hartman (1948). The species was redescribed by Carrera-Parra (2004) as part of the revision of the genus when also several new species were described. A new species has been recently described by Aguirrezabalaga and Carrera-Parra (2006).

Lumbrinerides Orensanz, 1973 (Fig. 7.12.6.21A–E)

Type species: *Lumbrinerides gesae* Orensanz, 1973. Mar del Plata, Argentina.

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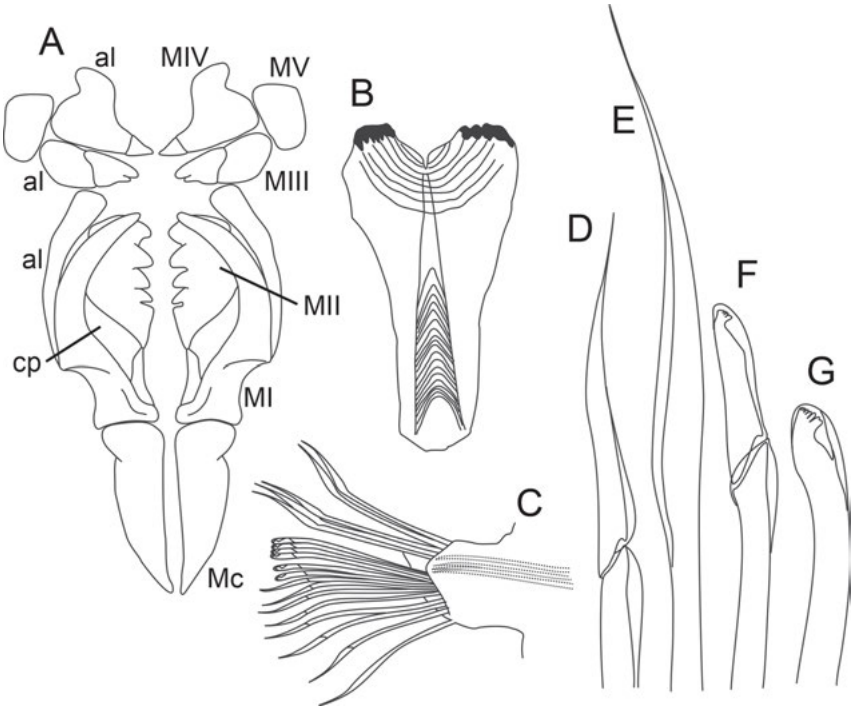


Fig. 7.12.6.20: Morphology of *Lumbricalus*; *Lumbricalus januarii* (Grube, 1879) (A) and *Lumbricalus aotearoae* (Knox & Green, 1972) (B–G). A, maxillary apparatus; B, mandibles; C, anterior parapodium with chaetae; D, compound spiniger; E, limbate chaeta; F, compound hooded hook; G, simple hooded hook. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MV, maxillae I–V. Modified from Carrera-Parra (2004) (A) and Knox and Green (1972) (B–G).

Diagnosis: Prostomium long, distally pointed, without antennae, without eyes. Parapodia with reduced notopodia, anterior parapodia small, almost vestigial, chaetae include simple limbate chaetae and simple bidentate hooded hooks. Pygidium without anal cirri. Maxillary carriers large, triangular, broad anteriorly. Maxillae I forceps-like, inner margin with sinuous border or 1–2 accessory teeth. Maxillae II with imperfectly dentate border or with short blunt teeth, without ligament and connecting plates. MIII and MIV completely pigmented. All maxillae with attachment lamellae. Maxillae V absent. Mandibles usually fused for entire length (adapted from Perkins 1979, and Carrera-Parra 2006a).

Composition: Sixteen species

Distribution: Widely distributed in tropical and temperate waters, shallow water, and deep sea.

Remarks: The genus *Lumbrinerides* was reviewed by Perkins (1979) and Miura (1980), who provided keys to species. New species from Japanese waters have later been described by Imajima (1985) and Miura (2017). Miura (2017) provided a thorough study of variation of morphological characters in nine species mainly based on Japanese material. A species having compound multidentate hooded hooks in addition to bidentate hooks was recognized by Uebelacker (1984) and later described by Carrera-Parra (2001b) as *Lumbrinerides uebelackerae* Carrera-Parra, 2001. Miura (2017) considered the inclusion of this species in *Lumbrinerides* as questionable.

Lumbrineriopsis Orensanz, 1973 (Fig. 7.12.6.22A–D)
Aotearia Benham, 1927

Type species: *Lumbriconereis mucronata* Ehlers, 1908. Outside estuary of river Congo, West Africa.

Diagnosis: Prostomium without antennae, without eyes, often prolonged. Parapodia with reduced notopodia, chaetae include simple limbate chaetae and simple bidentate hooded hooks. Pygidium without anal cirri. Maxillary carriers longer than maxillae I, slender, posteriorly dilated. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III completely pigmented, with two aliform expansions at inner border; maxillae IV completely pigmented, with denticulate inner border. All maxillae with attachment lamellae. Maxillae V absent. Mandibles fused up to three fourths of length (adapted from Miura 1980, and Carrera-Parra 2006a).

Composition: Five species

Distribution: Worldwide in warm and temperate seas.

Remarks: The genus was revised by Miura (1980), who provided a key to five species. The genus *Lumbrineriopsis* is a junior synonym of *Aotearia* Benham, 1927, that was erected for *A. sulcaticeps* from New Zealand. *Aotearia* was however originally stated to have asymmetric maxillae, a feature

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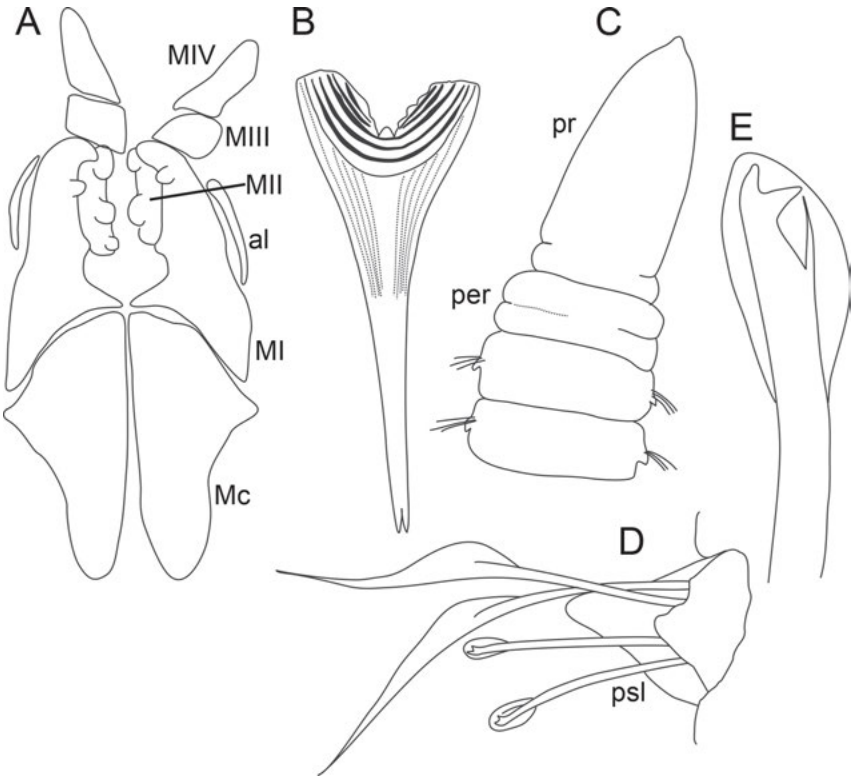


Fig. 7.12.6.21: Morphology of *Lumbrinerides bidentatus* Imajima, 1985 (= *L. shimodaensis* Imajima, 1985 fide Miura 2017). A, maxillary apparatus; B, mandibles; C, prostomium and anterior segments; D, posterior parapodium; E, hooded hook. al, attachment lamella; Mc, maxillary carriers; MI–MIV, maxillae I–IV; per, peristomium; pr, prostomium; psl, postchaetal lobe. Modified from Imajima (1985).

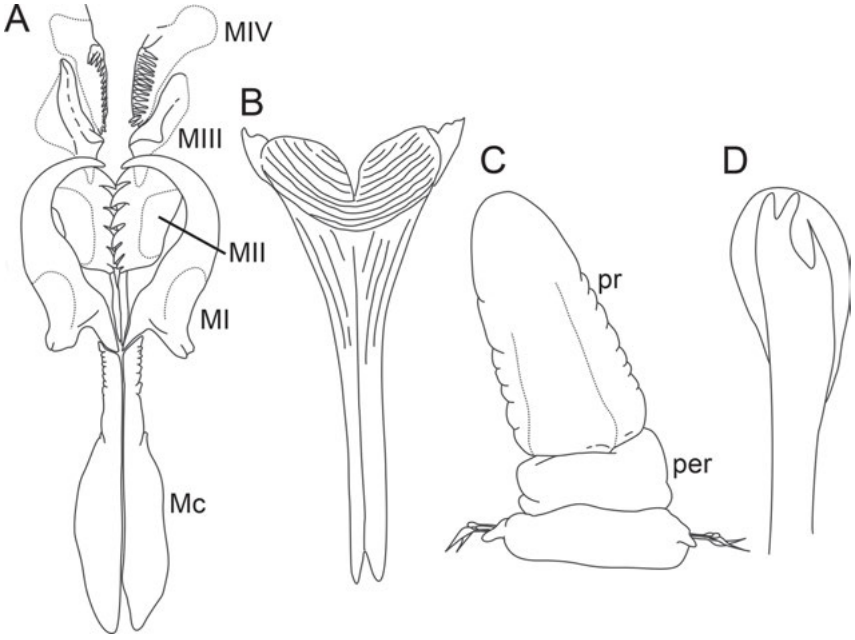


Fig. 7.12.6.22: Morphology of *Lumbrineriopsis*; *Lumbrineriopsis mucronata* (Ehlers, 1908) (A, B, D) and *Lumbrineriopsis paradoxa* (Saint-Joseph, 1888) (C). A, maxillary apparatus; B, mandibles; C, anterior body; D, hooded hook from posterior parapodium. Mc, maxillary carriers; MI–MIV, maxillae I–IV; per, peristomium; pr, prostomium. Modified from Orensanz (1973) (A, B, D) and Miura (1980) (C).

that led Hartman (1944) to exclude it from the Lumbrineridae. This was later corrected by Knox and Green (1972, 1973), but the species was then referred to *Lumbrineris*. The status of *Aotearia* is presently unresolved (see further comments below). Carrera-Parra (2006a) did not consider *Aotearia* in his account of the genera of Lumbrineridae.

Lumbrineris Blainville, 1828 (Fig, 7.12.6.23A–F)

Type species: *Lumbrineris latreilli* Audouin & Milne Edwards, 1833. Iles Chaussey, La Manche (British Channel), France.

Diagnosis: Prostomium without antennae, without eyes. Parapodia with notopodia slightly developed or reduced,

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with compound and simple multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament and wide poorly sclerotized connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles fused up to three fourths of length (adapted from Frame 1992, and Carrera-Parra 2006a, b).

Composition: The number of valid species is somewhat uncertain but may be about 50. In the latest revision of *Lumbrineris*, Carrera-Parra (2006b) considered 36 species to be valid according to the diagnosis given above from an assemblage of 57 named species.

Distribution: Worldwide.

Remarks: For a number of years the majority of lumbrinerid species was referred to the genus *Lumbrineris*, that was essentially rather widely defined (e.g., Fauvel 1923, Hartman 1944, 1959, Fauchald 1970, 1977). The genus has gradually become more restricted through taxonomic works by Orensanz (1973, 1990), Levenstein (1977), and Hartmann-Schröder (1979), who separated out species and species groups into new genera or resurrected synonymized genera based on maxillary and chaetal characters. This has been further followed up by Frame (1992) and Carrera-Parra (2006a). Nevertheless, as presently defined, the genus *Lumbrineris* is still the most speciose of the lumbrinerid genera. Further, many early described and poorly known species are by tradition still referred to *Lumbrineris* (in the wide sense) until their taxonomic status is clarified. New species have recently been described by Carrera-Parra (2001b) and Martins et al. (2012).

Blainville (1828) originally included three species in the genus *Lumbrineris*. Hartman (1959) considered all as indeterminable and designated *L. latreilli* as type species for the genus. Grube (1840) introduced the variant spelling *Lumbriconereis* of the genus name, without stating the reason for the name change. The variant spelling was commonly used up to mid twentieth century.

Lysarete Kinberg, 1865 (Fig. 7.12.6.24A–D)

Type species: *Lysarete brasiliensis* Kinberg, 1865. Off Rio de Janeiro, Brazil.

Diagnosis: Prostomium with three antennae, with eyes. Parapodia with notopodia well developed; neuropodia with limbate chaetae, without any kind of hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like with internal accessory teeth, maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III and IV completely pigmented, with several teeth; maxillae V and VI lateral to maxillae III and IV. Maxillae I–IV with attachment lamellae. Mandibles fused up to three fourths of length (adapted from Colbath 1989, and Carrera-Parra 2001b, 2006a).

Composition: Three species.

Distribution: West Atlantic, warm-temperate and tropical.

Remarks: Reports on the number of pairs of maxillae vary. Gilbert (1984), Colbath (1989), and Orensanz (1990) refer

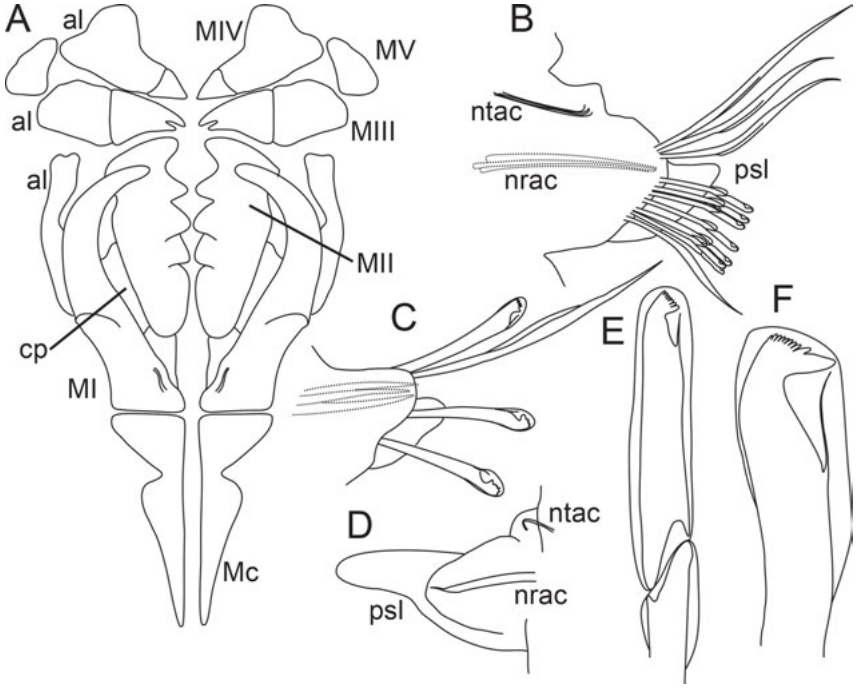


Fig. 7.12.6.23: Morphology of *Lumbrineris*; *Lumbrineris latreilli* Audouin & Milne Edwards, 1833 (A, D–F), *Lumbrineris* sp. (B), and *Lumbrineris cingulata* (Ehlers, 1897) (C). A, maxillary apparatus; B, parapodium 11; C, parapodium 37; D, parapodium 150; E, compound hooded hook; F, simple hooded hook. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MV, maxillae I–V; nrac, neuroaciculae; ntac, nototaciculae; psl, postchaetal lobe. Modified from Carrera-Parra (2006b) (A, D–F), Oug (2002) (B), and Frame (1992) (C).

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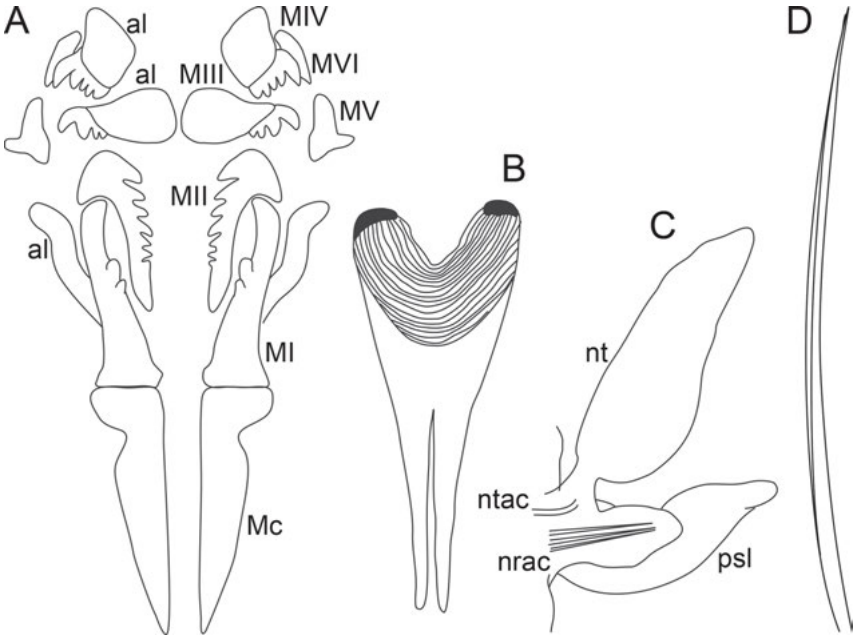


Fig. 7.12.6.24: Morphology of *Lysarete raquelae* Carrera-Parra, 2001. A, maxillary apparatus; B, mandibles; C, posterior parapodium, anterior view; D, simple chaeta. al, attachment lamella; Mc, maxillary carriers; MI–MVI, maxillae I–VI; nt, notopodial cirrus; nrac, neuroaciculae; ntac, nototaciculae; psl, postchaetal lobe. Modified from Carrera-Parra 2001b (A–C) and Gilbert 1984 (D).

to five pairs of maxillae, whereas Carrera-Parra (2001b, 2006a) refers to six pairs. Carrera-Parra (2001b) describes for *Lysarete raquelae* Carrera-Parra, 2001 that the number of maxillae increases during ontogenetic development from three in small specimens to five or six in large specimens. Different counts may also depend on whether maxillae V are considered as lateral lamellae or included as maxillae.

Ninoe Kinberg, 1865. (Fig. 7.12.6.25A–C)
Type species: *Ninoe chilensis* Kinberg, 1865. Valparaiso, Chile, shallow water, sand and stone.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with reduced notopodia; with simple multidentate hooded hooks, with postchaetal branchiae with two or more filaments in anterior body. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I, with ligament, without connecting plates; maxillae III and IV completely pigmented, maxillae IV or maxillae III and IV with denticulate incisive edge, maxillae V free, lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles fused up to three fourths of length (adapted from Orensanz 1990 and Carrera-Parra 2006a).
Composition: Thirty-three species
Distribution: Atlantic, Pacific, and Indian Oceans, warm-temperate and tropical.
Remarks: The genus has been recognized since its erection by Kinberg (1865), who indicated the presence of cirriform branchiae in anterior body as diagnostic. Fauchald (1970) extended the diagnosis to include all lumbrinerids with branchiae or vascularized structures irrespective of location on body. The genus was restricted by Levenstein (1977), who separated species with one parapodial branchial filament into the genus *Paraninoe* (later synonymized with *Cenogenus*) and Orensanz (1973, 1990), who reiterated Kinberg's genus concept and further defined the genus from maxillary characters. The genus is the second-most speciose of lumbrinerid genera and is represented by a number of species in warm waters. The genus has been partially revised by Orensanz (1973, 1990).

Reports of maxillae V vary. Several authors, e.g., Orensanz (1973, 1990) and Uebelacker (1984), did not mention maxillae V, whereas Hilbig (1995) stated that maxillae V were absent. Maxillae V or comparable lateral elements have however been described for several species (e.g., Miura 1980, Carrera-Parra 2001b, Oug 2002, Aguirrezabalaga and Carrera-Parra 2006). Whether the presence of maxillae V is a variable character may need further investigation.

Scoletoma Blainville, 1828 (Fig. 7.12.6.26A–D)
Type species: *Lumbricus fragilis* O.F. Müller, 1776. At Drøbak in Oslofjord, Norway.
Diagnosis: Prostomium without antennae, without eyes. Parapodia with notopodia reduced, with simple multidentate hooded hooks. Pygidium with anal cirri. Maxillae I forceps-like; maxillae II about as long as maxillae I,

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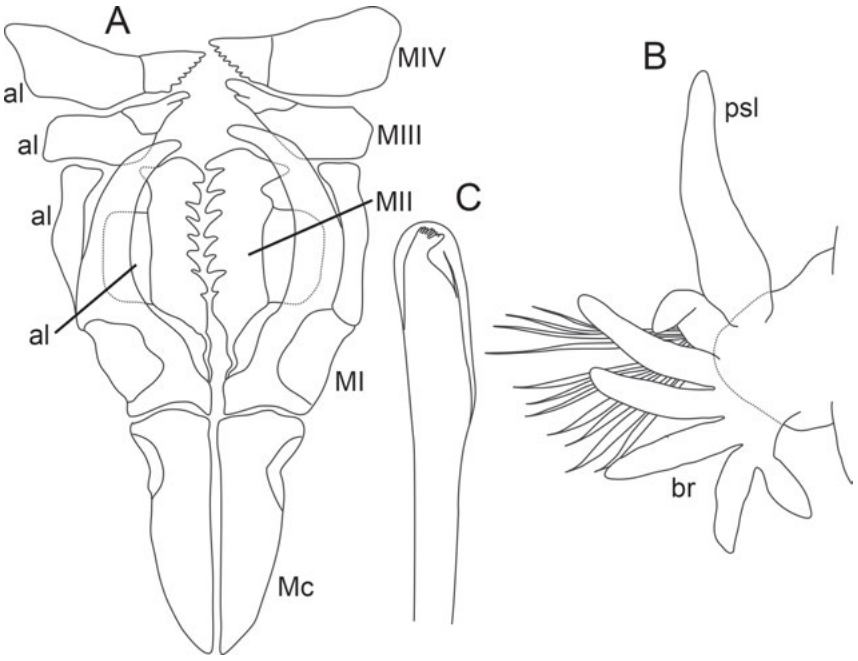


Fig. 7.12.6.25: Morphology of *Ninoe*; *Ninoe armoricana* Glémarec, 1968 (A) and *Ninoe leptognatha* (Ehlers, 1900) (B, C). A, maxillary apparatus; B, anterior parapodium from branchial region, posterior view; C, hooded hook. al, attachment lamella, al of MII shown below MI; br, branchia; Mc, maxillary carriers; MI–MIV, maxillae I–IV; psl, postchaetal lobe. Modified from Glémarec (1968) (A) and Orensanz (1990) (B, C).

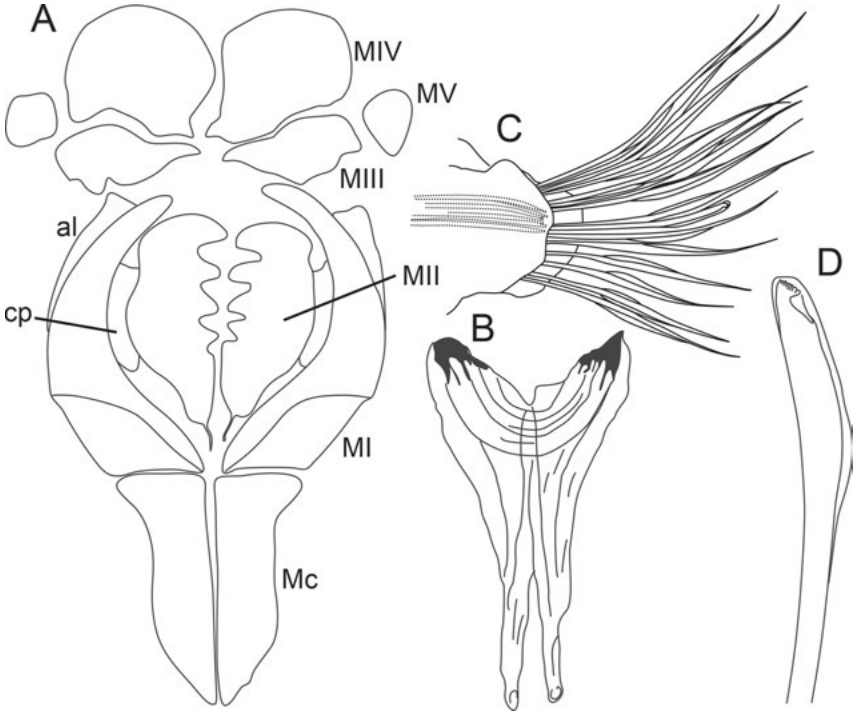


Fig. 7.12.6.26: Morphology of *Scoletoma fragilis* (O.F. Müller, 1776). A, maxillary apparatus; B, mandibles; C, ninth parapodium, anterior view; D, simple hooded hook. al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MV, maxillae I–V. Modified from Budaeva (2005) (A) and Frame (1992) (B–D).

with ligament and wide poorly sclerotized connecting plates; maxillae III and IV completely pigmented; maxillae V lateral to maxillae III–IV. Maxillae I–IV with attachment lamellae, maxillae V reduced to attachment lamellae only. Mandibles fused up to three fourths of length (adapted from Frame 1992, and Carrera-Parra 2006a).

Composition: Twenty-five species

Distribution: Worldwide.

Remarks: Frame (1992) resurrected *Scoletoma* as a valid genus to encompass species with simple hooded hooks and simple limbate chaetae, which previously had been referred to *Lumbrineris*. As currently defined, *Scoletoma* and *Lumbrineris* are rather close and are essentially

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distinguished only by the lack and presence of compound hooded hooks, respectively. Perkins (1979) reported for *S. tenuis* (as *Lumbrineris tenuis*) that Mx IV and Mx V (denoted as dorsolateral support) were interconnected by an isthmus, a state that is transitional to the complete fusion of Mx IV and V in *Abyssoninoe*.

Sergioneris Carrera-Parra, 2006 (Fig. 7.12.6.27A–D)
Type species: *Lumbrineris nagae* Gallardo, 1968. Nha Trang, South Vietnam.
Diagnosis: Prostomium with one antenna, without eyes. Parapodia with notopodia reduced; with simple multidentate hooded hooks. Pygidium with anal cirri. Maxillary carriers wide anteriorly and slender in middle and posterior end. Maxillae I forceps-like with wide base; maxillae II shorter than maxillae I, with ligament, with wide strongly sclerotized connecting plate from middle of maxillae I to lateral edge of maxillae II, with narrow incomplete connecting plate from base of maxillae I not reaching maxillae II. Maxillae III and IV completely pigmented. All maxillae with attachment lamellae. Maxillae V absent. Mandibles with shafts partially separated at posterior end (adapted from Carrera-Parra 2006a).
Composition: Monotypic
Distribution: Vietnam, Andaman Sea, Philippine Islands.
Remarks: Only limbate chaetae are present in anterior and midbody chaetigers. Simple hooded hooks first appear at chaetigers 40–60, in some specimens as far back as chaetiger 110 (Gallardo 1968, Oug 2002). *Sergioneris nagae* was previously referred to *Paraninoe* by Orensanz (1990) and later to *Cenogenus* by Carrera-Parra (2001a). The genus *Sergioneris* was erected (Carrera-Parra 2006a) because of the different and rather distinctive structure of the maxillary apparatus.

Genera of uncertain status or position
Aotearia Benham, 1927
Type species: *Aotearia sulcaticeps* Benham, 1927. New Zealand.
Remarks: Benham (1927) described and considered an asymmetrical pattern of anterior maxillae with an extra unpaired maxilla on the right-hand side as diagnostic. Knox and Green (1972, 1973), however, later showed that this was an artifact during the dissection for mouthparts. Hartman (1944) excluded *Aotearia* from Lumbrineridae because of the stated asymmetry of the maxillae, but later (Hartman 1959) considered *Aotearia* as a questionable junior synonym of *Lumbrineris*, a view that was followed by Fauchald (1970) and Knox and Green (1972, 1973). Orensanz (1990) discussed *Aotearia* briefly in relation to *Lumbrineriopsis* but contended that it should be declared a nomen oblitum according to ICZN's name rules because of no use except for the comments by Hartman (1944, 1959). Orensanz' view has later been disputed by e.g., Gil (2011), who considers *Aotearia* valid despite the error in the original diagnosis. The situation is presently

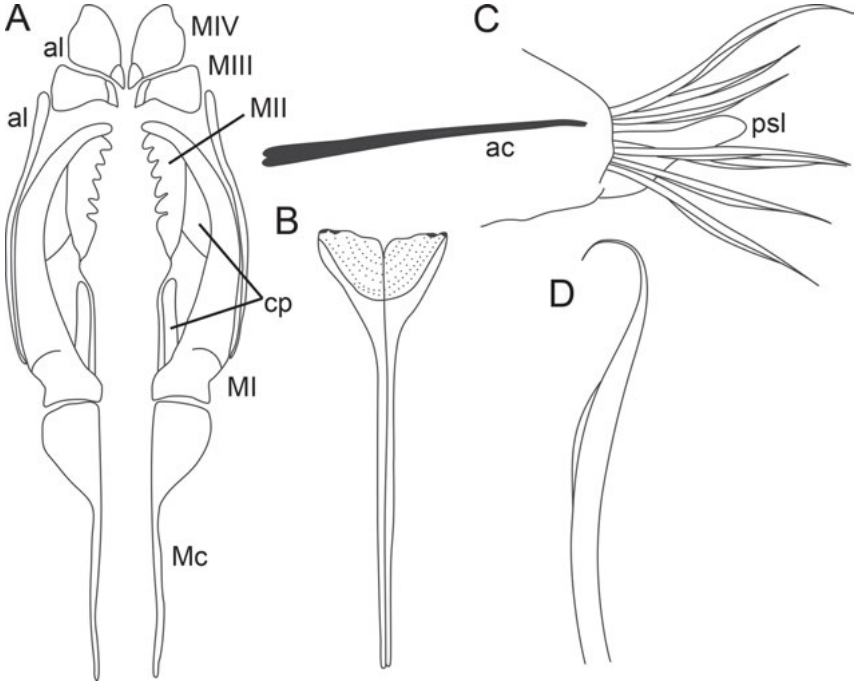


Fig. 7.12.6.27: Morphology of *Sergioneris nagae* (Gallardo, 1968). A, maxillary apparatus; B, mandibles; C, anterior parapodium, anterior view; D, limbate chaeta. ac, acicula; al, attachment lamella; cp, connecting plate; Mc, maxillary carriers; MI–MIV, maxillae I–IV; psl, postchaetal lobe. Modified from Carrera-Parra (2006a) (A) and Gallardo (1968) (B–D).

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unresolved, but it does not seem that *Aotearia* has come into common use in recent years, in contrast to *Lumbrineriopsis* that has been often reported. Carrera-Parra (2006a) did not consider *Aotearia* in his account of the genera of Lumbrineridae.

Ophiuricola Ludwig, 1905
Type species: *Ophiuricola cynips* Ludwig, 1905. Pacific Ocean, SW of Callao, Peru, 5200 m.
Composition: Monotypic
Distribution: Eastern Pacific Ocean, symbiont with ophiuroids.
Remarks: Ludwig (1905) reported two specimens in bad conditions that were dissected out from arms of the ophiuroid *Ophioglypha*. The short description refers to characters that are typical of lumbrinerids and oenonids (e.g., no antennae and palps, no parapodial cirri or branchiae, simple chaetae), but jaws were stated not to be present. Ludwig (1905) did not indicate a taxonomic position for the genus, but it has later been allocated to the lumbrinerids (Hartman 1944). Fauchald (1970) considered the affiliation with the lumbrinerids doubtful. The genus is not included in the phylogenetic analysis by Carrera-Parra (2006a).

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Tatiana Menchini Steiner

7.12.7 Oenonidae Kinberg, 1865

Introduction

The family Oenonidae is composed of medium-sized worms, mainly free living and burrowing in sand and mud, although some are parasites for at least one of their life stages. The species are notable for their filiform aspect and very iridescent cuticle (Fig.7.12.7.1A, B), which is generally thicker than that of other Eunicida, especially in free-living species. Among Eunicida, it is the only extant family that has a jaw apparatus of the prionognath type, which means that the maxillary jaws are composed of two parallel rows with dentate plates, forceps-like elements, and very long and slender maxillary carriers enclosed in a protractile ventral muscular pharynx.

Oenone is a Latinized form of the Greek "Oinone," derived from "oinos," which means wine. In Greek mythology, it is the name of a fountain nymph of Mount Ida, in Frigia, beloved of Paris and the mother of Corythus. The family Oenonidae was erected by Kinberg (1865) as Oenonidea [sic] to shelter the genus *Oenone* (erected by Savigny 1818), *Aglaura*, *Danymene*, and *Andromache*. However, the first described species was *Nereis iricolor* Montagu, 1804, later included in *Arabella*, erected by Grube (1850).

The history of the family is quite complex and includes the creation of three families, currently synonymous with Oenonidae, as well as 27 genera, 15 of which are currently synonymous with other genera or are unaccepted. Colbath (1989a), Hilbig (1995), Paxton (2000), Rouse and Pleijel (2001), and Zanol et al. (2021) presented the history of the family in detail. The genera of Oenonidae have been grouped in different ways since the family's creation, sometimes including *Lysarete* (currently in Lumbrineridae). Hartman (1944) erected the family Arabellidae to shelter *Arabella, Biborin, Drilonereis, Notocirrus,* and *Labidognathus* (today a junior synonym of *Drilonereis*). This reorganization grouped *Lysarete*, *Halla, Aglaurides* (today a junior synonym of *Oenone*), and *Iphitime* (currently in Dorvilleidae) in Lysaretidae because of the presence of three dorsal antennae at the base of the prostomium, among other characteristics (Hartman, 1944). Colbath (1986) analyzed the mineral composition of the jaws and detected the presence of calcite in *Lysarete* and other Lumbrineridae, whereas in *Oenone*, *Halla, Arabella*, and *Drilonereis,* the jaws are not calcified and have scleroprotein with minor amounts of traces metals. Colbath (1989a) added that *Lysarete* also has a labidognath maxillary pattern, as well as black aciculae, similar to members of Lumbrineridae. Thus, Colbath (1989a) resurrected Oenonidae to include *Oenone*, *Halla*, and the new genus *Tainokia*, all genera with antennae on the prostomium and prionognath maxillary apparatus, maintaining *Lysarete* as the only genus of Lysaretidae. Finally, Orensanz (1990) transferred *Lysarete* to Lumbrineridae, Lysaretidae became a junior synonym, and Arabellidae was merged with Oenonidae because of affinities related to the maxillary jaws. This reflects the current composition of the family, which is now composed of 12 genera and about 109 species (Zanol et al. 2021).

Arabella and *Drilonereis* represent about 76% of the valid oenonid species (Zanol et al. 2021). *Notocirrus* has nine valid species, and *Labrorostratus* has six (Read and Fauchald 2021). The other genera have either two species (*Halla, Haematocleptes, Oenone, Oligonathus,* and *Tainokia*) or are monospecific (*Biborin, Drilognathus,* and *Pholadiphila*). Some authors have adopted *Cenothrix* and *Notopsilus* as subgenera in an effort to differentiate

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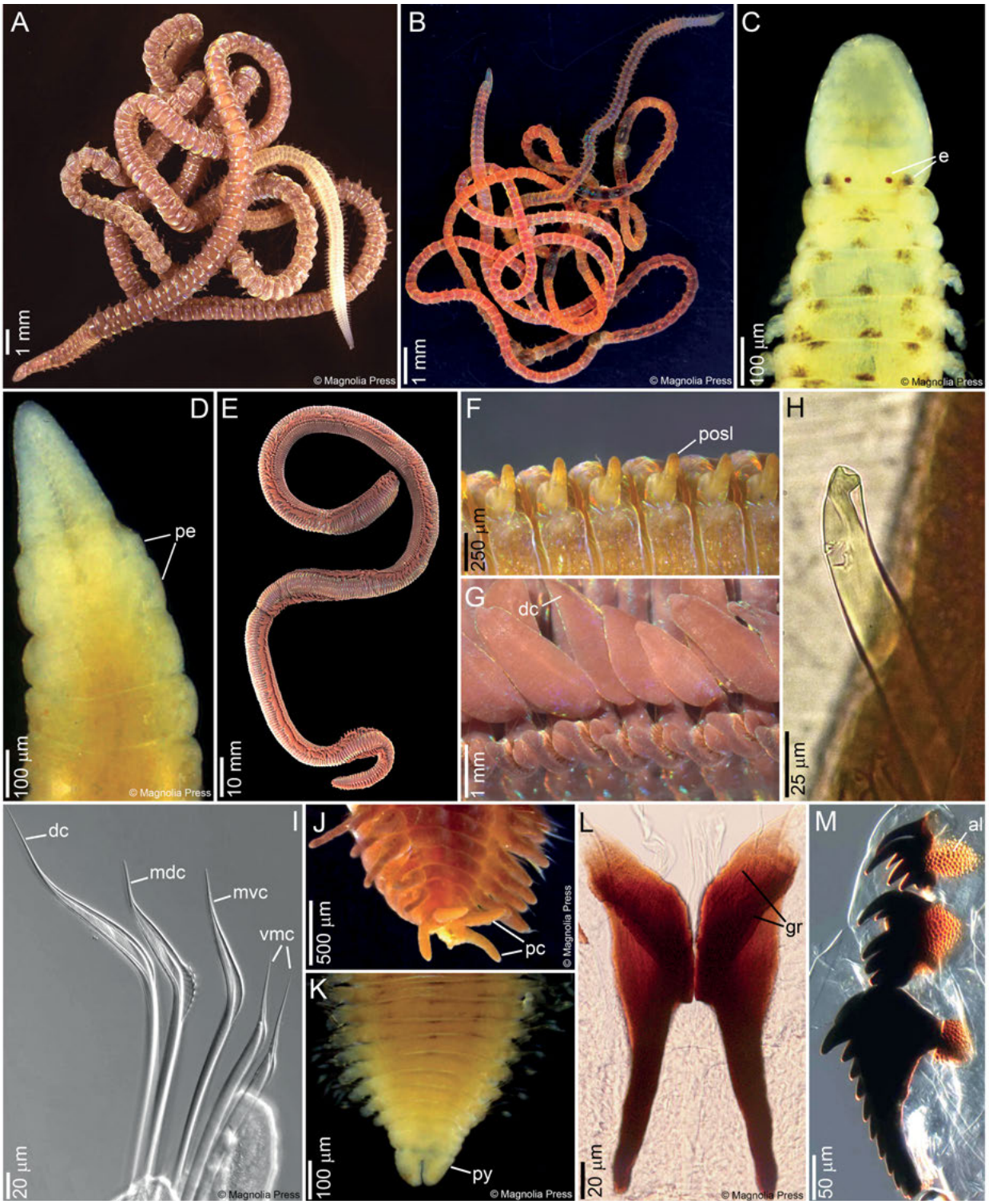


Fig. 7.12.7.1: Photographs of oenonids. A, F, *Arabella (Arabella) pulvinata*. B, *Drilonereis orensanzi*. C, K, L, *Arabella (Cenothrix) robusta*. D, *Drilonereis* cf. *logani*. E, G, *Halla okudai*. H, J, *Oenone fulgida*. I, M, *Arabella (Cenothrix) mutans*. A, B, entire specimens; C, D, anterior end, dorsal view; E, fragmented specimen, lateral view; F, parapodia from chaetigers 22 to 27, ventral view; G, parapodia from midbody, anterior view; H, subacicular bidentate hooded hook from chaetiger 147; I, chaetae from chaetiger 26; J, posterior end, ventrolateral view; K, posterior end, dorsal view; L, mandibles, ventral view; M, right MII to MV, dorsal view. A to D, F, H to M, from Lizard Island, Great Barrier Reef, Australia; E, G, from Fukue Island in the Goto Islands (Tomie Bay), Japan. A to D, I to L, © Magnolia Press (Zanol and Ruta 2015), reproduced with permission from the copyright holder; E, G, © CheckList (Kobayashi et al. 2020, CC BY 4.0, https://creativecommons.org/licenses/by/4.0/legalcode); F, © Alana dos Santos Leitão; H, M, © Joana Zanol. al, attachment lamella; dc, dorsal cirrus; doc, dorsal chaeta; e, eyespot; gr, growth lines; mdc, mediodorsal chaetae; mvc, medioventral chaeta; pc, pygidial cirrus; pe, peristomial rings; posl, postchaetal lobe; py, pygidium; vmc, ventral modified chaeta.

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Arabella species (Orensanz 1974, Perkins 1979, Zanol and Ruta 2015). The genera *Drilognathus*, *Haematocleptes*, *Oligognathus*, and *Pholadiphila* are exclusively parasitic, in addition to some species of *Arabella*, *Drilonereis*, and *Notocirrus*. Most *Labrorostratus* species are parasitic, but there are also records of some as free living.

Morphology

External Morphology

Body shape and color. Externally, oenonids are quite similar to lumbrinerids because of the general shape of the body and the globular prostomium without appendages in most species. Some species have one to three antennae in both families, in addition to less regionalization of the body, with a low morphological diversity of parapodia and chaetae. Both families can only be distinguished through careful observation of the jaws and chaetae.

Oenonids tend to be very long and thin, with a high number of chaetigers when complete, resulting in a filiform body, often with a moniliform aspect (Fig. 7.12.7.1A, B). The size varies from 3 mm in length and 60 chaetigers, as in *Drilognathus capensis* Day, 1960, up to 1 to 2 m and almost a thousand chaetigers, as in *Halla okudai* Imajima, 1967, when alive (Idris and Arshad 2013). *Drilonereis longa* Webster, 1879 can reach more than 70 cm in length and 1.5 mm width. Most adult forms are about 0.3 to 1 mm wide, can reach about 5 to 10 cm in length, and have about 150–300 chaetigers, when complete, including some parasite species.

The color is not very often recorded, but living specimens may have varying shades of white, yellow, and red to light brown or brown, sometimes with internal red hues from their blood vessels. *Halla* may show degrees of orange to light brown (Fig. 7.12.7.1E), and *Oenone* may be red or yellow to orange (Fig. 7.12.7.10A–C). Preserved specimens can be whitish, beige, yellow to light brown, or brown to dark brown. The parapodia of the anterior and posterior ends may be lighter, yellowish, or yellowish-orange to dark reddish-brown. Other coloration patterns in some species include brownish areas at the distal end of the postchaetal lobe, dark brown pigmentation on the dorsal portion of chaetigers (Fig. 7.12.7.1C), or whitish and dark orange spots regularly distributed on the dorsal side, which can be maintained after being fixed. Yellowish-orange to dark reddish-brown transverse bands may be found near the middle of each segment. *Oenone fulgida* (Savigny 1818) fixed in formalin may be dark brown to purple and yellow when fixed in ethanol. *Halla okudai* is light brown, emitting dark purple to violet secretions when under stress, turning the fixation and preservation solution purplish (Idris and Arshad 2013).

The body of most species is cylindrical, slender, and of uniform width throughout the body, especially the anteriormost segments that accommodate the large and muscular pharynx. Species may be slightly dorsoventrally flattened, oval, sometimes convex dorsally and flattened ventrally. The body may taper near the pygidial region. In *Oenone, Halla,* and *Pholadiphila*, the median region may be widest, evenly tapering towards the anterior and posterior ends (Fig. 7.12.7.10B, C).

Prostomium. The prostomium in general is conical, distally rounded, long or short (Figs. 7.12.7.2B, 7.12.7.5B, and 7.12.7.9A, B), sometimes slightly rounded and globular (Figs. 7.12.7.1C and 7.12.7.12B). In *Drilonereis*, it is pointed, triangular, compressed dorsoventrally, and contains a mediodorsal furrow or slit in most species (Figs. 7.12.7.1D and 7.12.7.4C, D). Species of *Arabella* may have a ventral median groove. Ventral pads, as in Lumbrineridae, are absent (Fig. 7.12.7.2F).

Species may have one or two pairs of eyespots in a transverse line at the base of the prostomium (Figs. 7.12.7.1C, 7.12.7.3A, and 7.12.7.10A), these may be absent in certain species, as in species of *Drilonereis* (Figs. 7.12.7.1D and 7.12.7.4A–C). In species with two pairs of eyes, the outer pair is usually larger. The inner pair may be more superficially located in the tissue. *Oenone ventriocu-lata* Zanol and Ruta, 2015 has one pair of ventral eyespots at the ventroanterior end of prostomium (Fig. 7.12.7.11D), and may thus represent a young stage (Çinar 2005), because larval eyes at the end of prostomium may be present in *Labrorostratus parasiticus* Saint-Joseph, 1888 and *Labrorostratus* sp. (Fig. 7.12.7.7E, H, I), as well as in other species of Eunicida. Two pairs of pigmented spots are documented in *Oligognathus bonelliae* Spengel, 1882, located deep under the fold of the first peristomial ring (Fig. 7.12.7.12C), as well as in *Drilonereis filum* (Claparède 1868) (Saint-Joseph 1888). Orensanz (1974) also found one pair in *D. filum*, which may represent the pair of nuchal organs (Fig. 7.12.7.4G). In other species, the pair of nuchal organs is represented by ciliated pits at the dorsal base of the prostomium, under the fold of the first peristomial ring; in some cases, they are eversible and papillae-like.

Most species do not have prostomial appendages, but *Tainokia* has a short dorsal antenna at the base of the prostomium (Fig. 7.12.7.14A), whereas *Halla* and *Oenone* have three juxtaposed antennae, long and cirriform in the former (Fig. 7.12.7.6A, E), short and digitiform in the latter (Figs. 7.12.7.10 and 11A, B).

Peristomium. Most species have two peristomial rings, without appendages, the anterior ring forming the lower lip ventrally (Figs. 7.12.7.2F, 7.12.7.4D, and 7.12.7.5A). *Oenone*

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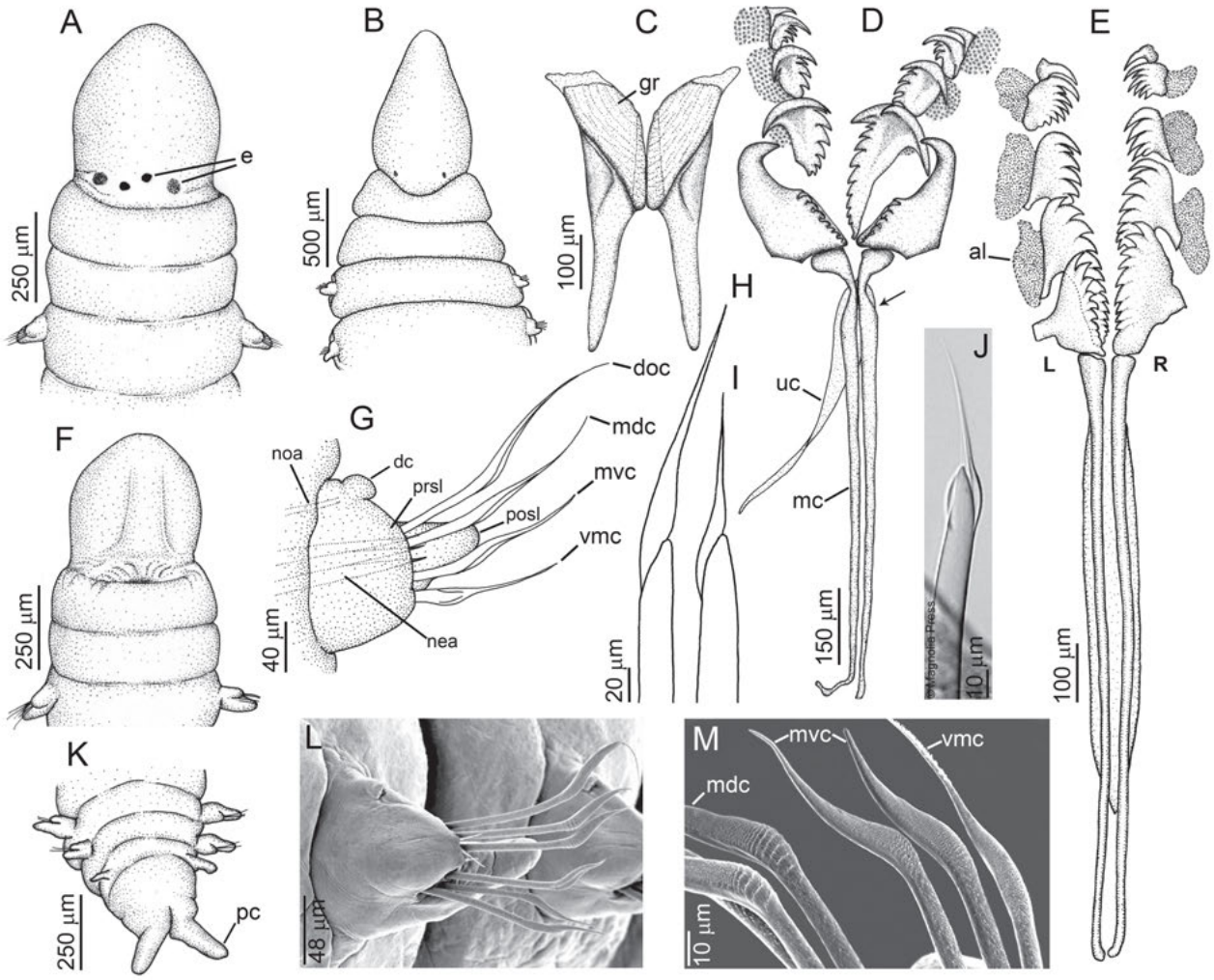


Fig. 7.12.7.2: Morphology of *Arabella*. A, C, D, F, G, K to M, *Arabella aracaensis* Steiner & Amaral, 2009. B, E, *Arabella (Notopsilus) acuta* (Kinberg, 1865). J, *Arabella (Cenothrix) mutans* (Chamberlin, 1919). H, I, *Arabella* sp., from Brazil. A, B, anterior end, dorsal view; C, mandibles, ventral view; D, E, maxillary apparatus, dorsal view; F, anterior end, ventral view; G, parapodium from chaetiger 6, anterior view; H, ventralmost modified chaeta from anterior chaetiger; I, ventralmost modified chaeta from posterior chaetiger; J, ventralmost modified chaeta from chaetiger 78; K, posterior end, ventral view; L, parapodium from chaetiger 45, anterior view; M, chaetae from chaetiger 73. A, C, D, F, G, K to M, © Taylor & Francis Ltd (Steiner and Amaral 2009), www.tandfonline.com; B, E, modified from Orensanz (1974); J, © Magnolia Press (Zanol and Ruta 2015), reproduced with permission from the copyright holder. al, attachment lamella; dc, dorsal cirrus; doc, dorsal chaeta; e, eyespot; gr, growth line; mc, maxillary carrier; mdc, mediodorsal chaeta; mvc, medioventral chaeta; nea, neuropodial acicula; noa, notopodial acicula; pc, pygidial cirrus; posl, postchaetal lobe; prsl, prechaetal lobe; uc, unpaired carrier; vmc, ventral modified chaeta; L, left; R, right. Arrow indicates the beginning of the furcula.

has one ring (Figs. 7.12.7.10 and 7.12.7.11A, B), whereas in *Pholadiphila*, the peristomium neither can be distinguished from the prostomium nor can the number of rings be determined (Fig. 7.12.7.13A). In the parasite *Labrorostratus prolificus* Amaral, 1977, specimens asexually generated within the host, with up to 15 chaetigers, have the first ring fused to the prostomium, meaning that only the second can be distinguished (Fig. 7.12.7.7F, G, P). In more advanced stages of growth, even within the host, the first ring becomes well defined (Fig. 7.12.7.7Q). *Halla*, *Oenone* and *Tainokia* have a mediodorsal anterior incision in the first peristomial ring where the antennae are positioned, below or between the eyes. (Figs. 7.12.7.10, 7.12.7.11A, B, and 7.12.7.14A). In addition, *Halla* has a small notch that extends to the middle of the first chaetiger, where the antennae can be positioned (Figs. 7.12.7.6A). Also, in this genus, the first peristomial ring forms small longitudinal folds ventrally (Fig. 7.12.7.6B) that allow an increase in the diameter of the oral opening when the protraction of pharynx occurs (Idris and Arshad 2013).

Jaws. The jaw apparatus is enclosed in a short (Fig. 7.12.7.9A) or long (Fig. 7.12.7.4A) ventral muscular pharynx that can protrude from the mouth. It is well

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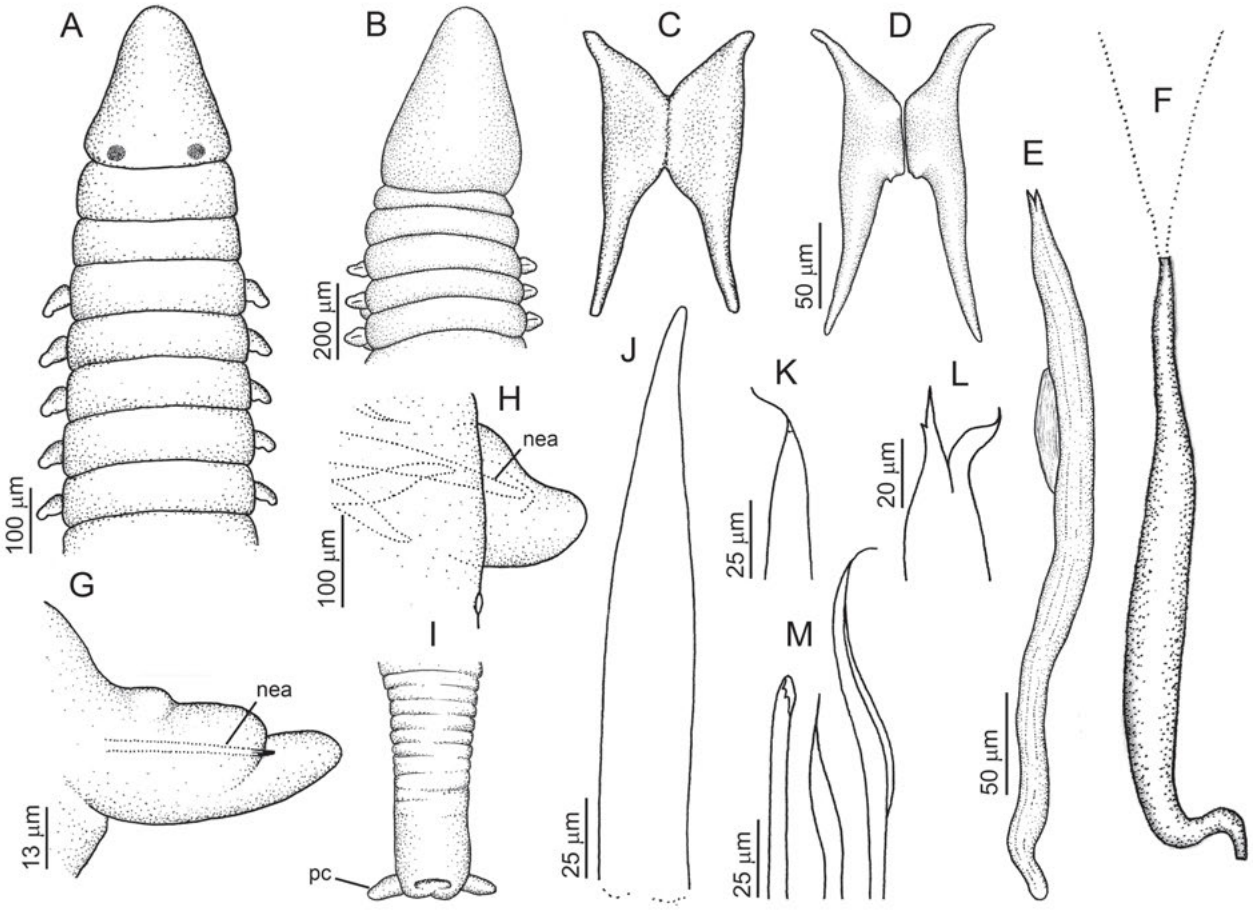


Fig. 7.12.7.3: Morphology of *Drilognathus*. A, C, F, G, I, *Drilognathus capensis* Day, 1960. B, D, E, H, J to M, *Drilognathus* sp., from Argentina. A, anterior end, dorsal view (scale bar based on species' original description); B, anterior end, dorsal view; C, D, mandibles, ventral view; E, F, maxillary apparatus; G, parapodium from midbody, anterior view (scale bar based on species' original description); H, parapodium from midbody, anterior view; I, posterior end; J, neuropodial acicula; K, internal chaeta; L, anterior end of maxillary apparatus; M, internal chaetae. A, C, F, G, I, modified from Day (1960) (no scale bars in the original figures); B, D, E, H, J to M, modified from Orensanz (1974). nea, neuropodial acicula; pc, pygidial cirrus.

developed in free-living species and sometimes reduced in parasites, possibly indicating lifestyle adaptations (Pettibone 1957, Martin and Britayev 1998). According to Colbath (1987, 1989a), the prionognath jaws of oenonids are composed primarily of scleroprotein with minor amounts of traces metals, no crystalline mineral phases, and not calcified.

The ventral mandibles are present in all genera and follow the pattern described to Eunicida (Zanol and Budaeva 2021). In *Oligognathus*, two rods are connected by a sclerotized bridge at the anterior end, forming a single horseshoe-shaped piece (Fig. 7.12.7.12J, K), whereas the shafts are reduced to two small triangular areas of sclerotized tissue in *Haematocleptes terebellidis* Wirén, 1886 (Fig. 7.12.7.5I). In *Labrorostratus parasiticus*, a peculiar hook-shaped crossbar joins the pieces, in addition to a pair of spines (Fig. 7.12.7.8K). In *Labrorostratus jonicus* Tenerelli, 1961, the mandibles are unfused, with two hook-shaped structures at the anterior end, a flat oval base, and two rounded protuberances at the posterior end (Fig. 7.12.7.8M). The two hook-shaped structures may represent a single broken structure (Fig. 7.12.7.8L). The mandibles are very small, diamond-shaped, or drop-shaped in *Drilonereis* (Fig. 7.12.7.4N–Q), although absent in some species of this genus. The mandibles are usually small in comparison to the maxillae set, as in *Drilonereis* and *Oligognathus* (Fig. 7.12.7.12E, F), but can occasionally be larger, as in *Notocirrus scoticus* McIntosh, 1869 (Fig. 7.12.7.9A).

According to Colbath (1987) and Paxton (2009), the mandibles grow throughout life, although growth rings in the ventral cutting plates in oenonids are not as evident and easily visible as in Lumbrineridae, often because of the intensely dark coloration and dull surface. Another reason is their reduced size, which requires observation under a microscope, not allowing the surface view, where the rings are visible. Growth rings have been recorded

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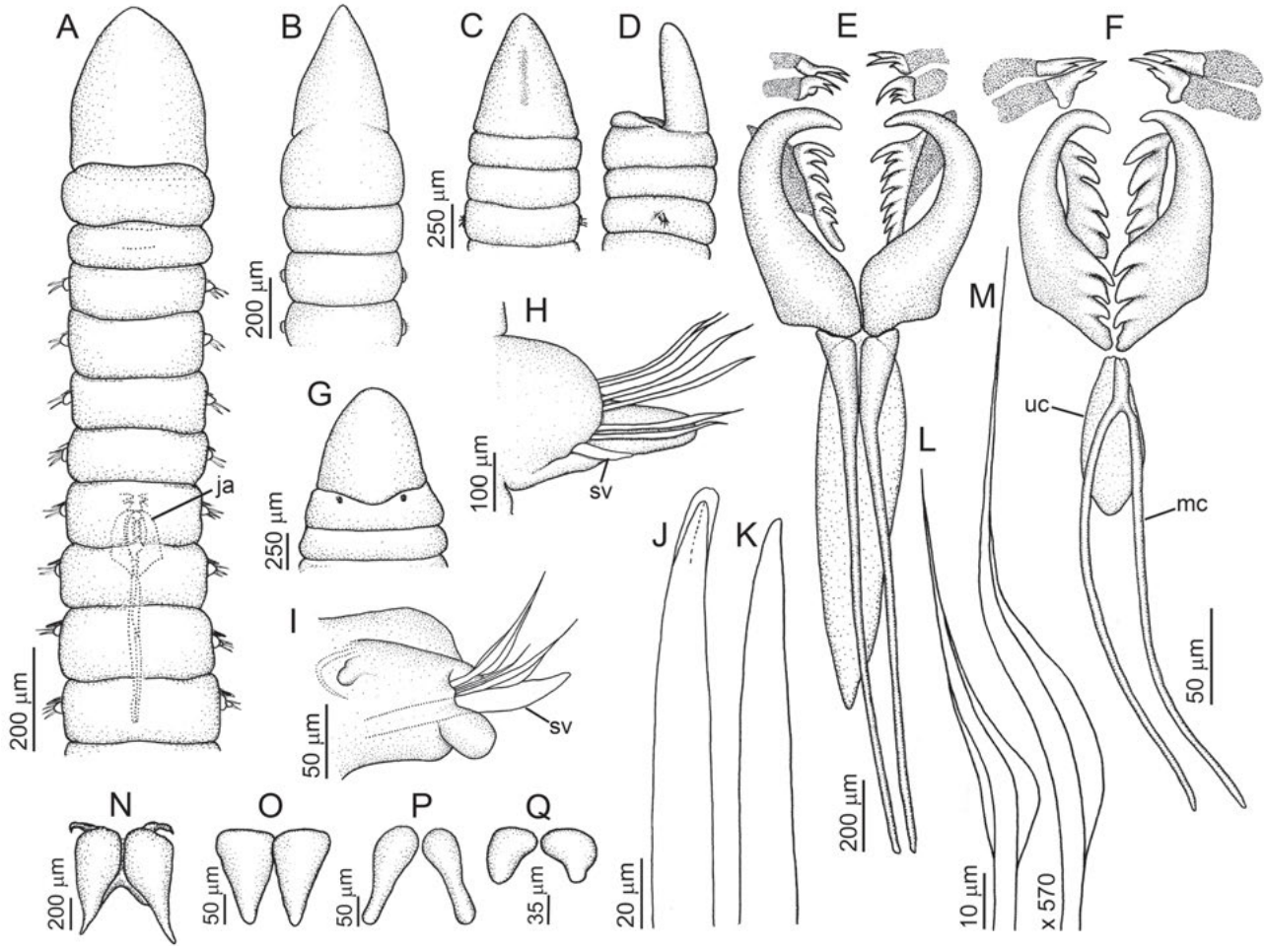


Fig. 7.12.7.4: Morphology of *Drilonereis*. A, I, *Drilonereis filum* (Claparède, 1870), from Mediterranean. E, G, H, *D. filum*, from Argentina; B, F, L, *Drilonereis simplex* Orensanz, 1974; C, D, Q, *Drilonereis tenuis* (Ehlers, 1900); J, K, O, P, *Drilonereis* sp., from Brazil; M, *Drilonereis mexicana* Fauchald, 1970; N, *Drilonereis falcata* Moore, 1911. A to C, anterior end, dorsal view; D, anterior end, lateral view; E, F, maxillary apparatus, dorsal view; G, anterior end, dorsal view; H, parapodium from midbody, anterior view; I, parapodium from anterior region, superior view; J, K, stout ventral spine; L, geniculate chaeta; M, geniculate chaeta from chaetiger 125; N to Q, mandibles. A, I, modified from Ramos (1976); B, E to H, L, N, Q, modified from Orensanz (1974); C, D, modified from Orensanz (1990); M, modified from Fauchald (1970). ja, jaw apparatus; mc, maxillary carrier; sv, stout ventral spine; uc, unpaired carrier.

in several genera, such as *Arabella* (Figs. 7.12.7.1L and 7.12.7.2C), *Oenone* (Fig. 7.12.7.11F), and *Halla* (Fig. 7.12.7.6D).

Most species have five pairs of well-defined maxillae (MI to MV) distributed in two longitudinal rows (Figs. 7.12.7.1M and 7.12.7.2D, E). The paired MI is generally attached basally to the maxillary carriers. The MI may be distally falcate and basally smooth (Fig. 7.12.7.4E), or dentate basally (Figs. 7.12.7.2D, 7.12.7.4F, and 7.12.7.14B), or along the entire inner margin (Figs. 7.12.7.2E and 7.12.7.9E); sometimes, the distal tooth is fang shaped (Figs. 7.12.7.9M and 7.12.7.11C). The MII is located below MI, not connected to it by ligaments, as in Lumbrineridae, dentate along the entire inner margin, sometimes similar in size to MI (Figs. 7.12.7.2D and 7.12.7.14B), and may also contain a large number of teeth. The paired multidentate MIII and MIV are located in front of MII; MV has one sharp tooth, rarely two (Figs. 7.12.7.2D and 7.12.7.9E). The distal tooth of MII to MV is frequently fang shaped. Attachment lamella that protrudes ventrally may be present in all maxillae, sometimes absent in MI (Figs. 7.12.7.2E, 7.12.7.4E, 7.12.7.9E, and 7.12.7.14B). Colbath (1989b) proposes the classification of “gracile” or “robust” for MI and “long” or “short” for MII, which has since been eventually adopted (Zanol and Ruta 2015).

In *Haematocleptes*, the maxillae are reduced to two very small pieces (Fig. 7.12.7.5C, D, F), whereas in *Oligognathus parasiticus* Cerruti, 1909 there are three unidentate pairs of equivalent sizes (Fig. 7.12.7.12D) (Cerruti 1909). The jaw apparatus of *Pholadiphila* is similar to Lumbrineridae, with falcate MI, internally dentate MII, and MIII a small bidentate plate (Fig. 7.12.7.13F). *Labrorostratus*, on

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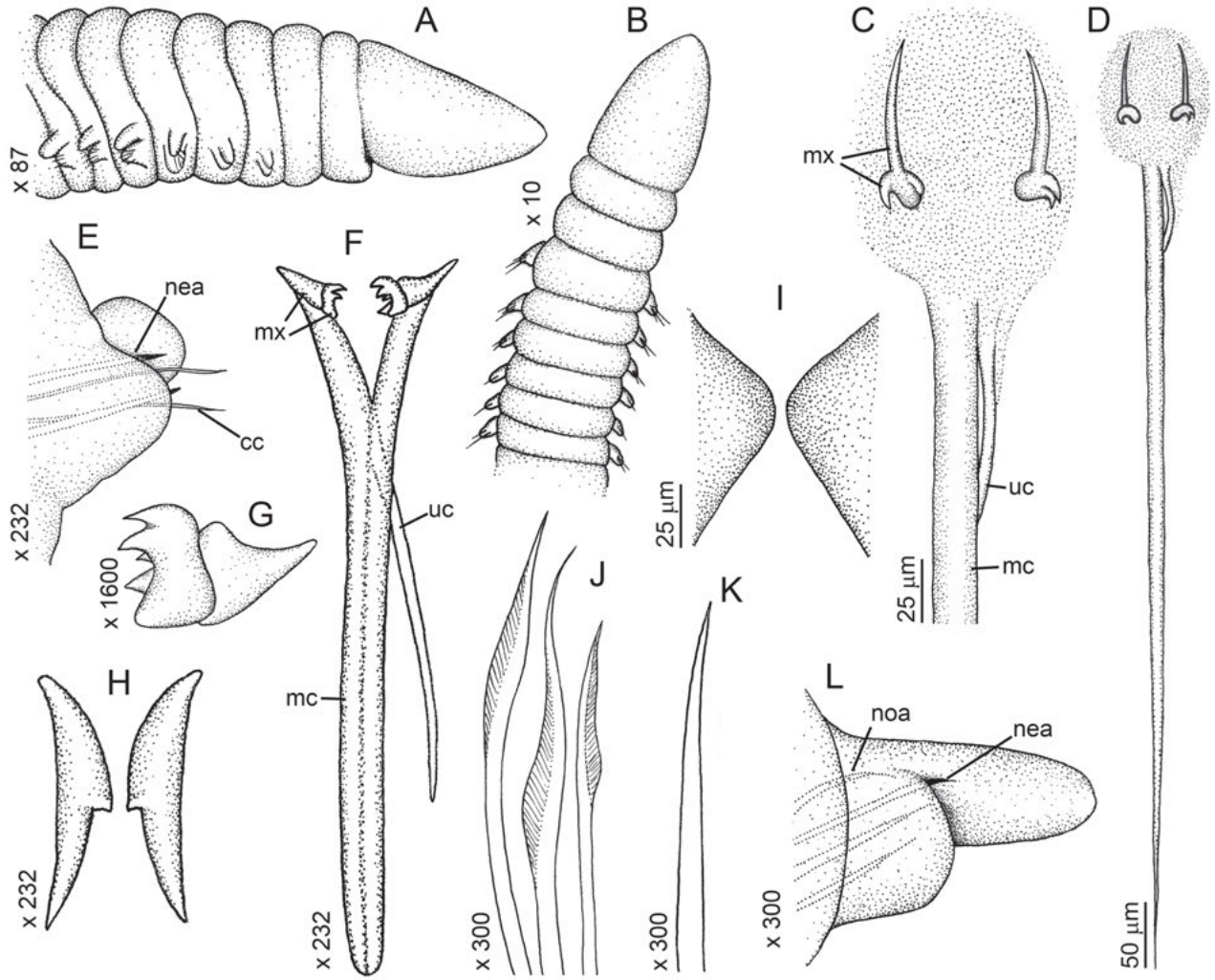


Fig. 7.12.7.5: Morphology of *Haematocleptes*. A, E to H, *Haematocleptes leaenae* Hartman & Fauchald, 1971. B, C, D, I to L, *Haematocleptes terebellidis* Wirén, 1886. A, anterior end, lateral view; B, anterior end, dorsal view; C, anterior end of maxillary apparatus, dorsal view; D, complete maxillary apparatus, dorsal view; E, parapodium from anterior third of body, anterior view; F, maxillary apparatus, dorsal view; G, maxillae from right side, dorsal view; H, I, mandibles; J, limbate chaetae; K, acicula; L, parapodium from anterior region, anterior view. A, E to H, modified from Hartman and Fauchald (1971); B, C, D, I to L, modified from Wiren (1886). cc, capillary chaeta; nea, neuropodial acicula; mc, maxillary carrier; mx, maxillae; noa, notopodial acicula; uc, unpaired carrier.

the other hand, exhibits a questionable diversity of maxillary structures, in the sense of the morphological scope of the genus. The maxillae are very small pieces, one pair (Fig. 7.12.7.8H, I) or two pairs (Fig. 7.12.7.8B, C, E, J) with varied shapes and connected to many different structures. *Labrorostratus prolificus* has only one pair of large triangular plates (Fig. 7.12.7.8F). Meanwhile, maxillae are absent in *Biborin, Drilognathus*, and *Labrorostratus caribensis* Hernández-Alcántara, Cruz-Pérez, & Solís-Weiss, 2015.

The maxillary apparatus is symmetrical in number of plates, meaning that plates are always paired (Zanol et al. 2021). There may be an asymmetry in shape and size, especially in MI and MII. In general, some asymmetry is always observed. In *Arabella aracaensis* Steiner & Amaral, 2009, the paired MI are similar in size, although the number of teeth is smaller on the right side, which is balanced in MII, where the right side has more teeth than the left (Fig. 7.12.7.2D). In some *Arabella* and *Notocirrus* species, the left MI may be smaller than the right, which is compensated in turn by the presence of a left MII that is larger than the right (Figs. 7.12.7.2E and 7.12.7.9E). A more extreme case of asymmetry occurs in *Oenone*, *Halla*, and *Tainokia logachevae* Ravara & Cunha, 2017, where the right MI is extremely small relative to the left (Figs. 7.12.7.6C, 7.12.7.11C, and 7.12.7.14D). In most species of *Drilonereis*, the paired MI are quite symmetrical (Fig. 7.12.7.4E, F), as in *Pholadiphila* (Fig. 7.12.7.13F), *Haematocleptes* (Fig. 7.12.7.5C, F), and *Labrorostratus* (Fig. 7.12.7.8A–F, H).

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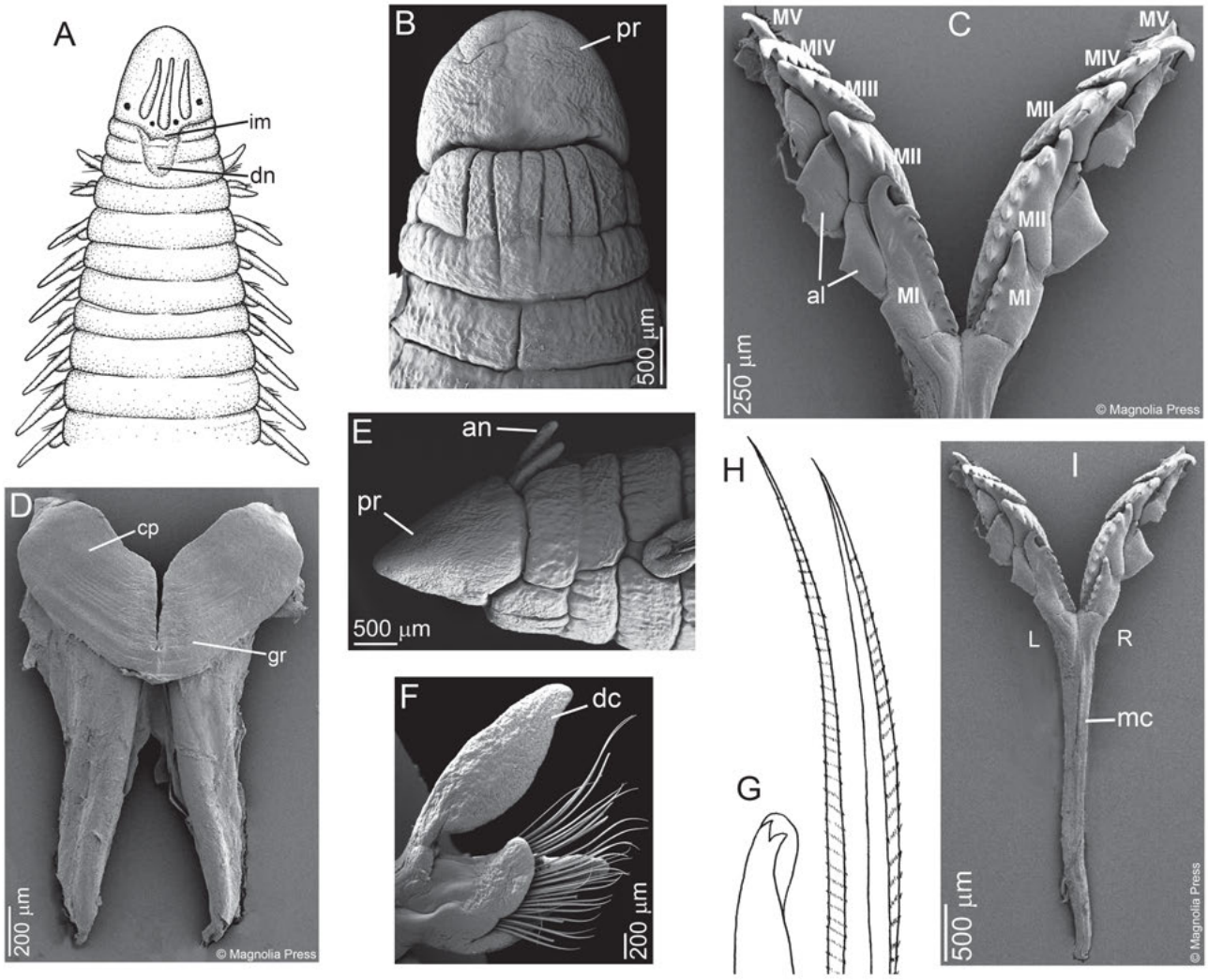


Fig. 7.12.7.6: Morphology of *Halla*. A, G, H, *Halla parthenopeia* (Delle Chiaje, 1828). B to F, I, *Halla okudai* Imajima, 1967. A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end of maxillary apparatus, dorsal view; D, mandibles, ventral view; E, anterior end, lateral view; F, parapodium from anterior end, anterior view; G, subacicular bidentate hooded hook; H, capillary chaetae; I, complete maxillary apparatus, dorsal view. A, G, H, modified from Fauvel (1923) (no scale bars in the original figures); B, E, F, © Sue Lindsay (Macquarie University); C, D, I, © Magnolia Press (Paxton 2009), reproduced with permission from the copyright holder. al, attachment lamellae; an, antenna; cp, cutting plate; dc, dorsal cirrus; dn, dorsal notch; gr, growth lines; im, incision mediodorsal; mc, maxillary carrier; MI to MV, paired maxillae; pr, prostomium; L, left; R, right.

Unlike the mandibles that demonstrate growth throughout life, Kielan-Jaworowska (1966), Colbath (1987), and Paxton (2009) suggest periodic and rapid maxillary replacement by shedding and molting. However, the paucity of evidence on how the apparatus changes during the species' growth and development hampers support of this hypothesis (Paxton 2006). Rather, it has been posited because the maxillae of some species of *Arabella*, *Notocirrus,* and *Drilonereis* show polymorphism among adult specimens, especially MI and MII. Orensanz (1974) noted that both left and right MI of *Notocirrus virginis* (Kinberg 1865) might be larger, with compensation in the size of the MII, as well as the presence of distal tooth that may or may not be fang shaped (Fig. 7.12.7.9M–O). Furthermore, differences in jaw structure also occur between adults and juveniles (Day 1960, Ramos 1976, Colbath 1989b). The intraspecific variation in jaw morphology is particularly important from a paleontological perspective since isolated fossil jaw elements have been largely studied (Kielan-Jaworowska 1966, Regali 1981, Van Erve 1981, Colbath 1989b, Szaniawski 1996).

The prionognath jaw apparatus has one pair of slender maxillary carriers that are longer than the set of maxillae and, in general, are anteriorly connected to each other by ligaments, and join loosely with MI. The paired carriers are present in *Arabella*, *Drilonereis*, *Notocirrus*, *Oenone*, *Halla*, and *Tainokia*, with both shafts straight,

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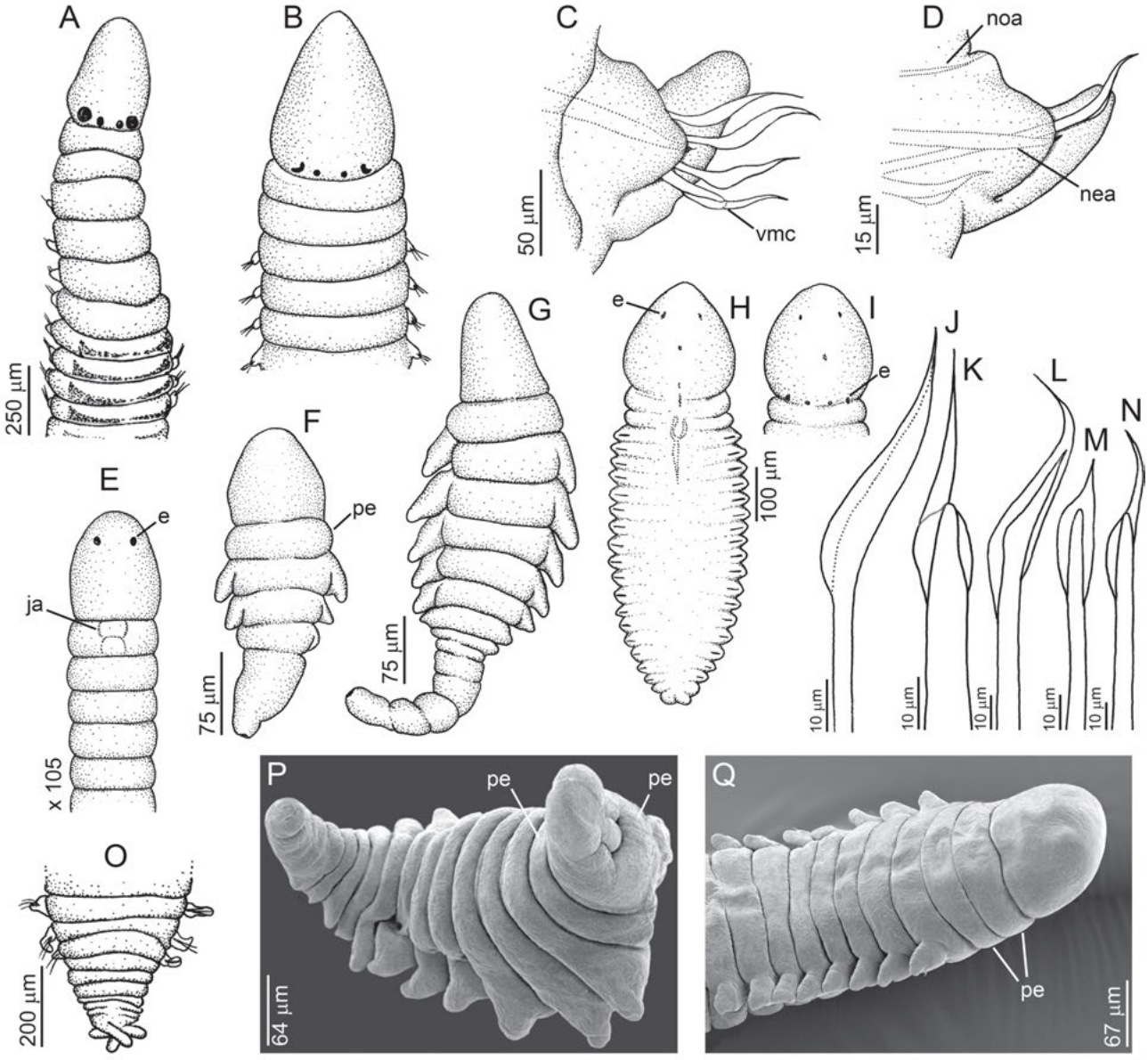


Fig. 7.12.7.7: Morphology of *Labrorostratus*. A, C, J, K, O, *Labrorostratus luteus* Uebelacker, 1978. B, D, F, G, P, Q, *Labrorostratus prolificus* Amaral, 1977. E, *Labrorostratus parasiticus* Saint-Joseph, 1888. H, I, *Labrorostratus* sp., from Spain. L, M, N, *Labrorostratus caribensis* Hernández-Alcántara, Cruz-Pérez, & Solís-Weiss, 2015. A, B, anterior end, dorsal view; C, D, parapodia from midbody, anterior view; E, young stage with nine chaetigers; F, young stage with three chaetigers; G, young stage with seven chaetigers with terminal stolon; H, young stage with eighteen chaetigers; I, young stage; J, limbate chaeta; K, ventralmost modified chaeta; L, limbate chaeta from posterior chaetiger; M, limbate chaetae from medium chaetiger; N, ventralmost modified chaeta from midbody; O, posterior end, ventral view; P, young stage with 10 chaetigers; Q, adult stage, anterior end, dorsolateral view. A, C, J, K, O, modified from Uebelacker (1978); B, modified from Amaral (1977) (no scale bar in the original figure); D, F, G, modified from Steiner and Amaral (2009); P, Q, © Taylor & Francis Ltd (Steiner and Amaral 2009), www.tandfonline.com; E, modified from Saint-Joseph (1888); H, I, modified from San Martin and Sardá (1986); L, M, N, modified from Hernández-Alcántara and Solís-Weiss (1998). e, eyespot; ja, jaw apparatus; nea, neuropodial acicula; noa, notopodial acicula; pc, pygidial cirrus; pe, peristomial ring; vmc, ventral modified chaeta.

frequently broad at the anterior region (Figs. 7.12.7.2E, 7.12.7.9E, and 7.12.7.14C), sometimes followed by two other lateral expansions, marking the beginning of the furcula (Figs. 7.12.7.2D and 7.12.7.14B) and the divergence of the shafts in posterior direction (Zanol and Ruta 2015, Joana Zanol, personal communication). In *Drilonereis*, shafts can be straight, very narrow, and fused in the anterior portion (Fig. 7.12.7.4F). In *Oligognathus*, the two distinguishable shafts are fused along the entire length (Fig. 7.12.7.12E, G), whereas the fusion is more evident in

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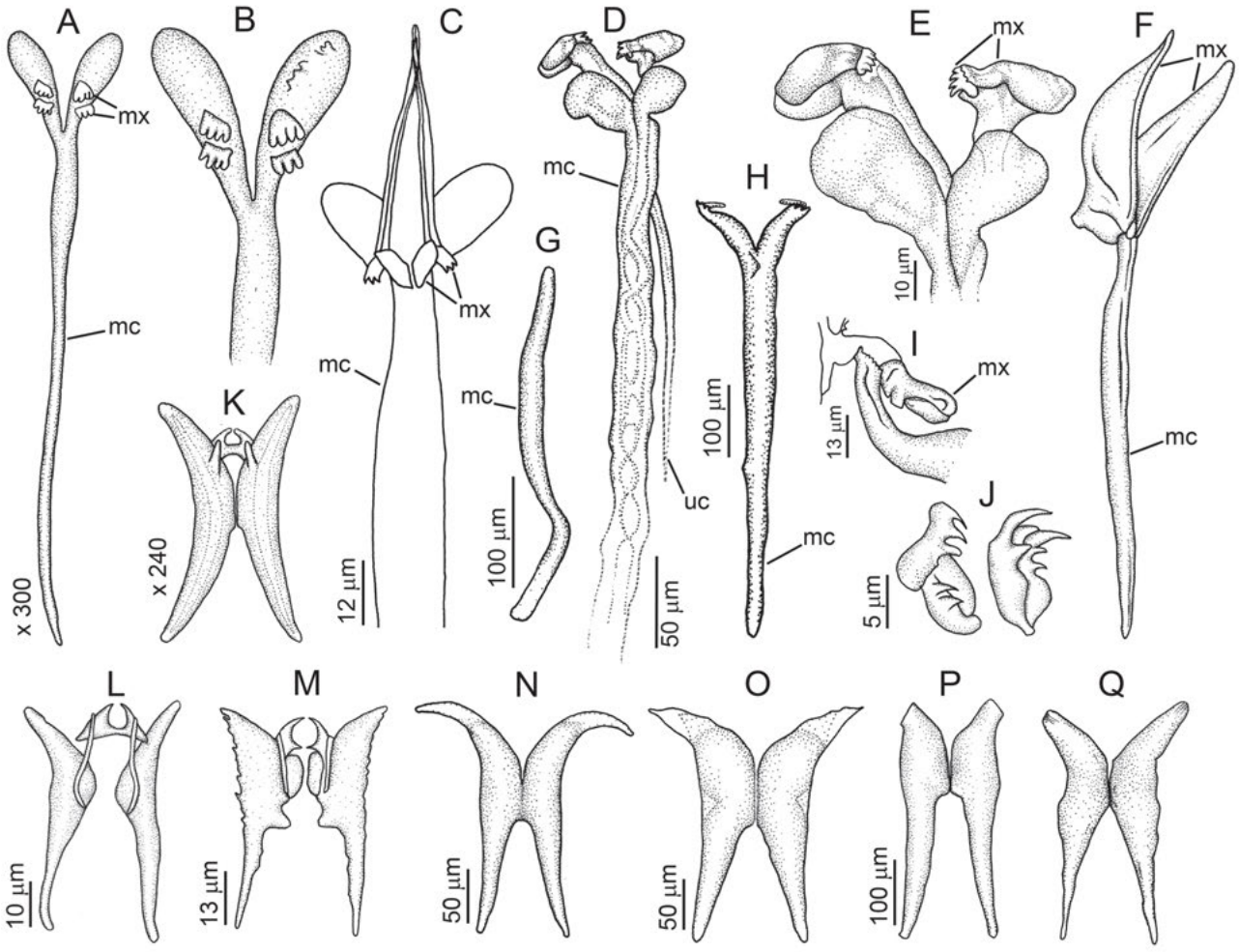


Fig. 7.12.7.8: Jaws of *Labrorostratus*. A, B, K, *Labrorostratus parasiticus* Saint-Joseph, 1888. C, J, M, *Labrorostratus jonicus* Tenerelli, 1961. D, E, O, *Labrorostratus luteus* Uebelacker, 1978. H, I, P, *Labrorostratus zaragozensis* Hernández-Alcántara & Solís-Weiss, 1998. L, *Labrorostratus* sp., from Spain. G, N, *Labrorostratus caribensis* Hernández-Alcántara, Cruz-Pérez, & Solís-Weiss, 2015. F, Q, *Labrorostratus prolificus* Amaral, 1977. A to H, maxillary apparatus; I, J, maxillae; L to Q, mandibles. A, B, K, modified from Saint-Joseph (1988); C, J, M, modified from Tenerelli (1961); D, E, O, modified from Uebelacker (1978); H, I, P, modified from Hernández-Alcántara and Solís-Weiss (1998); L, modified from San Martin and Sardá (1986); G, N, modified from Hernández-Alcántara et al. (2015); F, Q, modified from Amaral (1977) (no scale bars in the original figures). mc, maxillary carrier; mx, maxilla; uc, unpaired carrier.

Haematocleptes (Fig. 7.12.7.5D, F). In *Labrorostratus*, the carriers are fused along their entire length (Fig. 7.12.7.8A, D, F, H), except in *Labrorostratus jonicus*, which has an obscure and dubious maxillary apparatus. It possesses two anterior filiform structures that support, in its anterior portion, two serrated jaws, which connect to a pair of wide lateral and rounded plates, which in turn connect to the paired carriers (Fig. 7.12.7.8C, J). In *Labrorostratus parasiticus*, *Labrorostratus luteus* Uebelarcker, 1978, and *Labrorostratus zaragozensis* Hernández-Alcántara & Solís-Weiss, 1998, the fused carrier diverges anteriorly in two large plates that support small jaws.

An unpaired ventral median carrier (also named third carrier or ventral ligament) is present in *Arabella*, *Drilonereis*, *Haematocleptes*, *Notocirrus*, *Labrorostratus luteus*, and *Tainokia iridescens* Knox & Green, 1972 (Figs. 7.12.7.2D, 7.12.7.4E, 7.12.7.5F, 7.12.7.8D, 7.12.7.9E, and 7.12.7.14B). In *Oenone*, *Halla*, *Tainokia logachevae,* and other genera, it has not been verified, which may indicate that it is very short or absent, although it has been reported for *Oenone fulgida* by Hartman (1944). The unpaired carrier is shorter than the paired one, generally wider and moderately to poorly sclerotized, lighter in color, and sometimes difficult to visualize. The three carriers are parallel and have a longitudinal arrangement.

In *Pholadiphila turnerae* Dean, 1992, there is a single and slender rod-like maxillary carrier, shorter than the jaws, possessing a tripartite anterior end, which appears

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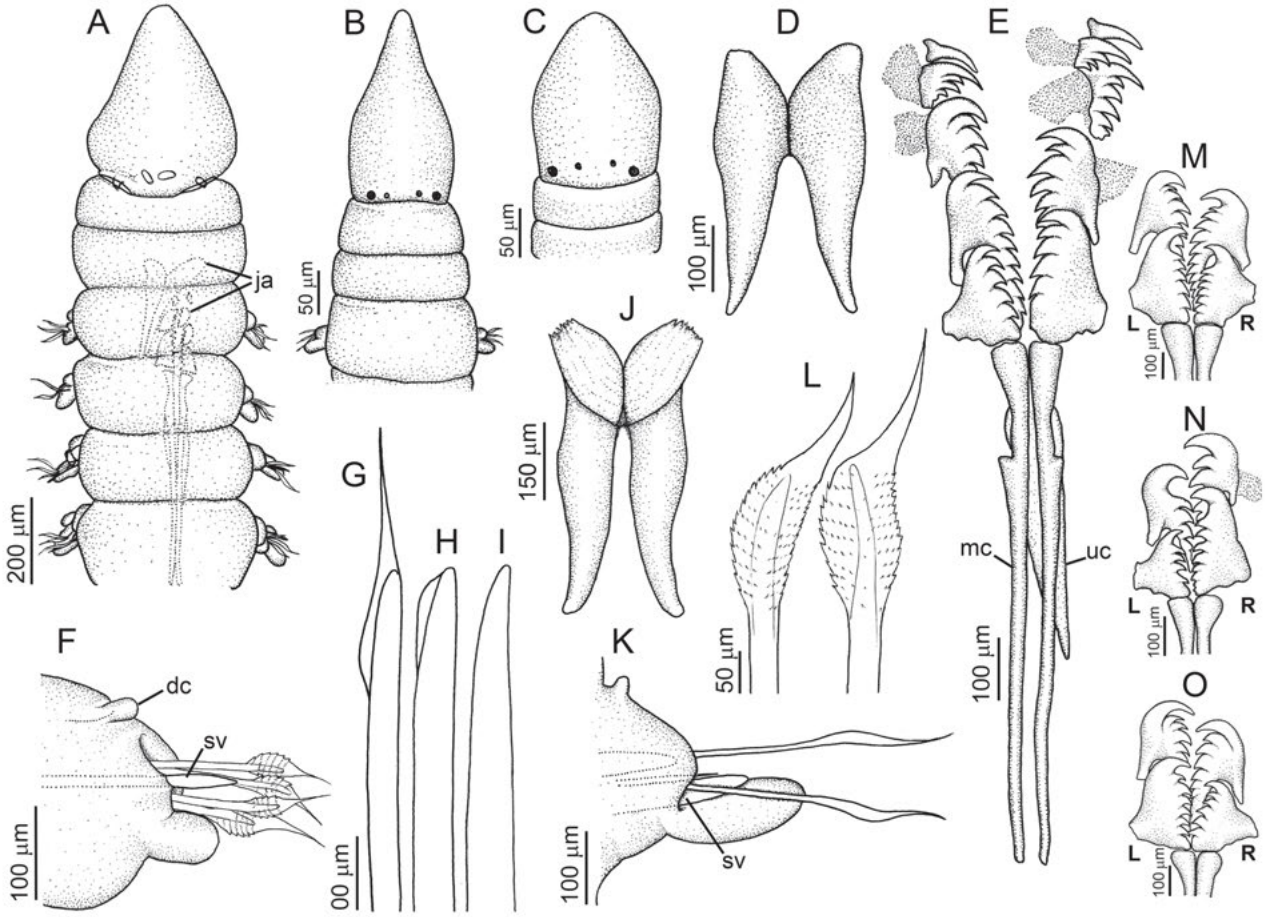


Fig. 7.12.7.9: Morphology of *Notocirrus*. A, F, L, *Notocirrus scoticus* McIntosh, 1869. B, *Notocirrus* sp., from Brazil. C, E, G to K, *Notocirrus lorum* Ehlers, 1897. D, *Notocirrus australis* Day, 1960. M, N, O, *Notocirrus virginis* (Kinberg, 1865). A, B, C, anterior end, dorsal view; D, mandibles; E, maxillary apparatus; F, parapodium from chaetiger 7; G, stout ventral spine from first chaetigers; H, stout ventral spine from median region; stout ventral spine from posterior region; J, mandibles; K, parapodium; L, geniculate chaetae; M, MI and MII, larger specimen; N, O, MI and MII, smaller specimens. A, F, L, modified from Ramos (1976); E, modified from Orensanz (1990); K, M, N, O, modified from Orensanz (1974). dc, dorsal cirrus; ja, jaw apparatus; mc, maxillary carrier; sv, stout ventral spine; uc, unpaired carrier; L, left; R, right.

to indicate the fusion of the three original carriers (Fig. 7.12.7.13D, F) (Dean 1992). The maxillary apparatus of *Drilognathus* and *Labrorostratus caribensis* lacks maxillae, and the fused carriers are reduced to an elongated and rod-like sclerotized structure (Fig. 7.12.7.3E, 3F and 7.12.7.8G).

Parapodia. The parapodia are uni- or subbiramous, similar throughout the body, generally elongated and well developed. They can be very small in some species of *Drilonereis* (Fig. 7.12.7.4A) and some parasites. The notopodium is reduced to the dorsal cirrus with embedded thin notoaciculae (Figs. 7.12.7.2G, 7.12.7.7D, 7.12.7.9F, and 7.12.7.11E). In most genera, the dorsal cirrus is knob-like, papilliform, or a small protrusion of the epidermis (Figs. 7.12.7.2G, 7.12.7.7D, and 7.12.7.9F), but *Oenone ventrioculata*, *Halla*, and *Tainokia* have a cirriform to digitiform dorsal cirrus (Fig. 7.12.7.14E), becoming wider and flattened in posterior chaetigers in *Halla* (Fig. 7.12.7.6F). In *Oenone fulgida*, the dorsal cirrus is broad, foliaceous (Figs. 7.12.7.10C and 7.12.7.11E), and may perform the function of branchia (Hartman 1944). However, specific branchial structures, as occurring in Eunicidae and Onuphidae, are absent. One to several very thin internal notopodial aciculae are present in most genera, but their presence is not documented in *Pholadiphila*. Occasionally, the aciculae may be unnoticed or absent in some species of other genera. The neuropodium has a rounded (Fig. 7.12.7.3G) or slightly conical (Fig. 7.12.7.11E) or truncate prechaetal lobe, and an even longer postchaetal lobe, which can be papilliform (Figs. 7.12.7.4I and 7.12.7.9F), rounded (Fig. 7.12.7.5E), digitiform, conical (Fig. 7.12.7.7D), triangular (Fig. 7.12.7.4H), or rectangular, even in adult stages of parasitic species. The ventral cirrus is absent.

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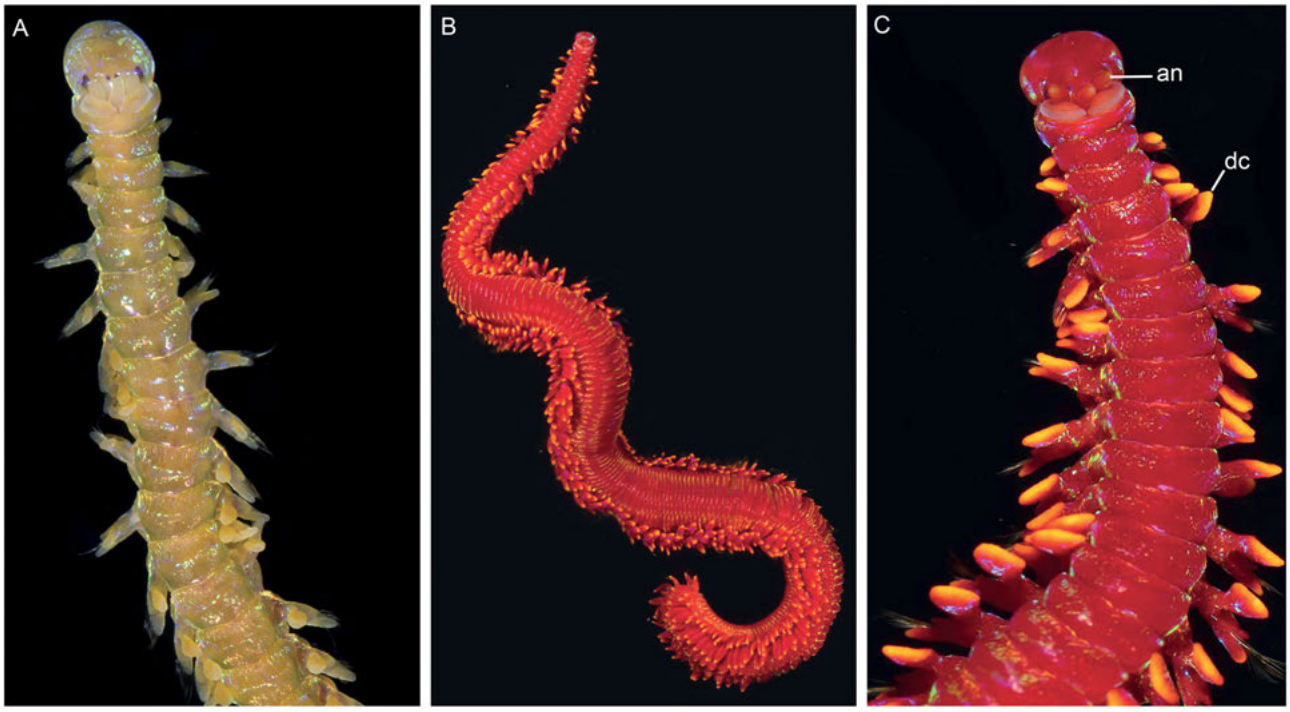


Fig. 7.12.7.10: Morphology of *Oenone*, photographs of live specimens, dorsal view. A, *Oenone fulgida* (Savigny, 1818), from Kaneohe Bay, Honolulu, Hawaii. B, C, *Oenone* sp., from Salt Creek, Bocas del Toro Province, Panama. © Florida Museum of Natural History, Invertebrate Zoology group (CC BY-NC 3.0, http://creativecommons.org/licenses/by-nc/3.0/). an, antenna; dc, dorsal cirrus.

One to five neuropodial aciculae are present, larger, and more robust than the notopodial ones, often protruding slightly from the parapodia (Figs. 7.12.7.3G and 7.12.7.11E). In *Pholadiphila*, the parapodia are uniramous, and there are no pre- or postchaetal lobes, which is a considerable difference from the pattern found in Oenonidae (Fig. 7.12.7.13G).

There are few types of chaetae in Oenonidae. In upper and lower bundle of the neuropodium, long and thin capillaries (Figs. 7.12.7.5E, 7.12.7.6H, and 7.12.7.11H), or limbates (Figs. 7.12.7.1I, 7.12.7.4M, and 7.12.7.9L), are present. The limbates have blades with different degrees of bending, with smooth (Fig. 7.12.7.4M), finely, or coarsely serrated blades (Fig. 7.12.7.2M), sometimes with small spines (Fig. 7.12.7.9L). The bundle of chaetae in the parapodium is not randomly distributed but exhibits an evident morphological pattern from the most dorsal to the most ventral. In *Arabella aracaensis*, the dorsal chaeta of the upper bundle is the longest (Fig. 7.12.7.2G: doc), whereas the mediodorsal is shorter and more bent (Fig. 7.12.7.2G, M: mdc). The medioventral chaeta of the lower bundle is similar to the mediodorsal but less bent and with a different morphology (Fig. 7.12.7.2G, M, mvc). The ventral chaeta is the most differentiated from the parapodium, showing torsion of the blade, becoming distally narrower than the medioventral but equal in length (Fig. 7.12.7.2G, M, vmc). Also, the thickness and the length of the blade can vary along the body (Figs. 7.12.7.1I, vmc, 7.12.7.2H, I and 7.12.7.9G–I). The ventral chaeta does not have a hood or a guard (Colbath 1989b, Steiner and Amaral 2009). Other *Arabella* species may have the dorsal chaetae more bent than the mediodorsal (Fig. 7.12.7.1I), as well as other variations can be found in other genera. The ventalmost modified chaeta is noticed in *Arabella* (Fig. 7.12.7.2J), *Labrorostratus* (Fig. 7.12.7.7C, N), *Notocirrus* sp. (Fig. 7.12.7.9G), and *Tainokia* (Fig. 7.12.7.14E), among other species. In *Drilonereis* and *Notocirrus*, one or two, rarely three, stout spines occur in each parapodium, sometimes varying along the body, with those in the anterior region quite similar to the ventral modified chaeta in some species (Fig. 7.12.7.9G–I). In the lower bundle, uni- or bidentate hooded hooks on chaetigers of the median and posterior regions are present in *Oenone*, *Halla*, and *Tainokia logachevae*, all genera with antennae (Figs. 7.12.7.6G, 7.12.7.11E, G, and 7.12.7.14H). In adults of *Halla*, this hook may appear between chaetigers 70 to 100, continuing along the body (Fauvel 1923, Idris and Arshad 2013), although it has been reported as being absent in large specimens (Ehlers 1864–1868, Imajima and Hartman 1964, Colbath 1989a). Ventral chaeta, acicular spine, and subacicular hooded hook may be homologous structures.

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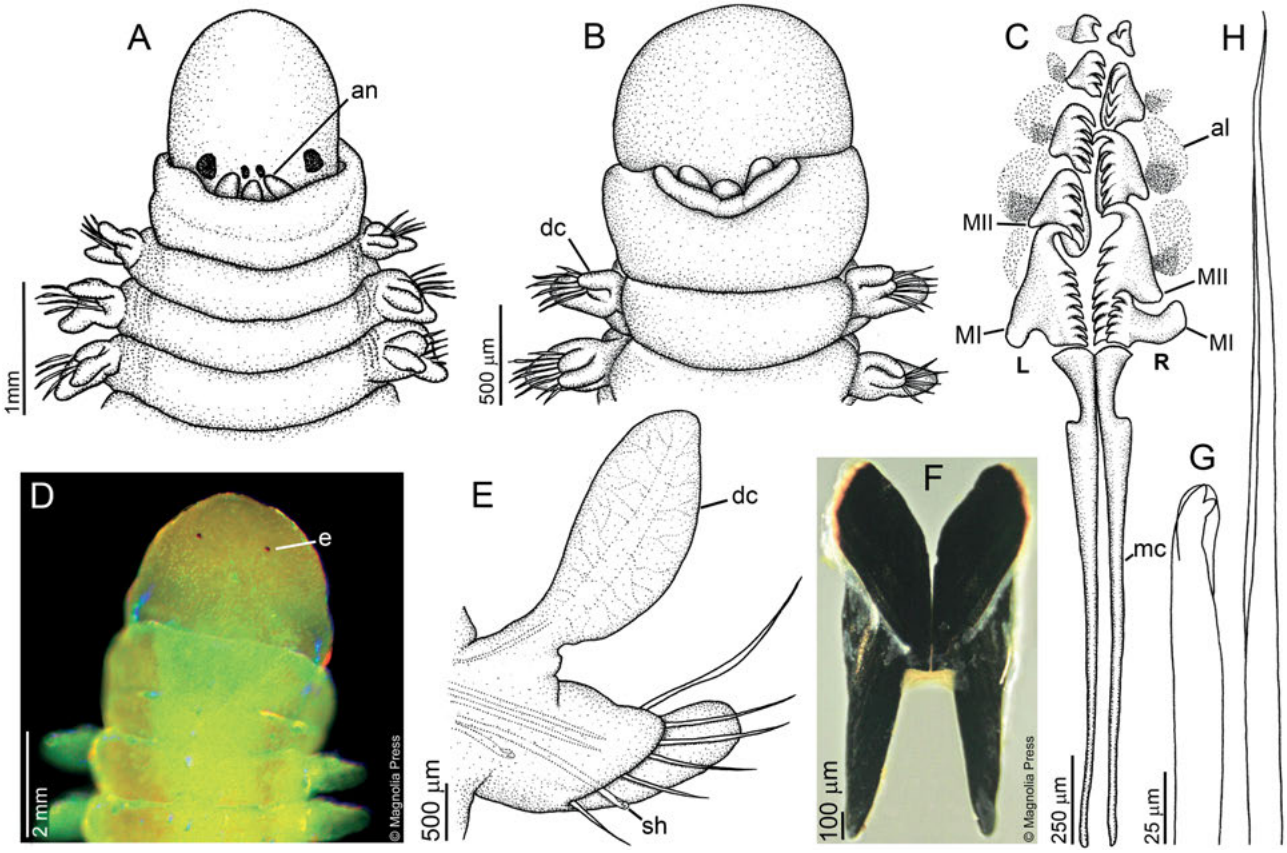


Fig. 7.12.7.11: Morphology of *Oenone*. A, C, E to H, *Oenone fulgida* (Savigny, 1818). B, *Oenone* sp., from Japan. D, *Oenone ventrioculata* Zanol & Ruta, 2015. A, B, anterior end, dorsal view; C, maxillary apparatus, dorsal view; D, anterior end, ventral view; E, parapodium from chaetiger 45, anterior view; F, mandibles, ventral view; G, subacicular bidentate hooded hook, chaetiger 45; H, capillary chaetae from chaetiger 45. A, C, E, F, G, modified from Paxton (2000); B, modified from Rouse and Pleijel (2001) (based on SEM micrograph); D, F, © Magnolia Press (Zanol and Ruta 2015), reproduced with permission from the copyright holder. al, attachment lamella; an, antenna; dc, dorsal cirrus; e, eyespot; mc, maxillary carrier; MI and MII, maxillae; sh, subacicular hook; L, left; R, right.

Drilognathus capensis has no chaetae (Fig. 7.12.7.3G), but very small chaetae emerge internally at the base of the parapodia (Fig. 7.12.7.3H) in *Drilognathus* sp. (Orensanz 1974) and, *Haematocleptes* (Fig. 7.12.7.5E, L). The absence of chaetae has also been verified in specimens of *Labrorostratus prolificus* generated asexually, with up to 30 chaetigers (Steiner and Amaral 2009) (Fig. 7.12.7.7F, G, P), as well as young stages of *Drilonereis caulleryi* Pettibone, 1957 and adults stages of *Drilonereis benedicti* Pettibone, 1957. *The chaetal pattern of Pholadiphila turnerae is distinct from* the other genera of Oenonidae, with capillary or limbate chaetae absent and different types of stout hirsute spines (Fig. 7.12.7.13G).

Pygidium. The pygidium, with terminal anus, can be a simple ring (Fig. 7.12.7.13B), or have two lateral and inflated pads (Fig. 7.12.7.1K), or rounded at the end without appendages, or with two (Figs. 7.12.7.2K and 7.12.7.3I) to four short anal cirri (Figs. 7.12.7.1J and 7.12.7.7O). Colbath (1989b) considered the presence and number of anal cirri as an important specific character but recognized the difficulty of obtaining complete specimens.

Biology and ecology

Habitat, distribution, and abundance

Oenonids are distributed worldwide in intertidal to abyssal depths of about 3600 m. They have been recorded in all oceans, including areas of the Arctic and Antarctic, although they are most common in the tropical and temperate regions (Zanol et al. 2021). Although they are present in all oceans, many regions are poorly studied, suggesting that oenonid diversity is still underestimated (Zanol et al. 2021).

Usually, oenonids occur at low densities, with few exceptions. They are rare intertidally, but some species

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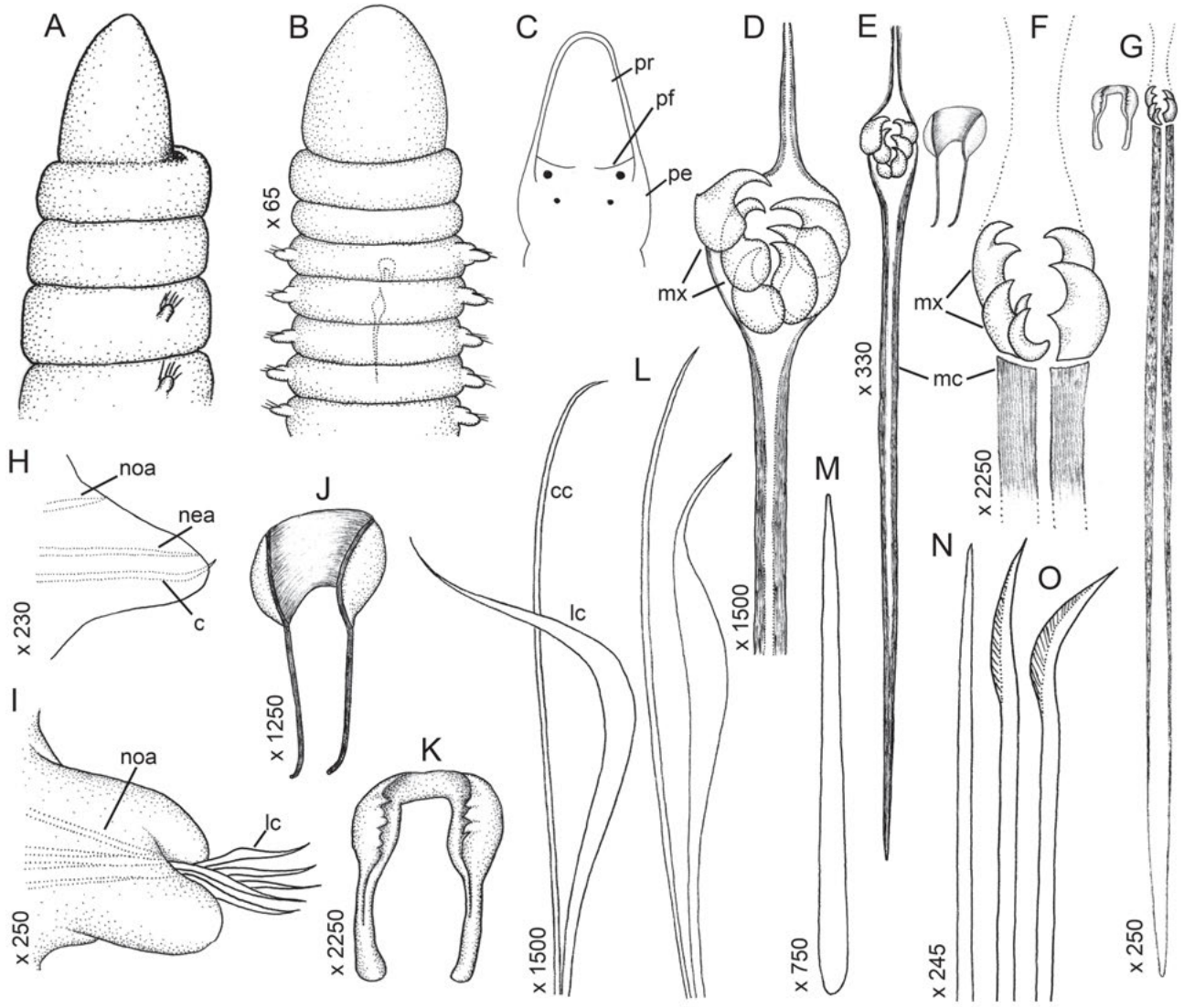


Fig. 7.12.7.12: Morphology of *Oligognathus*. A, C, F to I, K, N, O, *Oligognathus boneliae* Spengel, 1882. B, D, E, J, L, M, *Oligognathus parasiticus* Cerruti, 1909. A, anterior region, lateral view (no scale bar in the original figure); B, anterior region, dorsal view; C, prostomium and peristomium scheme; D, anterior end of maxillary apparatus; E, complete jaw apparatus; F, anterior end of maxillary apparatus; G, complete jaw apparatus; H, vertical midsection of a parapodium; I, parapodium; J, K, mandibles; L, chaetae; M, N, acicula; O, chaetae. A, C, F to I, K, N, O, modified from Spengel (1882); B, D, E, J, L, M, modified from Cerruti (1909). c, chaeta; cc, capillary chaeta; lc, limbate chaeta; mc, maxillary carrier; mx, maxillae, nea; neuropodial acicula; noa, notopodial acicula; pe, peristomial ring; pf, peristomial fold; pr, prostomium.

of *Arabella*, *Halla*, and *Oenone* can occur in high density. Many species are more frequent in the sublittoral and deeper areas. In soft bottoms, oenonids can occur in coarse to fine sands or different mixtures of sand, mud, clay, and silt; or coarse calcareous sand on coral, coral rubble, sand with gravel, or pebbles and shell fragments, sand close to mangroves, as well as underneath stones and coral, and rocky shores. *Arabella* has also been collected in oyster and mussel beds, rhizoids of Phaeophyceae, and among *Zostera* holdfasts. *Oenone* may inhabit rocky shores in association with algae. There are also records of commensal and endofaunal species, such as *Arabella*, composing the fauna associated with bryozoans and other colonial marine invertebrates, and *Oenone* participating of the endofauna in *Schizoporella unicornis* (Johnston in Wood 1844) (in Morgado and Amaral 1981), or as a commensal species in the sponge *Spheciospongia vesparium* (Lamarck, 1815) (in Pearse 1932). Both species of *Tainokia* were found in reduced habitats, T. *iridescens* was found in the lower eulittoral zone, in gray, slightly sulfurous sand, in New Zealand, whereas T. *logachevae* was retrieved from a dredge sample across the crater of the Mercator mud volcano, in the Gulf of Cadiz.

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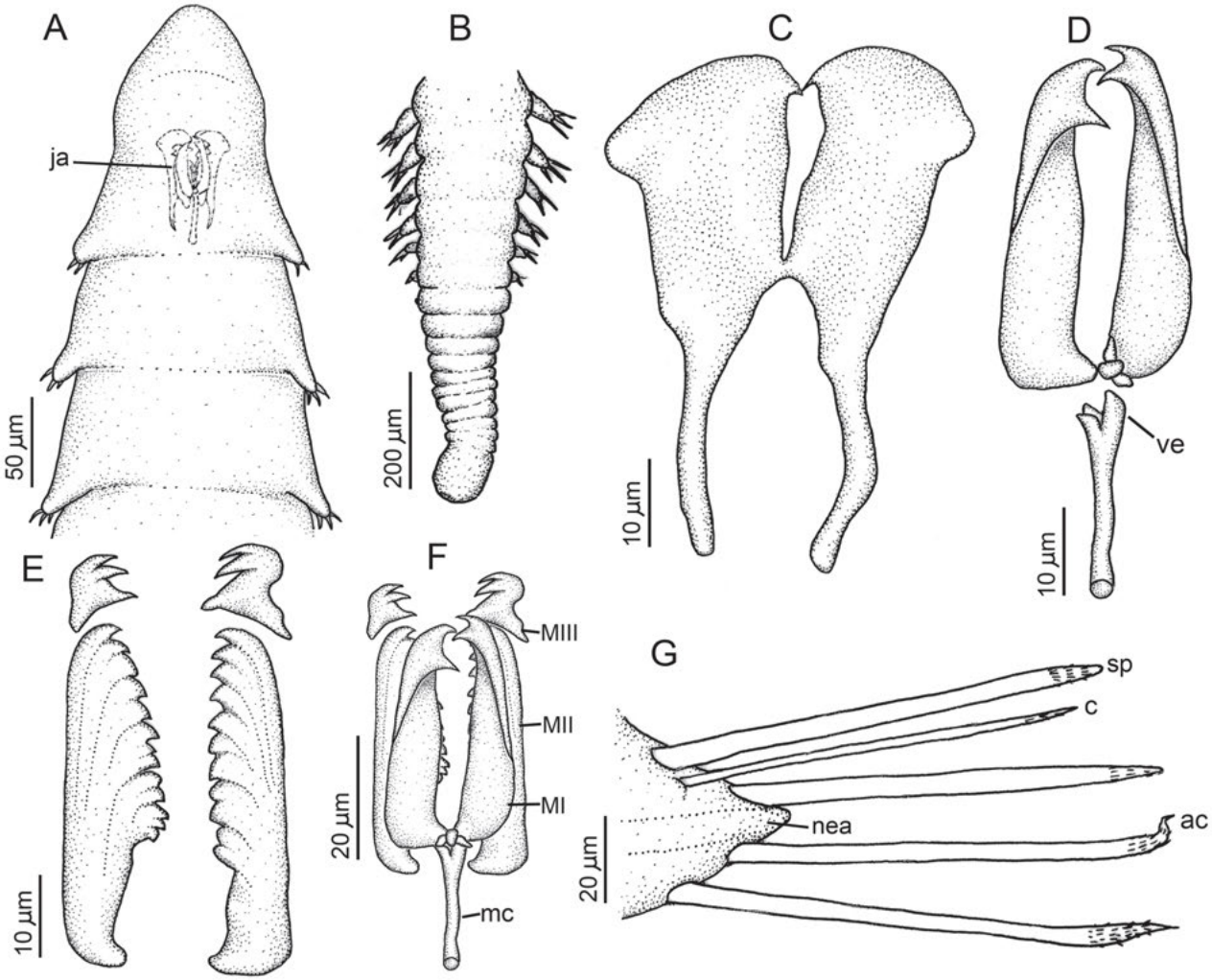


Fig. 7.12.7.13: Morphology of *Pholadiphila turnerae* Dean, 1992. A, anterior end, dorsal view; B, posterior region; C, mandibles; D, MI and maxillary carrier; E, MII and MIII; F, complete maxillary apparatus, dorsal view; G. parapodium from midbody. Modified from Dean (1992). ac, acuminate chaeta; c, capillary chaeta; mc, maxillary carrier; MI to MIII, maxillae; nea, neuropodial acicula; sp, stout spine; ve, ventral extension.

Despite the low abundance of oenonids, large populations of *Halla okudai* inhabit sandy bottoms of intertidal and shallow subtidal zones, in Japan and Malaysia (Idris and Arshad 2013, Kobayashi et al. 2020), whereas *Halla parthenopeia* (Delle Chiaje, 1828) is widely distributed in similar environments in Mediterranean, including the Suez Canal (Osman et al. 2010a, b, Baeta et al. 2019, Ibrahim and Abd-Elnaby 2021). Many species considered cosmopolitan, as *Oenone fulgida*, *Arabella iricolor*, and *Drilonereis filum*, should be revised. However, the scarce material available and the difficulty of obtaining specimens for study, due to their rarity, make it difficult to clarify their taxonomic status. The ectoparasite *Pholadiphila turnerae* was recorded living inside the mantle cavity of wood-boring Pholadoidea bivalves at depths of 3600 m, in wooden panels, in the North Atlantic Ocean (Dean 1992).

Little is known about the distribution of parasites. Most species are known only from the original description, sometimes made on the basis of a single specimen, when eventually detected inside the fragmented or dissected host's body. The taxonomic validity of some descriptions thus remains doubtful. Even so, each record is important because of the scarcity of specimens found worldwide (Hernández-Alcántara et al. 2015). The distribution of parasitic species can be reasonably given based on their hosts, which are found in a variety of habitats, such as soft bottoms, from intertidal to more than 1000 m (host of *Haematocleptes leaenae* Hartman & Fauchald, 1971), or coral rocks at 4.5 m (host of *Labrorostratus caribensis*), or intertidally among calcareous algae (host of *Oligognathus bonelliae*).

Information about oenonid ecology is scarce. They are not frequently collected or recorded, and their abundance

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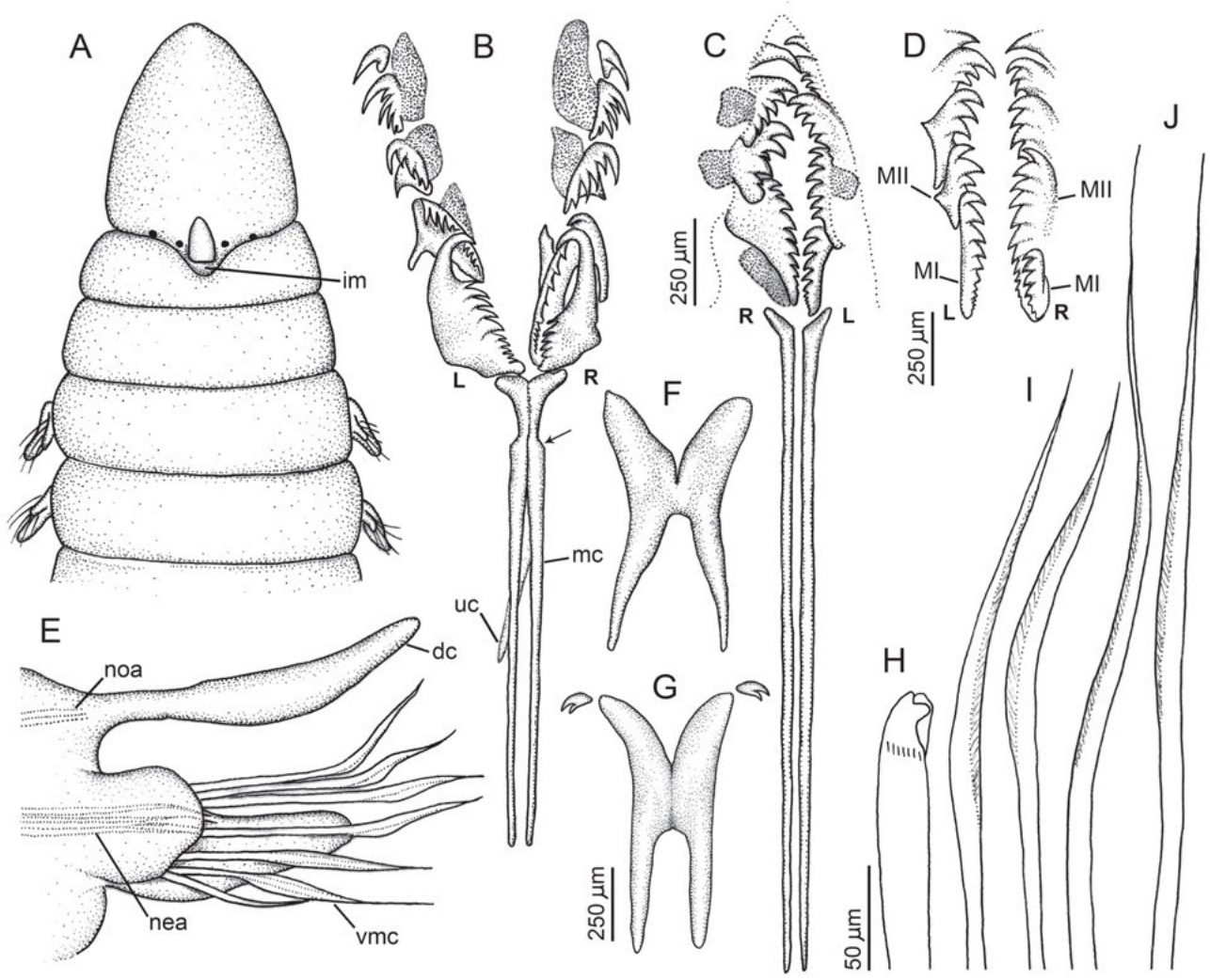


Fig. 7.12.7.14: Morphology of *Tainokia*. A, B, E, F, *Tainokia iridescens* Knox & Green, 1972. C, D, G to J, *Tainokia logachevae* Ravara & Cunha, 2017. A, anterior end, dorsal view; B, maxillary apparatus, dorsal view; C, maxillary apparatus, ventral view; D, maxillary apparatus, dorsal view; E, parapodium from midbody, anterior view; F, G, mandibles; H, subacicular bidentate hooded hook; I, lower limbate chaetae; J, upper limbate chaetae. A, B, E, F, modified from Knox and Green (1972) (no scale bars in the original figures); C, D, G to J, modified from Ravara and Cunha (2017). dc, dorsal cirrus; im, incision mediodorsal; mc, maxillary carrier; MI and MII, maxillae; nea, neuropodial acicula; noa, notopodial acicula; uc, unpaired carrier; vmc, ventral modified chaeta; L, left; R, right. Arrow indicates the beginning of the furcula.

is always low in large ecological samples, meaning that the relationships between free-living species and other species are rarely discerned. Moreover, specific analyses regarding their behavior in relation to the environment are rare. Studies that assess the infestation rates by parasitic oenonids and their ecological relationships with their hosts are likewise few in number (Martin and Britayev 1998).

Feeding modes and life styles

There are no records of tube construction in free-living oenonids, although they dig their galleries, cementing the walls with mucus (Hilbig 1995). *Arabella iricolor*, from New England, burrows readily and deeply, encased in a thick coat of mucus secreted in abundance (Pettibone 1963). *Notocirrus virginis* buries itself in the sand rapidly, aided by abundant mucous secretion (Ramos 1976). *Tainokia iridescens* is extremely active, burrowing rapidly into the sand when exposed and secreting copious amounts of mucus to which sand grains adhere, making a soft encasing tube (Knox and Green 1972).

Little is known, meanwhile, about the life histories of endoparasites. Currently, about 20 species are known, encompassing exclusively parasitic genera such as *Drilognathus* (2 species), *Haematocleptes* (2 species), *Oligognathus* (2 species), *Labrorostratus* (5 species, and one unidentified in San Martin & Sardá 1986), in addition to some species of *Arabella* (2 species), *Notocirrus* (1 species,

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and two unidentified in Koch 1847 and Ehlers 1864–1868), and *Drilonereis* (5 species, and two unidentified in Orensanz 1974 and Pérès 1949). The hosts are mostly annelids belonging to the families Syllidae (10 species), Onuphidae (6 species), Eunicidae (3 species), Nereididae (2 species), Trichobranchidae (2 species), Terebellidae (2 species), Ampharetidae (1 species), Serpulidae (1 species), Arenicolidae (1 species), and an additional echiuran species, *Bonellia viridis* Rolando, 1822. Some species appear to demonstrate specificity in the choice of the host, such as *Oligognathus bonelliae*, which has been exclusively recorded in the echiurid *B. viridis*. *Labrorostratus parasiticus*, on the other hand, can be found in six different species of Syllidae but has also been recorded as free living among calcareous algae (Pettibone 1957). The parasite *Labrorostratus luteus* was also found as free living in soft bottoms, at 37–69 m (Uebelacker 1984). *Labrorostratus jonicus* was found among algae, together with syllids (Tenerelli 1961), being, therefore, a free-living species. The species *Biborin ecbola* Chamberlin, 1919a has no maxillae and has been considered to be a parasite (Orensanz 1990, Carrera-Parra 2009, Zanol et al. 2021). However, it was collected among *Phyllospadix* seagrass (Chamberlin 1919b), where it was confirmed as free living (Chamberlin 1919a), meaning that the absence of maxillae cannot be the only criterion to be deemed a parasite.

Most parasitic species have been found in the body cavity, immersed in the coelom. They have also been recorded in blood vessels in the body wall, tissues of the digestive tract, peri-intestinal blood sinus, vascular body wall, and vascular system. An interesting case is the parasite *Labrorostratus luteus*, found in the body cavity of *Haplosyllis spongicola* (Grube, 1855): the latter, in turn, is a parasite of the sponge *Gelliodes digitalis* (see Martin and Britayev 1998) from coral heads on Grand Bahama Island (Uebelacker 1978). A single and large specimen of *Drilonereis benedicti*, with 240 mm in length and about 1200 chaetigers, was found in the body cavity of *Americonuphis magna* (Andrews, 1891) (Pettibone 1957), whereas about 60 individuals of *Labrorostratus prolificus*, from young stages with three chaetigers to mature individuals with more than 60 chaetigers (Steiner and Amaral 2009) were found in *Perinereis cultrifera* (Grube, 1840). Some parasites can grow to a larger size than their hosts (Pettibone 1957, Hernández-Alcántara and Solís-Weiss 1998).

Observations of feeding behavior and analyses of the gut contents of oenonids are still rare. Fauchald and Jumars (1979) referred to free-living oenonids as carnivores, based on Pettibone (1957, 1963), or selective surface deposit feeders, based on Sanders et al. (1962). The ingestion of detritus, diatoms, and filamentous algae has been observed in *Drilonereis longa* and *Oenone fulgida* from the Caribbean Sea (Ebbs 1966) and the Marshall Islands (Hartman 1954), as well as boring in coral. Analyses based on stable isotopes (δ15N) in three unidentified individuals of the family, in addition to *Halla parthenopeia* and *Arabella iricolor* (Carlier et al. 2007, Fanelli et al. 2011, Deudero et al. 2014), indicate a very high trophic level and unambiguous carnivory (Jumars et al. 2015). The latter species has been observed feeding on the mussel *Mytilus edulis* Linnaeus, 1758 while secreting a jellylike substance (Iwasaki 1997).

The feeding mode of the two species of *Halla* has been studied in detail because they are of commercial interest. *Halla parthenopeia*, known in Catalonia (Spain) as "cuc-llobarrer," feeds on different species of clams from areas of the Suez Canal. However, it grows better feeding on some specific species, such as *Paratapes undulatus* (Born, 1778) and *Cerastoderma glaucum* (Bruguière, 1789), therefore considered selective, seeking out suitable and profitable prey (Osman et al. 2010a). Osman et al. (2010a) reported that *H. parthenopeia* secretes a jellylike substance when handling and feeding upon the prey and described its eating behavior. The secretion of such a substance is considered to be confined to predatory polychaetes that feed on macroinvertebrates (Kawai et al. 1999). However, the species' activity has also been described as scraping along hard substrate (Fauchald and Jumars 1979) because of the presence of algae, diatoms, and copepods in the gut content (Yonge 1954). This species secretes another type of purple mucus under stress conditions, which is lethal and might be a chemical defense against competitors and parasites (Iori et al. 2014). Purple mucus secretion also occurs in species of *Oenone* when they are under handling stress (Carrera-Parra 2009).

Halla okudai, known in Japan as "akamushi" (Kawai et al. 1999) and "tai-mushi" (Saito et al. 2014), has well-studied feeding behavior (Saito and Imabayasi 1994, Imabayashi et al. 1996, Saito et al. 1999, Kawai et al. 1999, Saito et al. 2000, 2003, 2004). The species feeds preferentially on short-manila clams *Ruditapes philippinarum* (A. Adams & Reeve, 1850) (Saito et al. 1999). Imabayashi et al. (1996) studied its feeding activity in detail, identifying four phases: (1) response, when the worm reacts to the presence of the prey, projecting part of the anterior region above the sand; (2) research, when chasing the prey with different body movements, including movement of the antennae that become erect; (3) capture, when pulling the prey to the entrance of the gallery, wrapping itself around it while secreting a large amount of mucus, which serves to relax and paralyze its prey; and (4) feeding process, when the worm penetrates the shell, entirely consuming

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the soft tissues, including the mantle, with large amounts of mucus remaining at the end of the process (Imabayashi et al. 1996, Kawai et al. 1999). Three different types of mucus are produced for different functions related to the cementation of the gallery, locomotion, and food activity (Kawai et al. 1999, Osman et al. 2010a).

The food of the ectoparasite *Pholadiphila turnerae* may come from the mucus coat of the branchial filaments or the partially digested material within the bivalve's wood-storing cecum (Dean 1992). Little is known about the possible food sources of parasitic oenonids. For *Arabella endonata* Emerson, 1974, which was found in the coelomic cavity of a female of *Diopatra ornata* Moore, 1911, oocytes could be a source of food for the larger specimens (Emerson 1974), which would allow space in the cavity, whereas the smaller ones, without jaws, may feed on the nutritious coelomic fluid. Individuals of *Labrorostratus prolificus* Amaral, 1977 in different stages were also found in the coelom of a female of *Perinereis cultrifera* with oocytes (Steiner and Amaral 2009).

Reproduction and development

The reproductive biology of the two economically important species of *Halla* has been studied in detail. The ultrastructure of male germ cells and the character of spermatozoa of *Halla parthenopeia* were studied by Abd-Elnaby (2009), who found sperm of the ect-aquasperm type and morphologically simple and primitive spermatozoa, with two peaks of mature sperm appearing in late April and late December, and spawning occurring in May and January. Osman et al. (2010b) studied the reproductive biology and described three maturity stages for oogenesis in females, with two reproductive periods, one in May and another in November, lasting until January, with oocytes free in the coelomic cavity. Similarly, the reproduction, early development, growth, and regeneration of *Halla okudai* have been previously studied (Itazaki 1982a, b, 1983a, b, Itazaki and Yoshida 1983, 1986a, 1b).

The reproduction of other free-living species remains poorly understood. The breeding of *Arabella iricolor* occurs throughout summer in Woods Hole region (USA), but mature specimens are rare, and regeneration occurs with ease, with annulation abnormalities observed with some frequency (Pettibone 1963). Paxton (2000) suggested that oenonids are dioecious, without sexual dimorphism. Rouse (2006) posited that all Eunicida have lecithotrophic development with various degrees of parental care from broadcast spawning to viviparity, whereas Zanol et al. (2021) stated that the information available suggests that most families of Eunicida have limited dispersal ability, although neither study cites specific information related to Oenonidae.

The reproduction of parasitic species is even less understood. According to Hilbig (1995) and Pettibone (1963), not all species appear to be parasitic for their entire life, but rather some have a parasitic phase, likely during the early stages of development, leaving the host's body to become sexually mature as free-living forms. This is because, in general, the morphology of adult parasites is not particularly different from free-living species with respect to body size, parapodia, chaetae, and jaws, which would be expected in exclusively parasitic species (Martin and Britayev 1998, Poulin 2001). However, the mode of infestation is still unknown (Pettibone 1957). Amaral (1977) and Steiner and Amaral (2009) reported asexual reproduction by scissiparity in *Labrorostratus prolificus* with specimens between 3 and 60 chaetigers found in the host, some with 8 chaetigers generating new stolons (Fig. 7.12.7.7F, G, P), meaning that one larva could have penetrated the host, and the other individuals would have been asexually generated. *Notocirrus spiniferus* (see Moore 1906) and *Arabella endonata* also occur in greater numbers within a host (Allen 1952, Pettibone 1963, Emerson 1974), but asexual reproduction has not been mentioned.

Some insights about the development of parasitic species within the host are therefore possible (Pettibone 1957, Amaral 1977, San Martín and Sardá 1986, Steiner and Amaral 2009). Basically, the chaetae, aciculae, jaws, and eyespots are absent in initial stages, whereas parapodial lobes are simple projections of the body wall (Fig. 7.12.7.7F, G). As growth occurs, aciculae appear (Fig. 7.12.7.7H, I), jaws are rudimentary (Fig. 7.12.7.7E), and chaetae begin to form but do not protrude (Fig. 7.12.7.7D). According to Fauchald (1970), parasites, while in the host, tend to have fewer chaetae. In small specimens of *Drilonereis caulleryi* and *Notocirrus spiniferus*, the maxillary carriers appear as a single elongated rod. In more advanced stages of these species, as well as in *Labrorostratus prolificus*, the chaetae are already evident, and the jaw apparatus is developed (Fig. 7.12.7.7F, Q). In *Haematocleptes*, however, the chaetae never protrude from the parapodium (Fig. 7.12.7.5E, L), as well as *Drilonereis benedicti*, that can reach 1200 chaetigers. Paxton (2000) suggested that *N. spiniferus* is parasitic only in the early stages of its life cycle and leaves its host before sexual maturity (Pettibone 1957), whereas *Haematocleptes terebellidis* might spend its entire life as a parasite (Wirén 1886). Poulin (2001) posited that the rate of segmentation per unit body length is greater in parasitic oenonids than in their free-living eunicid relatives.

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Because each segment can produce gametes later in life, the proliferation of segments in oenonids may be an adaptation to their parasitic lifestyle, since more segments would be filled with accumulating gametes (Poulin 2001).

Drilognathus may represent juvenile stages of other oenonid species (Day 1960, Orensanz 1974, Martin and Britayev 1998) because of its small size, rod-like maxillary apparatus, without maxillae (Fig. 7.12.7.2), as seen in the early stages of *Drilonereis caulleryi*. By contrast, the Caribbean species *Labrorostratus caribensis* has a jaw apparatus similar (Fig. 7.12.7.8G) to that of *Drilognathus capensis*. However, the size of the Caribbean specimen (10 mm for 153 segments) suggests that the absence of maxillae is not associated with juvenile stages (Hernández-Alcántara et al. 2015).

Economic uses

The species of *Halla* have been exploited as fishing bait. Large populations of *Halla okudai* are harvested and sold commercially as quite expensive fishing bait in Japan and Malaysia (Idris and Arshad 2013, Kobayashi et al. 2020). They are popular among recreational anglers in Malaysia, with harvesting carried out by digging using shovels and forks during low tide (Idris and Arshad, 2013). The Japanese population of the species is decreasing along with populations of its primary prey species, the manila clam *Ruditapes philippinarum* (Kobayashi et al. 2020). Therefore, it has been regarded as Near Threatened in Japan, based on the categories of the Japanese Red List (Kobayashi et al. 2020). Large populations of *Halla parthenopeia* are also exploited for fishing bait in Mediterranean Sea (Osman et al. 2010a, Baeta et al. 2019), with a thriving bait industry along the Suez Canal with potential applications in commercial aquaculture because of its high market price (Osman et al. 2010a). On the Maresme Coast (Catalonia, Spain), fishers are swapping their target species for worm bait dredges and sell them on the local market because of the decline in other populations used as bait, such as some species of clams and fishes (Baeta et al. 2019).

The biochemical composition of the purple pigment from *Halla parthenopeia* has been studied, both hallachrome and other biochemical compounds (D'Agostino et al. 1986, Prota et al. 1972, Cimino et al. 1986), in search of natural marine products. Ibrahim and Abd-Elnaby (2021) found that the crude extract of this species has a broad-spectrum antimicrobial effect, especially against some types of bacteria and fungi, and is clearly safe for aquaculture applications as an alternative to synthetic antibiotics to inhibit microbial fish and invertebrate pathogens.

Phylogeny and taxonomy

Phylogeny

The fossil records of the jaw apparatuses of Eunicida are very rich. They are represented by isolated fossil jaws elements, named scolecodonts by Croneis and Scott (1933), and they have been studied since Pander (1856). Scolecodonts are resistant to chemical degradation and usually well preserved, occurring worldwide (Lange 1950, Kielan-Jaworowska 1966, Regali 1981, Van Erve 1981, Colbath 1989b) in rocks in which most of the other fossils have been diagenetically destroyed (Szaniawski 1996). The Prionognatha includes the extant Oenonidae and the extinct Atraktoprionidae and Skalenoprionidae. The origin of this group goes back at least to the lower Ordovician (Kielan-Jaworowska 1966, Rouse and Pleijel 2001).

The phylogenetic position of Oenonidae within the Eunicida is still undefined. Fauchald and Rouse (1997) considered as evidence for monophyly the presence of maxillary carriers highly sclerotized and loosely attached to the posterior end of Mx I. The hypothesis proposed by Tzetlin (1980) showed that the prionognath apparatus of Oenonidae places this taxon at the most basal position in the recent Eunicida. On the other hand, Orensanz (1990) placed Oenonidae as the sister group of Lumbrineridae, sharing as synapomorphy the absence of the ventral cirrus. This author also pointed out that the latter family has an intermediary apparatus between sub-labidognath and prionognath. Finally, in the study by Orensanz (1990), the sister group of (Oenonidae + Lumbrineridae) was formed by [(Eunicidae + Onuphidae) + Hartmaniellidae]. The sister-group relationship between Oenonidae and Lumbrineridae was also corroborated by Rouse and Fauchald (1997), Rouse and Pleijel (2001), and Struck et al. (2015). The phylogeny proposed by Struck et al. (2006), based on the sequence data of four genes, showed Oenonidae as sister group of Onuphidae + Eunicidae and Lumbrineridae as sister group of this clade together with Dorvilleidae, in a more basal position within Eunicida. These same relationships were recovered by Zanol et al. (2014), using morphological and molecular data, but with Dorvilleidae positioned basally. Struck et al. (2006) also stated that Histriobdellidae and Hartmaniellidae might be related to Oenonidae, although Tzetlin et al. (2020) correlated the structure of the jaws of the former family to a ctenognath type.

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Based on jaw morphology, Paxton (2009) also confirmed that Oenonidae is more related to Eunicidae + Onuphidae, sharing the presence of a delicate third carrier, absent in Lumbrineridae, therefore, corroborating Struck et al. (2006). Zrzavý et al. (2009), based on a combined data set with morphological and molecular data, showed similar results, with Lumbrineridae positioned basally. However, they found Oenonidae as the sister group of Dorvilleidae and both as sister group of Eunicidae, in line with Tilic et al. (2016). On the other hand, Budaeva et al. (2016) recovered Oenonidae as the sister group of [(Eunicidae + Onuphidae) + Dorvilleidae], with Lumbrineridae at the basal position.

The phylogenetic relationships of the genera within Oenonidae are also poorly known. So far, the source of information is represented by the studies of Struck et al. (2006) and Kobayashi et al. (2020). Struck et al. (2006) revealed a close relationship of [(*Arabella* + *Drilonereis*) + *Oenone fulgida*], supported by nearly all analyses. Using mitochondrial 16S rRNA sequences, Kobayashi et al. (2020) found the same result, including *Halla* + *Oenone* in a monophyletic clade with *Tainokia* (the old "Lysaretidae"). Both results also confirmed the current composition of the Oenonidae previously proposed by Orensanz (1990).

Taxonomy

So far, no genus of Oenonidae has been taxonomically reviewed. From the twentieth century, some studies were dedicated to the family, but only with descriptions of new species (Pettibone 1957, Ramos 1976, Perkins 1979, Uebelacker 1984, Orensanz 1974, 1990, Hilbig 1995, Zanol and Ruta 2015). Therefore, all genera require further revision for solving some knowledge gaps in the family. Among them are the validity of *Drilognathus* and the revision of the species currently included in *Labrorostratus* (see more information below).

The genus *Pholadiphila* deserves more attention, as it has a morphological pattern that differs from the other genera of the family: the anterior and posterior region with indistinct segmentation; a single, short, and rod-like carrier; only three pairs of maxillae; indistinct pre- and postchaetal lobes; bundle of chaetae composed of robust and hirsute spines; and absence of capillary or limbate chaetae. The jaws structure of *Pholadiphila* resembles that of the Symmetrognatha group (sensu Paxton 2009), differing not only from Oenonidae but also from the other families of Eunicida.

Given the few external morphological characters present in Oenonidae, the jaws have great taxonomic value, both at generic and specific levels. The presence of maxillary polymorphism requires careful and extensive analysis. This is especially true for MI and MII, which can be size dependent, and, therefore, young specimens should be identified with caution. In *Drilonereis*, species-level variations should be noted with respect to MI inner dentition, which may be absent or present. In *Notocirrus*, there may also be variation in the MI morphology. The carriers can provide important characters in species differentiation, so analysis of the dorsal and ventral sides of maxillae is important. The external morphology is also important as it can bring informative variations. Accordingly, it is necessary to analyze the parapodial lobes throughout the body, as well as the shape and serration of capillary and limbate chaetae, the degree of bent of geniculate chaetae, and the shape of ventral modified chaetae and its blade length, as well as the acicular spine, in anterior, median, and posterior regions.

Oenonidae Kinberg, 1865

Type genus: *Oenone* Savigny in Lamarck, 1818

Diagnosis: Body very long and filiform, or shorter and tapered at the ends and broad in the midbody. Prostomium rounded to conical, usually with two pairs of eyes and rarely with one to three dorsal antennae. Two peristomial rings and well-defined chaetigers. Jaw apparatus composed of three to five pairs of maxillae distributed in two longitudinal rows, in addition to one pair of very long maxillary carriers, rarely short and/or fused together, and an unpaired carrier generally shorter, when present. Parapodia subbiramous, notopodium with dorsal cirrus usually very reduced, rarely absent, with fine internal aciculae. Neuropodium with short prechaetal lobe and elongated postchaetal lobe, both absent in *Pholadiphila*. Branchiae and ventral cirri absent. Capillary, limbate, and geniculate neuropodial chaetae in both upper and lower bundles. Some genera with modified ventral chaeta, stout spine or hooded hook in the lower bundle. Pygidium a simple ring, pad-like, or one to two pairs of pygidial cirri. Several parasitic species.

Arabella Grube, 1850 (Figs. 7.12.7.1A, C, F, I, K–M and 7.12.7.2A–M)

Aracoda Schmarda, 1861; *Maclovia* Grube, 1871.

Type species: *Nereis iricolor* Montagu, 1804

Diagnosis: Live individuals reddish or whitish to yellowish, internal red hues due to blood (Fig. 7.12.7.1A, C). Dark spots on dorsal side, or transverse band near middle of each chaetiger, kept on preserved worms, sometimes present (Fig. 7.12.7.1C). Preserved specimens beige, yellowish, light brown to brown, anterior and posterior region lighter or light yellowish-orange. Species can reach

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60 cm long, 5 mm wide, and about 500 chaetigers. Body generally cylindrical, dorsoventrally rounded, somewhat flattened, well-defined segments, about the same width along the whole body, tapered in the posterior region. Prostomium conical to spatulate, sometimes slightly depressed ventrally or with median groove dorsal or ventrally (Fig. 7.12.7.1A, B, F). One or two pairs of eyespots, rarely absent. Two peristomial rings clearly demarcated. Black to dark brown jaw apparatus. Five pairs of maxillae, MI and MII symmetrical (Fig. 7.12.7.2D) or asymmetrical (Fig. 7.12.7.2E) in shape and size. MI distally falcate, sometimes bidentate, and basally dentate or dentate along the entire inner margin, as well as MII to MIV; sometimes distal tooth fang shaped, MV with one sharp tooth. Attachment lamellae in MII to MV (Fig. 7.12.7.1M). Long and slender maxillary carriers, anterior end not fused and more inflated; furcula often present. Unpaired carrier larger, shorter, and less sclerotized. Paired mandibles well developed, connected medially, cutting plates with growth rings (Figs. 7.12.7.1L and 7.12.7.2C). Parapodia subbiramous (Fig. 7.12.7.2G, L), notopodium with dorsal cirrus reduced to a small papilla, 1–3 internal aciculae. Neuropodium usually with rounded or truncate prechaetal lobe and postchaetal longer and conical, digitiform, or triangular. Neuropodial aciculae present, sometimes mucronate. Limbate to geniculate chaetae (Fig. 7.12.7.2G, L, M) with or without finely or coarsely serrated margin, in upper and lower bundle. Ventralmost modified chaeta present in different degrees: from similar to others with long and strait limb (Fig. 7.12.7.2G, M) to stout with reduced and mucronate limb (Figs. 7.12.7.1I and 7.12.7.2I). Pygidium with two lateral lobes (Fig. 7.12.7.1K) or with a pair of digitiform dorsal and/or ventral cirri, placed laterally (Fig. 7.12.7.2K).

Composition: Currently, 33 species are valid of the 55 already described (Fauchald 1970).

Remarks: Some authors have adopted the inclusion of subgenera in defining species (Orensanz 1974, 1990, Zanol and Ruta 2015). *Arabella* (*Arabella*) have MI distally falcate and ventralmost chaetae similar to the others of the bundle; *Arabella (Cenothrix)* have MI distally falcate and ventralmost chaetae with reduced limb, tapering abruptly, mucronate, and generally stout; *Arabella* (*Notopsilus*) have MI dentate along entire inner margin and ventralmost chaetae as *Arabella* (*Cenothrix*). *Arabella iricolor* and *Arabella endonata* have been reported as parasites in the body cavity of *Diopatra ornata* (Hartman 1968, Emerson 1974).

Distribution: Worldwide. Intertidal to abyssal areas, in coarse to fine sand, different mix of sand, mud, clay, silt, muddy sand close to mangroves, coral rubble, sand under rocks and rocky crevices, oyster and mussel beds, rhizoids of *Zostera*, holdfasts of *Laminaria*, bryozoans, ascidians, and other colonial marine invertebrates, rocky shores, and coarse calcareous sand on coral.

Biborin Chamberlin, 1919a

Type species: *Biborin ecbola* Chamberlin, 1919a

Diagnosis: Live specimens greenish and preserved specimens greyish brown of a dull bluish green cast. Body strongly attenuated and pointed caudad, more moderately cephalad. Species can reach 92 mm long, 2.2 mm wide, without parapodia, and 277 chaetigers; body tapering in posterior direction. Prostomium longer than wide, longer than the two peristomial rings, conical, flattened dorsoventrally, eyespots absent. Two peristomial rings, second slightly longer. Maxillae absent, but with a thickening of tissue. Paired mandibles well developed, short and broad, not toothed, the edges meeting at an acute angle in front; shafts shorter behind the point of ligament than the blades in front of this point, rather slender, blunt behind. Parapodia subbiramous, notopodium with internal aciculae. Neuropodium with subcylindrical and conical postchaetal lobe. Aciculae not registered. Chaetae long, only limbates.

Composition: One species, *Biborin ecbola*.

Remarks: This genus is known only from its original description by Chamberlin (1919a), which did not include schematic drawings with morphological details.

Distribution: Pacific Ocean: USA (Laguna Beach, California), collected among *Phyllospadix* seagrass (Chamberlin 1919a, b).

Drilognathus Day, 1960 (Fig. 7.12.7.3A–M)

Type species: *Drilognathus capensis* Day, 1960

Diagnosis: Preserved specimens creamy white. Species can reach less than 1 mm long, 0.5 mm wide, and about 60 segments when complete. Body with distinct segmentation. Prostomium conical, without appendages, with or without one pair of weakly visible eyespots (Fig. 7.12.7.3A, B). Two peristomial rings clearly demarcated. Black jaws, maxillae absent. Carriers reduced to a cuticular ridge, no teeth or maxillary plates (Fig. 7.12.7.3E) or bifid anteriorly with a less sclerotized lateral portion (Fig. 7.12.7.3F, L). Paired mandibles well developed, connected medially (Fig. 7.12.7.3C, D). Parapodia subbiramous (Fig. 7.12.7.3G, H), notopodium reduced to a small protrusion, aciculae in *Drilognathus* sp. Neuropodium with short and rounded prechaetal and conical postchaetal lobes, well developed from the first chaetiger up to the middle of body, progressively reduced to a small lateral projection without lobes or chaetae, absent in last 10–15 chaetigers in *Drilognathus*

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capensis (Fig. 7.12.7.3I), or absent in the last 3 chaetigers in *Drilognathus* sp. Neuropodial aciculae present. All chaetae absent in *D. capensis*, one to two internal limbates in *Drilognathus* sp. Pygidium with one pair of ventrolateral cirri projecting outwards at right angles to the body (Fig. 7.12.7.3I) or bilobed with small and distal rounded papillae.

Composition: One species, *Drilognathus capensis*, parasite in the body cavity of *Onuphis holobranchiata* Marenzeller, 1879, and one undescribed species in the body cavity of *Onuphis setosa* (Kinberg 1865) (in Orensanz 1974), both known only from the original description.

Remarks: The cuticular ridge may represent the carriers, as stated by Orensanz (1974). There are doubts about the validity of this genus, with the possibility of being young stages of other species of the family (Day 1960, Orensanz 1974).

Distribution: *Drilognathus capensis* has been recorded in Lambert Bay, off Cape coast, South Africa, at 29 m deep, and *Drilognathus* sp. in off Punta del Este, Uruguay, at 112 m deep, in muddy sand.

Drilonereis Claparède, 1870 (Figs. 7.12.7.1B, D and 7.12.7.4A–Q)

Labidognathus Caullery, 1914.

Type species: *Lumbriconereis filum* Claparède, 1868

Diagnosis: Live specimens reddish, whitish to yellowish (Fig. 7.12.7.1B, D), internal red hues because of blood, anterior and posterior end yellowish to white. Preserved specimens with whitish anterior end or beige and rest of body yellowish to brownish, reddish, or brown to dark brown. Species can reach 365 mm long, 4 mm wide, and more than 300 chaetigers. *Drilonereis longa* can reach more than 70 cm and 1.5 mm wide. Body generally cylindrical, dorsoventrally rounded, somewhat flattened, aspect filiform, well-defined segments, about the same width along the whole body, tapered in posterior region. Prostomium conical to triangular (Fig. 7.12.7.4A–C), dorsoventrally flattened (Fig. 7.12.7.4D), middorsal longitudinal furrow or slit (Fig. 7.12.7.1D). Eyespots usually more evident in young specimens, absent in adults; when present, faded and covered by pigments of the epithelium. Two peristomial rings clearly demarcated, rarely first ring appear partially connected to prostomium. Black jaw apparatus. Four to five pairs of maxillae, symmetrical in shape and size (Fig. 7.12.7.4E, F). MI distally falcate, inner margin basally smooth (Fig. 7.12.7.4E) or dentate (Fig. 7.12.7.4F), teeth may be inconspicuous. MII dentate along the entire inner margin or smooth. MIII and MIV, sometimes MV, are small pieces with 1–3 teeth; species with five pairs of maxillae have two to three teeth in MIII. Attachment lamellae in MII to MIV or MV. Furcula rarely present. Long and slender maxillary carriers, anterior end inflated and fused (Uebelacker 1984; p. 42.19) or not fused (Fig. 7.12.7.4E), or narrower and fused (Fig. 7.12.7.4F), or sometimes slightly divergent before the fused region (Orensanz, 1974, p. 403). Unpaired carrier larger, shorter, and poorly sclerotized. Paired mandibles well developed in some species, connected medially, but frequently small, short shafts, subtriangular, drop shaped, or diamond shaped (Fig. 7.12.7.4N–Q); absent in parasitic species. Parapodia sometimes small, subbiramous (Fig. 7.12.7.4H, I), notopodium with dorsal cirrus reduced to a small papilla or a simple protrusion of epidermis, or absent; with internal aciculae. Neuropodium with short, truncate or rounded prechaetal lobe and a small, papilliform, digitiform, or conical postchaetal lobe. Neuropodial aciculae present, sometimes mucronate, projecting slightly from the parapodium. Limbate to geniculate chaetae (Fig. 7.12.7.4L, M) with or without serrated margin, in upper and lower bundle, and a stout ventral spine (Fig. 7.12.7.4H–K), sometimes absent in anterior region, parallel to limbate or geniculate chaetae. Pygidium composed of four globular lobes or four short cirri, two dorsal and two ventral, or a pair of button-shaped structures.

Composition: *Drilonereis* comprises about 33 valid species of the 39 already described, 5 of which are parasites: *Drilonereis parasiticus* (Caullery 1914); *Drilonereis* cf. *logani* Crossland, 1924 (in Zanol and Ruta 2015); *Drilonereis forcipes* Hartman, 1944; *Drilonereis benedicti* Pettibone, 1957; *Drilonereis caulleryi* Pettibone, 1957; in addition to two undescribed species in Orensanz (1974) and Pérès (1949). Parasites live in the body cavity of Onuphidae (2 species), Eunicidae (2), Terebellidae (1), and Serpulidae (1).

Remarks: Some species have been described as having one or two pairs of spots on the first peristomial ring (Fig. 7.12.7.4G), named as eyespots (Saint-Joseph 1888) or nuchal organs (Orensanz 1974). In parasitic species, mandibles are absent and MI is falcate with smooth inner margin.

Distribution: Worldwide. Rarely intertidal, more frequent in sublittoral, continental shelf to abyssal areas, 4.5 to 2000 m depth, in different types of soft bottoms: coarse to fine sand, mud, clay, silt, sand with gravel and shell fragments.

Haematocleptes Wirén, 1886 (Fig. 7.12.7.5A–L)

Type species: *Haematocleptes terebellidis* Wirén, 1886

Diagnosis: Preserved specimens can be whitish and transparent, or pale, white, and iridescent. Species can reach 25 mm long, 1 mm wide, and about 200 chaetigers.

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Body of *Haematocleptes leaenae* cylindrical, with a ventral longitudinal median groove, tapering in posterior direction. Prostomium conical, eyespots absent, flattened dorsoventrally in *Haematocleptes terebellidis* (Fig. 7.12.7.5A, B). Two peristomial rings. Black to dark brown jaw apparatus. Two pairs of maxillae, in *H. terebellidis*, MI rounded, bidentate, and MII a longitudinal and curved rod, both enclosed in a sclerotized area (Fig. 7.12.7.5C, D). *H. leaenae* with MI bidentate, basally inflated, and MII diamond shaped, free from carriers (Fig. 7.12.7.5F, G). Maxillary carriers fused along entire length, divergent at the anterior end in *H. leaenae*, very long and slender in *H. terebellidis*. Unpaired carrier elongated, shorter and narrower than the fused carrier. Paired mandibles not fused, *H. terebellidis* with two triangular and obtuse plates with outer faces without determined contours (Fig. 7.12.7.5I). Mandibles triangular shaped in *H. leaenae*, approached medially but not fused, larger than maxillae (Fig. 7.12.7.5H). Notopodium inconspicuous, no apparent dorsal cirrus, acicula in *H. terebellidis* (Fig. 7.12.7.5E, L). Neuropodium with rounded to conical prechaetal lobe and postchaetal lobe longer and conical, almost digitiform or rounded. Neuropodial aciculae present (Fig. 7.12.7.5K), yellow in *H. leaenae*. Parapodia not distinguishable at the end of body. Capillary or limbate chaetae (Fig. 7.12.7.5J) not projecting from the parapodia. Pygidium a simple ring.

Composition: Two parasitic species, *Haematocleptes terebellidis*, in the peri-intestinal blood sinus of *Terebellides stroemii* Sars, 1835, and in *Ampharete falcata* Eliason, 1955 (in Mackie and Garwood 1995); *Haematocleptes leaenae* is known only from the original description, in the body cavity of *Leaena minima* Hartman, 1965.

Distribution: Atlantic Ocean: Sweden (Gullmarfjord), Scotland (Clyde Estuary), St George's Channel, Irish Sea, Celtic Deep, Celtic Sea, USA (Northwest Atlantic). Continental shelf and slope depths, 95 to 130 m and 1102 m (Wirén 1886, Hartman and Fauchald 1971, Mackie and Garwood 1995, O'Reilly 2016).

Halla Costa, 1844 (Figs. 7.12.7.1E, G and 7.12.7.6A–I)

Cirrobranchia Ehlers, 1868.

Type species: *Nereis parthenopeia* Delle Chiaje, 1828

Diagnosis: Live individuals of *Halla okudai* are beige, orange, and reddish-brown to brown (Fig. 7.12.7.1E, G); *Halla parthenopeia is* orange with red dorsal cirrus (Costa 1844). Preserved specimens of *H. okudai* are light brown, sometimes purple due the secretion at the moment of fixation; *H. parthenopeia* is yellow to orange or dark brown, iridescent. Large-sized worms, live specimens of *H. okudai* can reach 1–2 m long, 90 cm when fixed, 13 mm wide, and more than 900 chaetigers. *H. parthenopeia* can reach 50 to 80 cm long and 700–800 chaetigers. Body with well-defined segments, somewhat larger at median region, both ends tapering. Prostomium conical, distally rounded, sometimes ventrally flattened (Fig. 7.12.7.6A, B, E). Three digitiform or slightly pointed and juxtaposed antennae, at the base of prostomium. Four pairs of eyespots. Two peristomial rings, the first with an incision mediodorsal where the antennae are positioned, in addition to a notch that may extend to half of the first or second chaetiger. Nuchal organs may be visible as two eversible pits in the anterior part of the incision. Black jaw apparatus. Five pairs of maxillae (Fig. 7.12.7.6C, I), MI and MII asymmetrical in shape and size, right MI shorter than left, right MII longer than left. MI dentate along entire inner margin, as well as MII to MIV; sometimes distal tooth fang shaped; MV with one sharp tooth. Attachment lamellae in MI to MV. Long and slender maxillary carriers, anterior end not fused and more inflated. Furcula not detected; unpaired carrier not registered. Paired mandibles well developed, connected medially, cutting plates with growth rings (Fig. 7.12.7.6D). Parapodia subbiramous (Fig. 7.12.7.6F), notopodium with digitiform dorsal cirrus, gradually increasing and somewhat flattened along the body; with internal aciculae. Neuropodium with rounded prechaetal lobe and postchaetal longer and conical or triangular, aciculae present. Capillary chaetae long and pointed in upper and lower bundle along the whole body, serrated margin (Fig. 7.12.7.6H). One or two uni- or bidentate subacicular hooded hook in chaetigers of median and posterior regions (Fig. 7.12.7.6G), sometimes not registered in adults and large specimens. Pygidium composed of four cirri.

Composition: Two species, *Halla parthenopeia* and *Halla okudai*.

Remarks: The presence of subacicular hooks in large specimens is controversial. Colbath (1989a) pointed out that the hooks are lost in adult stages because they have not been found by Ehlers (1864–1868) and Imajima and Hartman (1964). However, Idris and Arshad (2013) have reported in adults of *H. okudai* from Malaysia.

Distribution: *Halla parthenopeia* has been recorded in the Atlantic Ocean: Cádiz (Spain) (Fauvel 1923, Baeta et al. 2019) and Portugal (mapper.obis.org). Mediterranean: Spain, Italy, Egypt (Ibrahim and Abd-Elnaby 2021), Suez Canal (Osman et al. 2010a). *Halla okudai* has occurred in southern China (Saito et al. 2014), Japan (Kobayashi et al. 2020), Malaysia (Idris and Arshad 2013), Australia (Paxton 2009). The species were collected in sandy bottoms, in fine to coarse sediments from intertidal and shallow subtidal zones (Kobayashi et al. 2020).

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***Labrorostratus* Saint-Joseph, 1888** (Figs. 7.12.7.7A–Q and 7.12.7.8A–Q)

Type species: *Labrorostratus parasiticus* Saint-Joseph, 1888

Diagnosis: Preserved specimens may be light brown, bright orange-yellow, with brown spots dorsally at median region, prostomium colorless, pale yellow with minute grey spots, anterior and posterior end lighter. Species can reach 40 mm long, 1 mm wide, and about 350 chaetigers. Prostomium rounded to conical, sometimes slightly compressed dorsoventrally (Fig. 7.12.7.7A, B, Q). Two pairs of eyespots black or reddish, or absent. Two peristomial rings clearly demarcated. Maxillae composed of one or two pairs of small pieces (Fig. 7.12.7.8A–J), with margin dentate or not, or reduced to one pair of broad triangular plates; absent in *Labrorostratus caribensis*. Furcula absent. Maxillary carriers fused along its entire length, shafts divergent in the anterior end, sometimes broad, where maxillae are located, except in *Labrorostratus jonicus*, with unfused carriers. Unpaired carrier long and reported only to *Labrorostratus luteus*. Paired mandibles well developed, connected medially (Fig. 7.12.7.8L–Q). In *L. parasiticus, L. jonicus,* and *Labrorostratus* sp. structures as spines, transverse bars and protrusions are present medially. Parapodia uni- or subbiramous (Fig. 7.12.7.7C, D), notopodium with dorsal cirrus reduced to a knob-like structure, with internal aciculae. Neuropodium with rounded prechaetal lobe and conical or digitiform post chaetal lobe; up to three neuropodial aciculae. Parapodia gradually reducing from midbody to posterior end, with chaetigers indistinguishable. Limbate chaetae with smooth margin (Fig. 7.12.7.7J, L, M), up to six per parapodium. Presence of acicular spine in *L. jonicus* and ventral modified chaetae in *L. luteus* (Fig. 7.12.7.7K), *L. prolificus*, and *L. caribensis* (Fig. 7.12.7.7N). Pygidium rounded, with or without four cirri, two dorsal, and two ventral.

Composition: Six species and one undescribed in San Martin and Sardá (1986). All species are reported as parasites, but Tenerelli (1961) reported *L. jonicus* among algae, together with syllids. *Labrorostratus luteus* and *Labrorostratus parasiticus* have also been reported as free living in soft bottoms and among calcareous algae, respectively (Saint-Joseph 1888, Uebelacker 1984). Species of this genus are parasites in the body cavity of Syllidae (10 species), Nereididae (2), Eunicidae (1), and Trichobranchidae (1).

Remarks: The genus is composed of species that share similarities regarding the general shape of the body, parapodia, and mandibles. However, the morphological diversity of the jaws and the presence of ventral spine and modified ventral chaeta in some species convert this genus into a morphologically very diverse grouping, raising questions about the scope of the genus and the relationships between the species. In *L. parasiticus*, *L. jonicus*, *and Labrorostratus* sp. (San Martin and Sardá 1986), the characteristics of the mandibles differ from the pattern found in most Oenonidae species.

Distribution: Mediterranean Sea: English Channel, France, Italy, and Spain. Atlantic Ocean: Gulf of Mexico, Chinchorro Bank, Bahamas, Brazil. Pacific Ocean (Gulf of California), China. The hosts occur intertidally and subtidally to 69 m depth, in rocky shores and soft bottoms.

***Notocirrus* Schmarda, 1861** (Fig. 7.12.7.9A–O)

Type species: *Notocirrus chilensis* Schmarda, 1861

Diagnosis: Live specimens can be yellow or brown. Species can reach 25 cm long, 1 to 1.5 mm wide, and more than 220 chaetigers. Body cylindrical, sometimes dorsoventrally rounded, somewhat flattened, aspect filiform, well-defined segments, about the same width along the whole body, tapered in posterior region. Prostomium conical to triangular (Fig. 7.12.7.9A–C), sometimes slightly depressed ventrally or dorsoventrally. Two pairs of eyespots, sometimes absent. Two peristomial rings clearly demarcated. Black jaw apparatus. Four to five pairs of maxillae (Fig. 7.12.7.9E, M–O), MI and MII symmetrical or asymmetrical in shape and size. MI dentate along entire inner margin, as well as MII to MIV; sometimes distal tooth fang shaped. MV with one sharp tooth. Attachment lamellae in MII to MV. Long and slender maxillary carriers, anterior end not fused and more inflated; furcula often present. Unpaired carrier larger, shorter, and poorly sclerotized. Paired mandibles well developed, connected medially, cutting plates with growth rings (Fig. 7.12.7.9D, J). Parapodia subbiramous (Fig. 7.12.7.9F, K), notopodium with dorsal cirrus reduced to a small papilla or button-like, with internal aciculae. Neuropodium with rounded or truncate prechaetal lobe, longer and conical, digitiform, or triangular postchaetal lobe. Neuropodial aciculae present, sometimes mucronate, projecting slightly from the parapodium. Limbate to geniculate chaetae (Fig. 7.12.7.9F, K, L) with or without serrated margin, in upper and lower bundle, and one to three stout ventral spines, sometimes absent in anterior region, parallel to the capillary chaetae; morphology can vary along the body (Fig. 7.12.7.9G–I). Young specimens sometimes with spines absent. Pygidium of *Notocirrus scoticus* rounded and bilobed dorsally.

Composition: *Notocirrus* comprises 11 valid species of the 21 already described. *Notocirrus spiniferus* (Moore 1906),

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in Allen (1952), and *Notocirrus* sp., in Koch (1847) and Ehlers (1864–1868), are described as parasites in the body cavity and vascular body wall of *Diopatra cuprea* (Bosc, 1802) and *Marphysa sanguinea* (Montagu, 1813), respectively.

Distribution: Atlantic Ocean: USA, Gulf of Mexico, South America (Brazil to Southern Chile), North Sea, Irish Sea, English Channel. Mediterranean Sea: France, Italy, Greece, Turkey, Spanish Catalan Coast, South Africa (False Bay). Pacific Ocean: USA, Peru, Western Chile, Australia, Japan. Subtidal to continental shelf and slope depths, 0 to 400 m, in coarse to fine sand, different mix of sand, mud, clay, silt, and pebbles with or without fragments of shells.

***Oenone* Savigny in Lamarck, 1818** (Figs. 7.12.7.10A–C and 7.12.7.11A–H)

Aglaura Savigny in Lamarck, 1818; *Aglaurides* Ehlers, 1868.

Type species: *Aglaura fulgida* Savigny in Lamarck, 1818

Diagnosis: Live individuals yellow to orange, or reddish (Figs. 7.12.7.10A–C and 7.12.7.11D). Preserved specimens beige, yellow, brownish, or dark brown to purple. Species can reach more than 12 cm, 6 mm wide, and more than 190 chaetigers. Body cylindrical, well-defined segments, somewhat compressed dorsoventrally. Prostomium rounded (Figs. 7.12.7.10A–C and 7.12.7.11A, B, D), may be slightly flattened ventral- or dorsoventrally. Three digitiform, short, and juxtaposed antennae at the base of prostomium. Two pairs of dorsal eyespots; one pair at the ventroanterior end of the prostomium in *Oenone ventrioculata* (Fig. 7.12.7.11D). One inflated and relatively long peristomial ring that may have an incision mediodorsal where the antennae are located or it may be slightly covered by a fold of peristomium. Jaw apparatus strongly sclerotized, dark brown to black. Five pairs of maxillae (Fig. 7.12.7.11C), MI and MII asymmetrical in shape and size, right MI shorter than left, right MII longer than left. MI dentate along entire inner margin, as well as MII to MIV; distal tooth fang shaped, MV with one sharp tooth. Attachment lamellae in MI to MV. Long and slender maxillary carriers, anterior ends not fused and inflated; furcula often present. Unpaired carrier rarely registered. Paired mandibles well-developed, connected medially, cutting plates with growth rings (Fig. 7.12.7.11F). Parapodia subbiramous (Fig. 7.12.7.11E), notopodium with expanded, and foliaceous dorsal cirrus and internal aciculae. Neuropodium with rounded prechaetal lobe and longer and conical or triangular postchaetal lobe; aciculae present. Capillary chaetae long and pointed in upper and lower bundle along the whole body (Fig. 7.12.7.11H). Subacicular bidentate hooded hook, sometimes mucronate, in chaetigers of median and posterior regions (Fig. 7.12.7.11G).

Composition: Three species, *Oenone fulgida*, *Oenone diphyllidia* (Schmarda 1861), and *Oenone ventrioculata*.

Remarks: The only report of the presence of the unpaired carrier was for *O. fulgida*, by Hartman (1944), with symmetrical jaws and unpaired support as long as the paired ones.

Distribution: Worldwide. Intertidal to continental shelf, in coral rubble, undernet stones and coral (Zanol and Ruta 2015), endofaunal in *Schizoporella unicornis* (see Morgado and Amaral 1981), and commensal in the sponge *Speciospongia vespera* (see Pearse 1932).

***Oligognathus* Spengel, 1882** (Fig. 7.12.7.12A–O)

Type species: *Oligognathus bonelliae* Spengel, 1882

Diagnosis: Live individuals orange or transparent. Species can reach 100 mm long, 1 mm wide, and more than 200 chaetigers. Little iridescent and extremely delicate cuticle in *Oligognathus bonelliae*. Prostomium conical to rounded (Fig. 7.12.7.12A, B), two pairs of eyespots, or absent. Two peristomial rings clearly demarcated. First ring may cover considerably portion of prostomium, including nuchal organs and eyespots (Fig. 7.12.7.12C). Two or three pairs of small maxillae (Fig. 7.12.7.11D–G), similar in shape and size; transparent, thin, and difficult to visualize in *O. bonelliae*. Very long and slender maxillary carriers, fused along entire length, more sclerotized in both lateral, medially lighter. Unpaired carrier is a pigmented flat sclerotized band, restricted to the anterior region, not detected in *Oligognathus parasiticus*. Paired mandibles are two shafts connected by a transverse anterior ridge weakly sclerotized, horseshoe shaped (Fig. 7.12.7.12J, K). Parapodia subbiramous (Fig. 7.12.7.12H, I), dorsal cirrus not apparent externally; notopodial aciculae present. Neuropodium with short and rounded prechaetal lobe and conical to triangular postchaetal lobe. Neuropodial aciculae present (Fig. 7.12.7.12M, N). Chaetae are capillary and limbate (Fig. 7.12.7.12N, O), not projecting from the parapodium in *O. bonelliae*. Pygidium not described.

Composition: Two parasitic species, *Oligognathus bonelliae*, in the body cavity of *Bonellia viridis* (Echiura), and *Oligognathus parasiticus* Cerruti, 1909, known only from the original description, in the body cavity of *Microspio mecznikowiana* (Claparède, 1869) (as *Spio mecznikowianus* Claparède, 1869) (Spionidae).

Remarks: Spengel (1882) stated that the jaws are weakly sclerotized in *O. bonelliae*, so that it is not possible to clearly distinguish shape and number of maxillae.

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Distribution: Mediterranean Sea: Naples Gulf (Tyrrenian Sea), Corfu Channel (Jonic Sea), and Gulf of Geras (Aegean Sea) (Spengel 1882, Zenetos and Bogdanos 1987, Bogdanos and Satsmadjis 1983). Both species from intertidal areas; *Bonellia viridis* was collected among calcareous algae.

***Pholadiphila* Dean, 1992** (Fig. 7.12.7.13A–G)

Type species: *Pholadiphila turnerae* Dean, 1992

Diagnosis: Without pigmentation pattern registered in life; preserved specimens light yellow. Specimens can reach about 19 mm long, 0.27 mm wide, excluding parapodia, and about 260 chaetigers. Body slender, elongated, tapered anteriorly and posteriorly, flattened ventrally, weakly arched dorsally; segmentation indistinct in anterior and posterior region. Prostomium conical (Fig. 7.12.7.13A), without appendages, eyespots lacking, fused with the peristomium. Indistinct peristomial ring(s). Jaws translucent amber structure. Three pairs of symmetrical maxillae (Fig. 7.12.7.13D–F), MI forceps-like, distally bidentate, without teeth along inner margin. MII flattened, teeth along inner margin, MIII small, distally bidentate, apparently without attachment lamellae. Maxillary carrier is one single rod, short, slender, tripartite anteriorly (Fig. 7.12.7.13D). Unpaired carrier not detected. Paired mandibles partially fused medially, large plates shield-like, without apparent growth rings (Fig. 7.12.7.13C). Parapodium uniramous (Fig. 7.12.7.13G), conical, without distinction of pre- and post chaetal lobes, dorsal cirrus absent. Last seven to nine chaetigers without parapodia. Chaetae all simple, three types, upper bundle with stout emergent spines (Fig. 7.12.7.13G, s) and capillary chaetae (Fig. 7.12.7.13G, c), subacicular stout emergent spines, replaced by acuminate chaetae (Fig. 7.12.7.13G, ac); all chaetae hirsute at the distal end. Notopodial acicula absent, one neuropodial present. Pygidium formed by its terminal anus and an undifferentiated cylindrical region before it (Fig. 7.12.7.13B).

Composition: One ectoparasitic species, *Pholadiphila turnerae*, known only from its original description, inside the mantle cavity (infrabranchial chamber) of wood-boring bivalves of the family Xylophagaidae, *Xyloredo ingolfia* and another species of the superfamily Pholadoidea (Dean 1992).

Remarks: The presence of one or two peristomial rings is not clear and the presence of a vestigial notopodium was not mentioned. A tripartite anterior end of the carrier strongly suggests the fusion of the three carriers, so that the ventral portion (Fig. 7.12.7.13D, ve) may represent a vestigial third carrier (Dean 1992).

Distribution: North Atlantic Ocean (USA, near New Jersey-Virginia states), wooden panels, 3602 m deep.

***Tainokia* Knox & Green, 1972** (Fig. 7.12.7.14A–J)

Type species: *Tainokia iridescens* Knox & Green, 1972

Diagnosis: Live specimens of *T. iridescens* with anterior third of body luminescent, dark purple green or dull blue or red brown; rest of body brown with green iridescence, dorsal cirri red and chaetae colorless. Preserved specimens, in alcohol, with colors duller and iridescence not so evident. *Tainokia logachevae* is whitish in ethanol, with iridescent cuticle. Specimens of *T. iridescens* can reach 440 mm long, 5 mm wide, including parapodia, and about 550 chaetigers. The only specimen of *T. logachevae* is incomplete, 34 mm long, about 2 mm wide, and 75 chaetigers. Body with distinct segmentation. Prostomium conical (Fig. 7.12.7.14A), with one short central antenna at the base of prostomium. Two pairs of eyespots. Two peristomial rings, the first with an incision mediodorsal where the antenna is positioned. Black jaw apparatus. Five pairs of maxillae, MI and MII asymmetrical in shape and size, MI falcate and basally dentate (Fig. 7.12.7.14B) or dentate along entire inner margin (Fig. 7.12.7.14C, D). MII to MIV dentate along entire inner margin, sometimes distal tooth fang shaped; MV with one sharp tooth. When asymmetrical, right MI shorter than left and right MII longer than left. Attachment lamellae in MII to MV; in *T. logachevae*, present in MI. Long and slender paired maxillary carrier with anterior end not fused and more inflated; furcula present in *T. iridescens*. Unpaired carrier larger, shorter, and less sclerotized in *T. iridescens*; in *T. logachevae* not detected. Paired mandibles well developed, connected medially (Fig. 7.12.7.14F, G). Parapodia subbiramous (Fig. 7.12.7.14E), notopodium with cirriform to digitiform dorsal cirrus and internal aciculae; may be absent near pygidial region. Neuropodium with rounded to conical prechaetal lobe and long and conical postchaetal lobe. Neuropodial aciculae present, sometimes mucronate, projecting slightly from the parapodium. Chaetae are long and pointed capillary limbate (Fig. 7.12.7.14I, J) in upper and lower bundle along the whole body. Presence of ventral modified chaetae in *T. iridescens*, not confirmed in *T. logachevae*. Subacicular bidentate hooded hook in chaetigers of median and posterior regions in *T. logachevae* (Fig. 7.12.7.14H). Pygidium of *T. iridescens* formed by four globular lobes.

Composition: Two species, *Tainokia iridescens* and *Tainokia logachevae*.

Remarks: *Tainokia logachevae* was described based on a single specimen, so that the absence of the unpaired carrier must be confirmed. Ravara and Cunha (2017) considered that *T. logachevae* may represent a young stage because of the presence of the subacicular hook, a

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size-dependent morphological character absent in adults, according to Colbath (1989a) for the genus *Halla*. In addition, the MI with dentate inner margin could also indicate a young stage, as described for some *Arabella* species Colbath (1989b).

Distribution: *Tainokia iridescens* is known from lower eulittoral zone, in association with *Scoletoma brevicirra* (Schmarda, 1861) and *Scoloplos* sp., in gray, slightly sulphurous sand, in Armers Beach, Kaikoura Peninsula, New Zealand. *Tainokia logachevae* was retrieved from a dredge sample across the crater of Mercator mud volcano at 375–397 m, in Gulf of Cadiz, NE Atlantic Ocean.

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7.13 Phyllodocida

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7.13.1 Aphroditiformia

Introduction

Collectively referred to as scale worms, Aphroditiformia includes six traditionally recognized families: Acoetidae Kinberg, 1856; Aphroditidae Malmgren, 1867; Eulepethidae Chamberlin, 1919; Pholoidae Kinberg, 1958; Polynoidae Kinberg, 1856; and Sigalionidae Malmgren, 1867. The status of some lineages is, however, currently changing. In a recent molecular study, Norlinder et al. (2012) erected the family Iphionidae Kinberg, 1856 to replace Iphioninae, once a subfamily positioned in Polynoidae. Gonzalez et al. (2018) showed that the family Pholoidae should also be considered a subfamily in Sigalionidae. In this handbook, however, the Iphionidae will be treated in the chapter on Polynoidae.

Aphroditiformia belongs to the order Phyllodocida (Rouse and Pleijel 2001) and are characterized by the presence of elytra on some segments that may cover parts of the dorsum, and usually alternate with dorsal cirri on non-elytrigerous segments. The developmental origin of these elytra is still widely debated; they could correspond to either a greatly modified dorsal cirrus that forms a scale or could correspond to the development of dorsal tubercles (Rouse and Pleijel 2001). There are, however, some exceptions to this iconic character. Species formerly described as belonging to the family "Pisionidae" have been shown to have secondarily lost their elytra, and are now considered part of Sigalionidae (Gonzalez et al. 2017, Norlinder et al. 2012). Similarly, *Metaxypsamma uebelackerae* Wolf, 1986 (Sigalionidae) are also scaleless. Finally, the species *Palmyra aurifera* Savigny in Lamarck, 1818 is included in Aphroditidae (Wiklund et al. 2005, Norlinder et al. 2012), whereas other species of the genus are included in the family Chrysopetalidae.

Together, scale worm families comprise 237 recognized genera and exact number 1385 species (Tab. 7.13.1.1). The most speciose family is Polynoidae, with 943 species, followed by Sigalionidae with 252 species, and Aphroditidae with 108 species. Aphroditiforms have a worldwide distribution, from intertidal to abyssal depths, and with numerous habitat specializations. Adult sizes in Aphroditiformia range from about a millimeter for some Sigalionidae to about 2 m long for some of the long-bodied Acoetidae. Within Polynoidae, size ranges from a few millimeters for a large number of species to about 30 cm long and 12 cm wide in the Antarctic species *Eulagisca gigantea* Monro, 1939.

Tab. 7.13.1.1: Number of genera and species for the five families of Aphroditiformia. Numbers drawn from World Register of Marine Species (WoRMS Editorial Board 2017)

Family	Number of genera	Number of species
Acoetidae	8	58
Aphroditidae	13	108
Eulepethidae	6	24
Polynoidae	176	943
Sigalionidae	32	252
Total	237	1385

In the past, Aphroditiformia were the focus of a large treatise written by Darboux (1900), which still offers a wealth of information on this group. Since that treatise, numerous studies have focused on taxonomy, morphology, biology, development, and evolution of this annelid group. In this chapter, we aim to give an overview of these characters for Aphroditiformia in general. Families will then be the focus of dedicated chapters.

Morphology

Prostomium and peristomial appendages

The structure of the prostomium is a key character in the distinction between the different families of Aphroditiformia (Fig. 7.13.1.1). This region is usually covered by elytra and the associated appendages protrude anteriorly. The basic structure is the same for all families: the prostomium is surrounded by the first segment, which may be achaetous, and usually bears two pairs of tentacular cirri (a ventral pair and a dorsal pair). Although morphologically associated with the first segment, the pair of large palps is of prostomial origin. The number of antennae varies between zero and three, including a median and two lateral. The prostomium can be either deeply bilobed as in most Polynoidae or Acoetidae or more commonly form a single lobe. Some groups, however, differ from the typical anterior design. In the Pholoinae, the prostomium is typically rounded and fused to the first segment. In the genera formerly associated with the family "Pisionidae" (now included in Sigalionidae, see Gonzalez et al. 2017),

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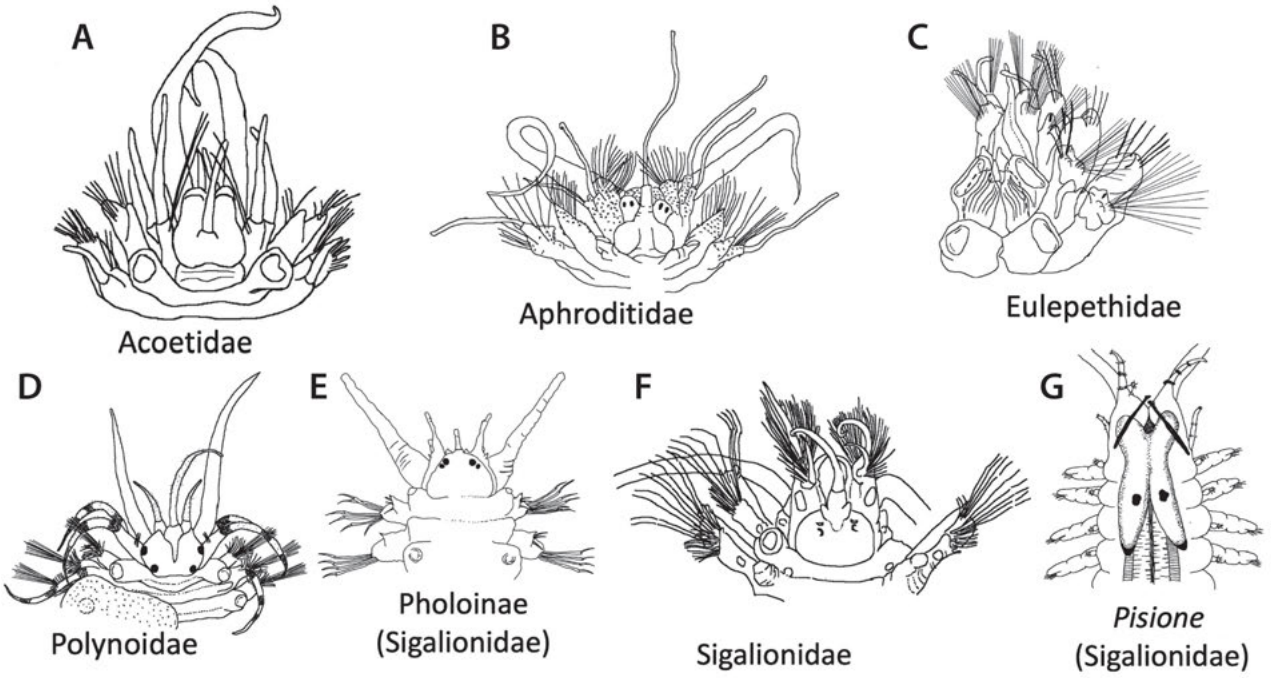


Fig. 7.13.1.1: Dorsal view of the anterior parts of different Aphroditiformia showing the prostomium. A, *Panthalis oerstedi* Kinberg, 1856 (Acoetidae). B, *Laetmonice hystrix* (Savigny & Lamarck, 1818) (Aphroditidae). C, *Grubeulepis augeneri* Pettibone, 1969 (Eulepethidae). D, *Harmothoe extenuata* (Grube, 1840) (Polynoidae). E, *Laubierpholoe swedwarki* (Laubier, 1975) (Sigalionidae, Pholoinae). F, *Sthenelais brachiata* Imajima, 2003 (Sigalionidae). G, *Pisione remota* (Southern, 1914) (Sigalionidae). Redrawn after Barnich and Fiege (2003) (A, C, D), Laubier (1975) (E), Imajima (2003) (F), and Akesson (1961) (G).

the prostomium is reduced and the first segment modified. Eyes are present and sessile in most families, on small mounds as in some Aphroditidae, or directed anteriorly on a pair of large structures called ommatophores as in some Acoetidae. The mouth opens ventrally and a facial tubercle may be present.

Studies on brain structures in the aphroditid *Aphrodita aculeata* Linnaeus, 1758; the polynoids *Lepidonotus clava* (Montagu, 1808) and *Harmothoe areolata* (Grube, 1860); and the sigalionids *Neoleanira tetragona* (Örsted, 1845) and *Sthenelais* cf. *limicola* showed that in accordance their active errant lifestyle, aphroditiforms have complex brain structures, morphologically reminiscent to that of insects, with paired mushroom body neuropils, unpaired midline neuropils, and olfactory glomeruli (Heuer and Loesel 2009, Heuer et al. 2010).

Elytral pattern

The presence of elytra (= scales) is a defining character of Aphroditiformia. These elytra vary in size along the body and may cover the dorsum completely or leave most of it exposed, as is the case in some symbiotic species (e.g., genera *Arctonoe*, *Branchipolynoe*, and *Lepidasthenia*). The anterior elytral pattern is common to all families until segment 19. Short-bodied species such as some members of the polynoid subfamilies Macellicephalinae and Branchinotogluminae deviate from this pattern. In particular, the posteriormost elytra may be missing in some males of the polynoid genus *Branchinotogluma* (Fig. 7.13.1.2). Segment 2, bears the first pair of elytra. Segment 3 bears a pair of dorsal cirri and the two following segments (4 and 5) each bear a pair of elytra. The following segments alternate between having cirri (even-numbered segments) and elytra (odd-numbered segments). In Eulepethidae, dorsal cirri are present only on segments 3 and 6, with branchiae starting on segment 8 onwards, whereas in Pholoinae, there are no dorsal cirri. Sigalionidae exhibit the most variability in the positioning of the dorsal cirri, either on all segments (e.g., *Pisione* sp.), only on segment 3 (e.g., *Pelogenia* sp.), or lacking dorsal cirri completely (most genera).

Beyond segment 19, the pattern varies throughout Aphroditiformia. In Aphroditidae, the segments alternate between elytra and cirri until the end of the body. In the polynoid subfamily Branchinotogluminae, the two last segments (20 and 21) both bear a pair of cirri, and the remaining members of the family with more than 19 segments have alternating cirri and elytra until segment 23.

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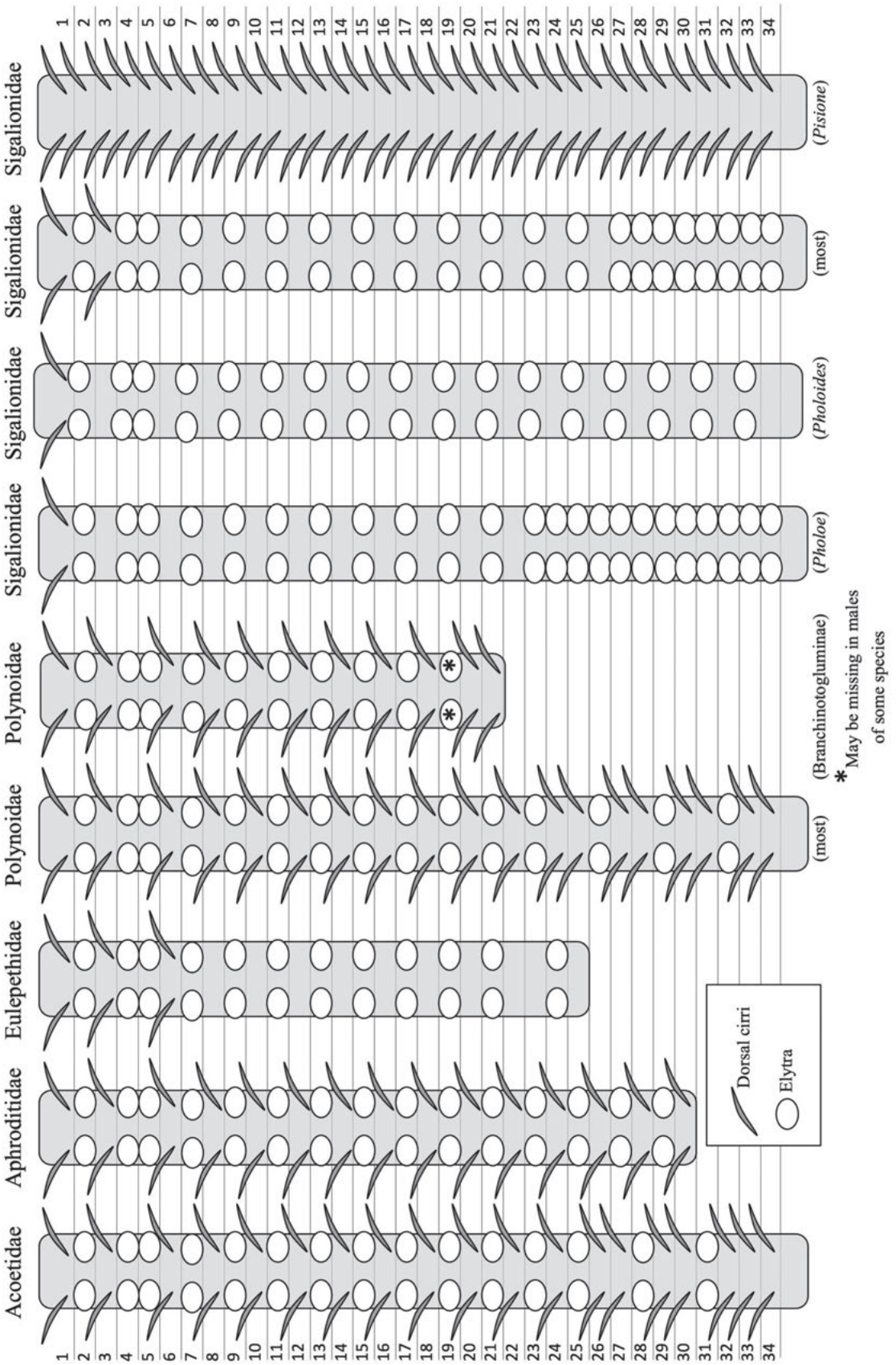


Fig. 7.13.1.2: Elytral patterns and position of dorsal cirri in Aphroditiformia for the first 34 segments.

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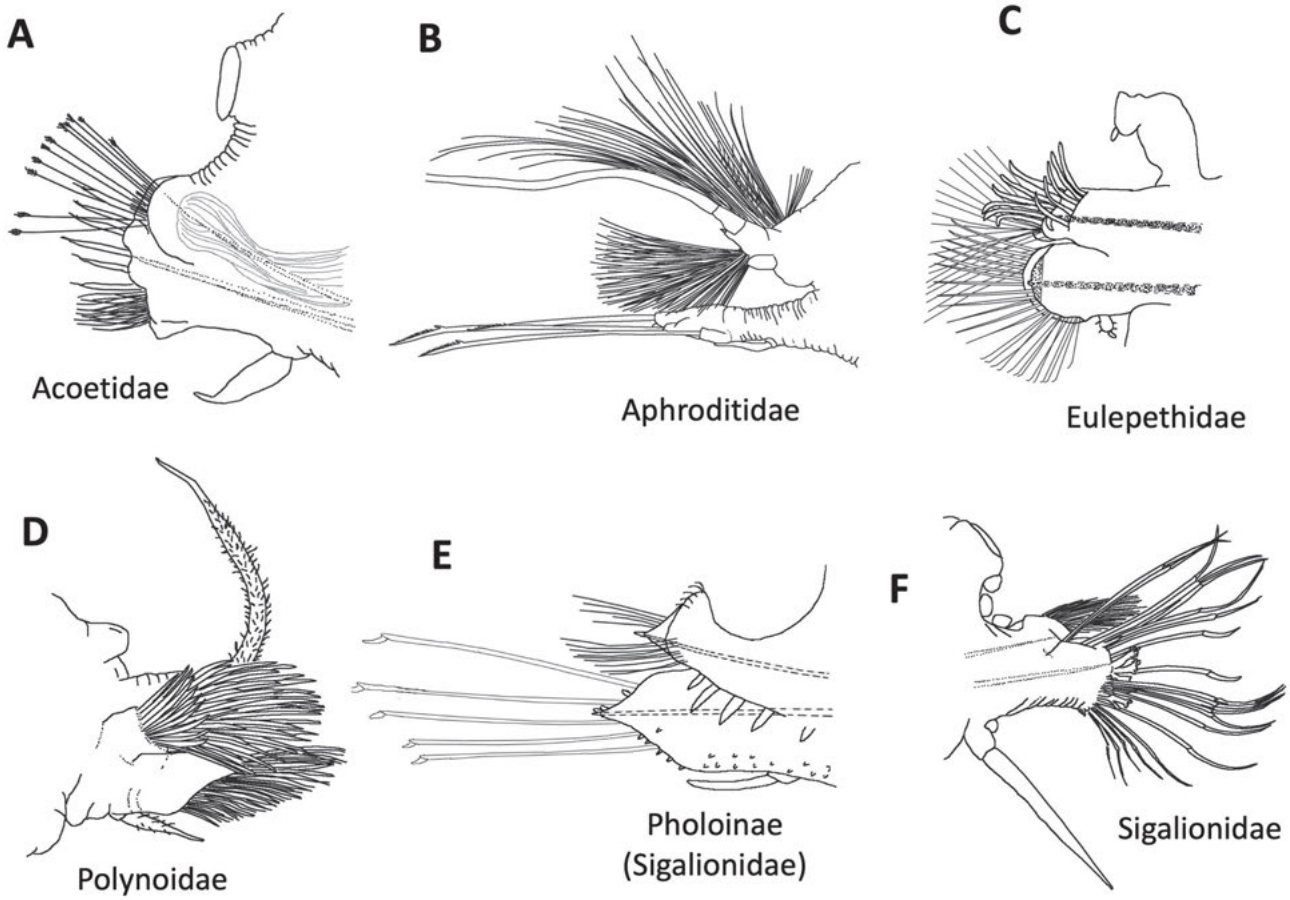


Fig. 7.13.1.3: Parapodial morphology in Aphroditiformia. A, *Acoetes jogasimae* (Izuka, 1912) (Acoetidae). B, *Laetmonice producta* Grube, 1877 (Aphroditidae). C, *Grubeulepis augeneri* Pettibone, 1969 (Eulepethidae). D, *Harmothoe imbricata* (Linnaeus, 1767) (Polynoidae). E, *Pholoe longa* (O.F. Müller, 1776) (Sigalionidae Pholoinae). F, *Sthenelais brachiata* Imajima, 2003 (Sigalionidae). Redrawn after Barnich and Fiege (2003) (C), Imajima (1997a) (A, D), Imajima (1997b) (B, F), and Pettibone (1992) (E).

Then the segments alternate between two with cirri, one with elytra, and so on until the last segment. Some polynoid genera lack elytra entirely on their posterior region (e.g., *Polynoe scolopendrina* Savigny, 1822), bearing only dorsal cirri. Sigalionidae have alternating elytra until segment 26, beyond which all segments bear elytra. In the genus *Pholoe* (Pholoinae), all segments beyond 23 bear elytra. In Acoetidae, segments having elytra or cirri alternate until segment 25, followed by two segments with cirri, one with elytra, two with cirri, one with elytra, and three segments with cirri.

In all genera forming the sigalionid subfamily Pisioninae, as well as in *Metaxypsamma uebelackerae* (Sigalionidae), and in *Palmyra aurifera* (Aphroditidae), elytra have been secondarily lost. In the latter, segments with palaeal fans and dorsal cirri alternate, following the typical pattern for Aphroditidae. Dorsal cirri are reduced but present on all segments in species found within the Pisioninae.

In addition to their position on the body, the overall shape of the elytra and their surface and border ornamentation are important taxonomic characters in species identification, but not at higher taxonomic levels.

Parapodia and chaetae

Parapodia are most often biramous, but the notopodium can be reduced or absent in some genera (Fig. 7.13.1.3). The segments can either be elytrigerous (bearing a pair of elytra) or cirrigerous (bearing a pair of dorsal cirri). Instances of parapodia bearing both a dorsal cirrus and an elytron have been reported (see Darboux 1900) but probably correspond to developmental anomalies. The elytrigerous parapodia bear a pair of thick elytrophores on their dorsal side, directed dorsally, and on which the

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elytra are attached, whereas those cirrigerous parapodia bear cirriphores that are directed laterally. Ventral cirri are present on all parapodia, usually digitiform. The supporting notoacicula is usually clearly visible, stout, pointed, and sometimes protruding in most families. In Eulepethidae, the neuroacicula is T-shaped and never protrudes. Notochaetae are all simple, with a great diversity of shapes, thickness, and number. In the family Sigalionidae, most or all neurochaetae are compound, either in the form of spinigers (long, apically pointed terminal article) or falcigers (short, apically blunt terminal article).

Digestive system

The digestive system is linear, with the mouth opening followed by a muscular proboscis (pharynx) connected to an intestine that contains paired, segmental lateral caeca (Fig. 7.13.1.4C). The latter extend into the parapodia, showing ramification and exhibiting physiological differentiation (Darboux 1900, Fauvel 1959, Dales and Pell 1971). Studies have shown that the pharynx, intestinal wall, and the caeca contain digestive enzymes and exhibit absorptive characteristics (Welsch and Storch 1970).

Pharynx and jaws

In most aphroditiforms, when extended, the pharynx opening is usually surrounded by papillae and is armed with two pairs of beak-like jaws (Fig. 7.13.1.4A). In Aphroditidae, some genera (e.g., *Aphrodita* and *Laetmonice*) lack jaws (Day 1962, Hourdez, personal observation), whereas others, including those of Eulepethidae, are reported to be plate-like (Pettibone 1986). Beak-like jaws are also absent in the polynoid *Vampiropolynoe embleyi* Marcus & Hourdez, 2002, in which only plates remain (Marcus and Hourdez 2002).

In some members of the families Acoetidae, Polynoidae, and Sigalionidae, structures interpreted as venom glands have been observed at the base of the jaws (Wolf 1986). Contrary to the best-known example of piercing jaws in annelids (Glyceridae), the jaws studied by Wolf (1986) possess a canal but no opening was present at the tip. In the families devoid of piercing jaws (Eulepethidae and Aphroditidae), Wolf (1986) did not observe any structure that is reminiscent of venom glands. Since then, no further studies have been carried out on the venom of aphroditiforms. In their review on venomics, von Reumont et al. (2014a) mentioned ongoing research on two species, a Polynoidae [*Harmothoe imbricata* (Linnaeus, 1767)] and a Sigalionidae [*Sthenelais boa* (Johnston, 1833)], in which preliminary data show that scale worms seem to possess a diverse set of putative toxin homologs, similar to what was observed in the well-studied *Glycera* (Glyceridae) (von Reumont et al. 2014b).

Biology and ecology

Feeding

The great majority of Aphroditiformia are predators, feeding on other annelids, small crustaceans, and mollusks (Fauchald and Jumars 1979, Jumars et al. 2015). Most are motile predators, but those that are commensal, or live inside tubes (i.e., Acoetidae and some Eulepethidae and Sigalionidae), are mostly sit-and-wait predators.

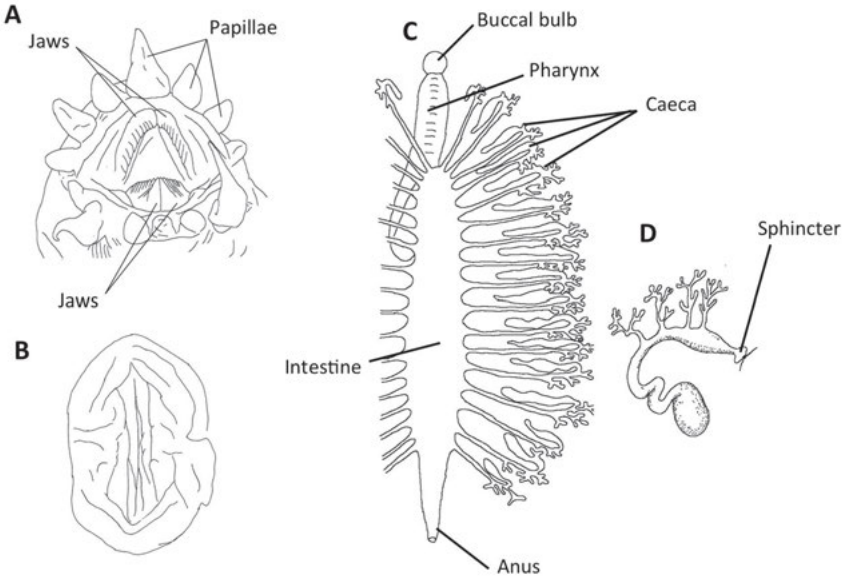


Fig. 7.13.1.4: Pharynx and digestive system. A, Pharynx opening of the polynoid *Lepidonotopodium piscesae* Pettibone, 1988. B, Pharynx opening of the aphroditid *Laetmonice producta* Grube, 1877. C, Digestive system of the aphroditid *Aphrodita aculeata* Linnaeus, 1758 (redrawn after Brusca and Brusca 1990). D, Detail of a cecum from *A. aculeata* (redrawn after Darboux 1900).

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Respiratory exchange and respiratory pigment

Although Aphroditiformia have a small, closed vascular system, it contains no circulating respiratory pigment. Scale worms typically lack branchiae; however, some groups do possess these structures (i.e., Eulepethidae, Polynoidae, and Sigalionidae). In Eulepethidae, branchiae start on segment 8 and continue onwards, whereas in some hydrothermal vent Polynoidae [subfamilies Branchipolynoinae, Branchiplicatinae, Branchinotogluminae, and the branchiate *Thermopolynoe* (Lepidonotopodinae)] branchiae are present in addition to dorsal cirri and elytra, and are considered as an adaptation to the chronic hypoxia they experience (Hourdez and Lallier 2007). In scale worms, oxygen diffuses through the body wall, and it has been shown that in shallow-water Polynoidae, water is renewed along the surface of the body by cilia and not the oscillating motion of the elytra (Lwebuga-Mukasa 1970). The elytra form a roof under which water flow is directional.

Aphroditiformia were previously well known for lacking circulating respiratory pigments (Weber 1978); however, a globin is present and is located within the nerve cells (neuroglobin). Its function is unclear, but it gives the nerve cord and prostomium a typical red color. Subsequently, the discovery of deep-sea hydrothermal vent polynoid species has changed this view. Most vent species are indeed red-colored and contain large amounts of hemoglobin (i.e., circulating globin) in their coelomic fluid (Hourdez et al. 1999a, b, unpublished data).

Reproduction and development

Sexes are separate in Aphroditiformia (Wilson 1991). Gametes develop in the epithelium that lines the coelomic cavity and nearly mature gametes are released into the coelomic cavity where their maturation progresses (Daly 1974). Oocytes contained in the coelomic cavity usually cannot be directly fertilized, and studies suggest that an endocrine factor may be necessary for oocytes to finish maturation and be fertilizable, in a way similar to that of *Arenicola marina* (Linnaeus, 1758) (Howie 1961, Bentley and Pacey 1992). In the polynoid *Lepidonotus sublevis* Verrill, 1873, however, the oocytes are fertilizable after a brief incubation in seawater (Simon 1965). Copulation takes place in members of the sigalionid subfamily Pisioninae (details in corresponding chapter). The presence of spermathecae in the polynoid genus *Branchipolynoe* suggests copulation also occurs in this lineage (Jollivet et al. 2000).

One of the most detailed studies of larval development in Aphroditiformia is that of Pernet (2000), who worked on the three closely related symbiotic polynoids *Arctonoe vittata* (Grube, 1855), *Arctonoe pulchra* (Johnson, 1897), and *Arctonoe fragilis* (Baird, 1863). The development is essentially the same for all Aphroditiformia that have been studied to date (Bhaud and Cazaux 1987). These species produce planktotrophic larvae with a prototroch but no metatroch or food groove cilia. Feeding starts after the development of episphere cilia (Fig. 7.13.1.5). After 6–12 weeks, metamorphosis occurs with the development of anterior appendages (palps, antennae, and

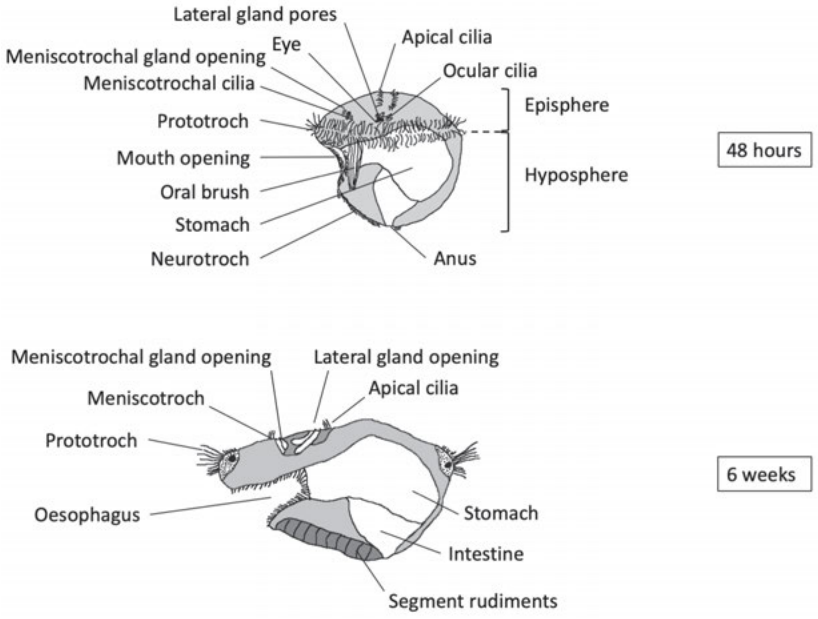


Fig. 7.13.1.5: Early development of *Arctonoe* spp. after 48 hours and 6 weeks (schematized after Pernet 2000).

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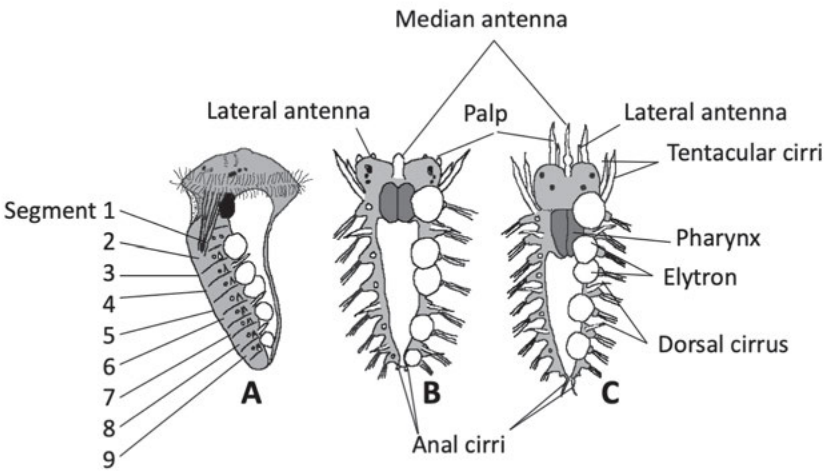


Fig. 7.13.1.6: Metamorphosis of *Arctonoe* spp. (schematized after Pernet 2000). A, Early metamorphosis with a now elongated hyposphere and appearance of dorsal cirri and elytra. Lateral view. B, appearance of adult head appendages. Prototroch and oral brush have disappeared. Dorsal view. C, Juvenile. Dorsal view.

Tab. 7.13.1.2: General morphology and age of fossil species of Aphroditiformia known to date.

Species	Morphology	Age (My)	Reference
Dryptoscolex matthiesae	Elongated and flexible	300	Fitzhugh et al. (1997)
Fatuoscolex gemmatus	Oval	300	Fitzhugh et al. (1997)
Hystriciola delicatula	Oval	300	Fitzhugh et al. (1997)
Palaeoaphrodite adeliae	Oval	165	Alessandrello et al. (2004)
Palaeoaphrodite anaboranoensis	Elongated and flexible	250	Alessandrello (1990)
Palaeoaphrodite briggsiana	Oval	165	Alessandrello et al. (2004)
Palaeoaphrodite gallica	Elongated and flexible	165	Alessandrello et al. (2004)
Palaeoaphrodite libanotica	Oval	94–100	Bracchi and Alessandrello (2005)
Palaeoaphrodite raetica	Oval	201–208	Alessandrello and Teruzzi (1986)
Protopholoe colombiana	Slender and stiff	86–90	Luque et al. (2015)
Protopholoe rhodanitis	Slender and stiff	165	Alessandrello et al. (2004)

tentacular cirri) and the beginning of elytra and dorsal cirri (Fig. 7.13.1.6).

The presence of elytra on late-stage larvae is a key character to identifying Aphroditiformia in the plankton. However, these are absent in the scaleless Pisioninae (Åkesson 1961). In *Pisione remota* (Southern, 1914), although the young larvae resemble those of Polynoidae (e.g., no metatroch) during metamorphosis, strong morphological differences appear. In particular, the first parapodia move forward, and the prostomium retracts between these parapodia. The dorsal cirri are also found on all segments but remain short.

For annelids, five larval stages are described in the literature (Cazaux 1968, Bhaud et al. 1999): trochophore I, trochophore II, metatrochophore I, metatrochophore II, and nectochaeta (bearing chaetae). Although the trochophore stages are very similar for all annelid families, at the metatrochophore stage in scale worms, some adult characters are present and can be used to identify families. Among larval Aphroditiformia, Sigalionidae is the only family with compound chaetae, whereas Acoetidae and Aphroditidae share the presence of thin, silken notochaetae, and in Eulepethidae, wide, distally truncated neuropodia bear the characteristic T-shaped acicula supporting the edge. Larval Polynoidae are identified, however, by the absence of these characters.

Phylogeny and evolution

Fossil record

As for all soft-bodied animals, fossilization is rare and very few fossils are available. There are currently 11 species of fossils dating from 86 to 300 million years in age with clear affinities to Aphroditiformia (Tab. 7.13.1.2). Affinities to lower taxonomic levels remain uncertain, as distinctive characters are usually not well preserved

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or are too small. Most paleoaphroditiforms described to date have about 24 segments, except *Dryptoscolex matthiesae* Thompson, 1979, which has up to 52 segments (Fitzhugh et al. 1997). Luque et al. (2015) distinguished three basic body shapes in the currently described fossil species (Tab. 7.13.1.2): an oval shape reminiscent of Aphroditidae, a more elongated and flexible shape that is reminiscent of Polynoidae or Sigalionidae, and a slender and possibly stiff shape that could correspond to Pholoinae or other short-bodied Sigalionidae. Additional work and probably a revision are needed to better interpret the relationships among these three shapes. In particular, species with two of these basic shapes are attributed to the same genus.

Molecular phylogenies and major taxonomic changes

In recent phylogenetic studies of Annelida, Aphroditiformia maintained its position within Errantia as part of Phyllodocida, a lineage that also includes Syllidae (Struck et al. 2015, Weigert and Bleidorn 2016). Aphroditiformia needs a systematic revision, and molecular studies combined with morphological data have been used to suggest some important modifications. In particular, studies such as Norlinder et al. (2012), Wiklund et al. (2005), and Struck et al. (2005) all strongly support the interpretation of the species formerly belonging to "Pisionidae" as scaleless Sigalionidae, and that of *Palmyra aurifera* as a scaleless member of Aphroditidae. Polynoidae forms the largest family, possibly a result of the fact that this family can be called the "default" family. Essentially, the species placed in this family lack morphological synapomorphies. Although this situation is not satisfactory, Polynoidae forms a monophyletic group in combined molecular and morphological studies (Norlinder et al. 2012, Gonzalez et al. 2018). Since 2012, the subfamily Iphioninae has been recovered independent of Polynoidae, often forming a clade with Acoetidae, and, as a consequence, Norlinder et al. (2012) elevated the polynoid subfamily Iphioninae to the family level (= Iphionidae).

It is important to note, however, that the relationship and position of Acoetidae with respect to Iphionidae (Iphioninae) and Polynoidae warrants further detailed molecular and morphological studies. Acoetidae and Iphionidae were recovered in a clade sister to Polynoidae by Gonzalez et al. (2018) using combined molecular and morphological analyses, and again by Zhang et al. (2018) using only molecules, both with higher support than first reported by Norlinder et al. (2012).

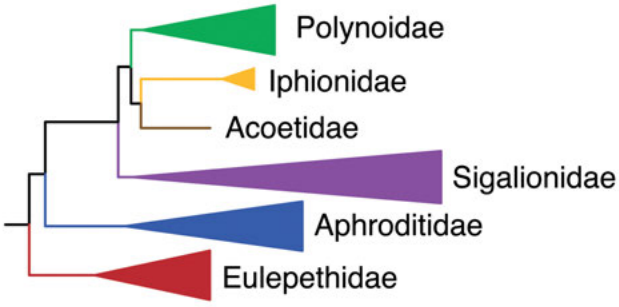


Fig. 7.13.1.7: Schematic representation of the current phylogenetic and systematic view of Aphroditiformia based on combined molecular and morphological analyses (from Gonzalez et al. 2018). Status of Iphionidae remains in question but continues to be recovered independent of Polynoidae (see Zhang et al. 2018). This lineage is here considered as subfamily Iphioninae in the handbook chapter on Polynoidae (chapter 7.13.1.4). Sigalionidae includes "Pholoidae" (see Gonzalez et al. 2018, Zhang et al. 2018) and the former "Pisionidae" (see Norlinder et al. 2012).

Based on the phylogenetic studies published by Zhang et al. (2018) and Gonzalez et al. (2018), Eulepethidae and Aphroditidae are deeply positioned in relationship to other aphroditiform families (Fig. 7.13.1.7). Although the relationship between the latter two families is unresolved in Norlinder et al. (2012), both Zhang et al. (2018) and Gonzalez et al. (2018) show good support for Eulepethidae being sister to all remaining scale worm families. Sigalionidae is consistently recovered as a sister group to Polynoidae, and morphological analyses indicate that their compound chaetae are secondarily derived. "Pholoidae" forms a clade within Sigalionidae that is sister group to Acoetidae—Polynoidae. Based on these results, Gonzalez et al. (2018) suggested that Pholoidae should be treated as members of family Sigalionidae.

The following chapters deal with the separate families of Aphroditiformia in greater depth.

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7.13.1.2 Acoetidae Kinberg, 1856

Introduction

Acoetidae is the fourth largest family within Aphroditiformia and includes eight genera and 58 species (Figs. 7.13.1.2.1–7.13.1.2.10). Species discovery was most prominent between 1817 and 1899 (n = 16) and between 1900 and 1988 (n = 25). In Pettibone's (1989) revision of Acoetidae, an additional 13 species were added, however, since then, only four species have been described. The most recent acoetid description was by Jimi et al. (2019) for a new species of *Polyodontes* from Japan. Most of our knowledge on Acoetidae stems from *Panthalis oerstedi* Kinberg, 1856 — being used by early scientists to understand structures of the brain, nervous system, and various morphological novelties.

Acoetidae comprises annelids with an unusually elongated body (≤2 m) and a prolific number of segments (>300). The true diversity of Acoetidae is unknown, but they have been found so far in diverse bottom types between the intertidal zone and 1500 m. The morphology of Acoetidae largely agrees with Polynoidae and Aphroditidae, possessing only simple chaetae and having dorsal cirri on nonelytragerous segments. Acoetids only inhabit self-constructed tubes, which they make from tightly woven feltage notochaetae and sediment (Fig. 7.13.1.2.4A, B). Unlike other scale worms, acoetids may possess highly modified prostomiums bearing large elaborate eyes (ommatophores), probably an adaptation to their sit-and-wait predatory lifestyle (Figs. 7.13.1.2.1–7.13.1.2.3 and 7.13.1.2.4B, C). These

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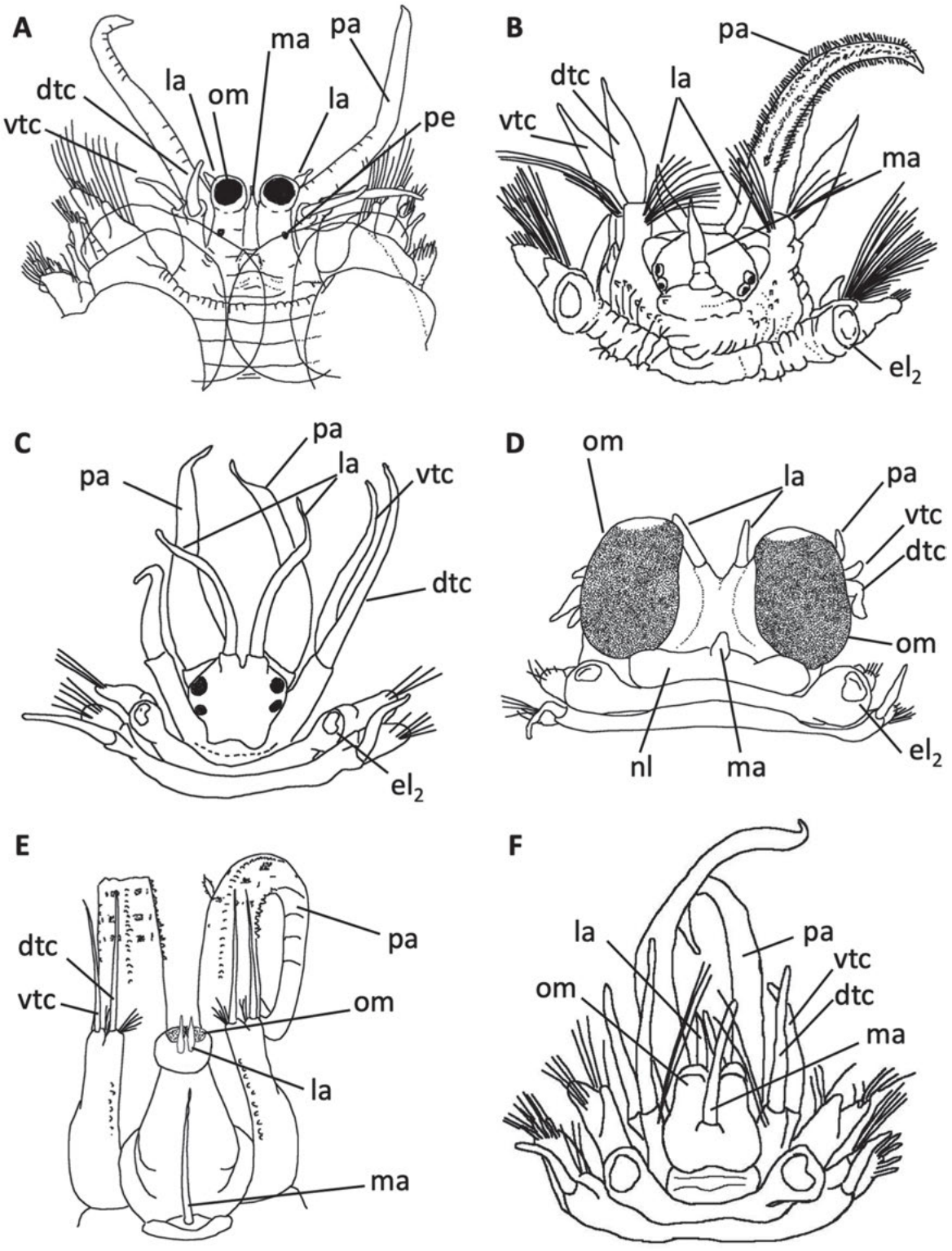


Fig. 7.13.1.2.1: Dorsal view of anterior regions of the different genera of Acoetidae. A, *Acoetes jogasimae* (Izuka, 1912). Prostomial type 3. Redrawn after Imajima (1997). B, *Euarche tubifex* Ehlers, 1887. Prostomial type 1. Redrawn after Imajima (1997). C, *Eupanthalis kinbergi* McInstosh, 1876. Prostomial type 1. Redrawn after Barnich and Fiege (2003). D, *Eupolyodontes gulo* (Grube, 1855). Prostomial type 2. Redrawn after Barnich and Fiege (2003). E, *Neopanthalis pelamida* Strelzov, 1968. Prostomial type 4. Redrawn after Strelzov (1968). F, *Panthalis oerstedi* Kinberg, 1856. Prostomial type 3. Redrawn after Barnich and Fiege (2003). Images not drawn to scale. dtc, dorsal tentacular cirrus; el_2, elytrophore segment 2; la, lateral antenna; ma, median antenna; nl, nuchal lobe; om, ommatophore; pa, palp; pe, posterior eyes; pr, prostomium; vtc, ventral tentacular cirrus.

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highly evolved structures may occupy the entire width of the prostomium or be pedunculate. Early literature suggested that Acoetidae possessed several morphological apomorphies (i.e., ommatophores, feltage chaetae, and denticulate jaws) but continued discovery across scale worms has proven that these structures are not unique because they are now known to be shared among the aphroditiform families.

Morphology

External morphology

Body shape, size and color. Acoetids are among the largest of the scale worms, having a dorsoventrally flattened body that is relatively broad in its entirety, reaching upward of 300 segments or more. In cross section, they appear rectangular, with blunt subconical parapodia and elytra positioned toward their lateral borders (Pettibone 1989).

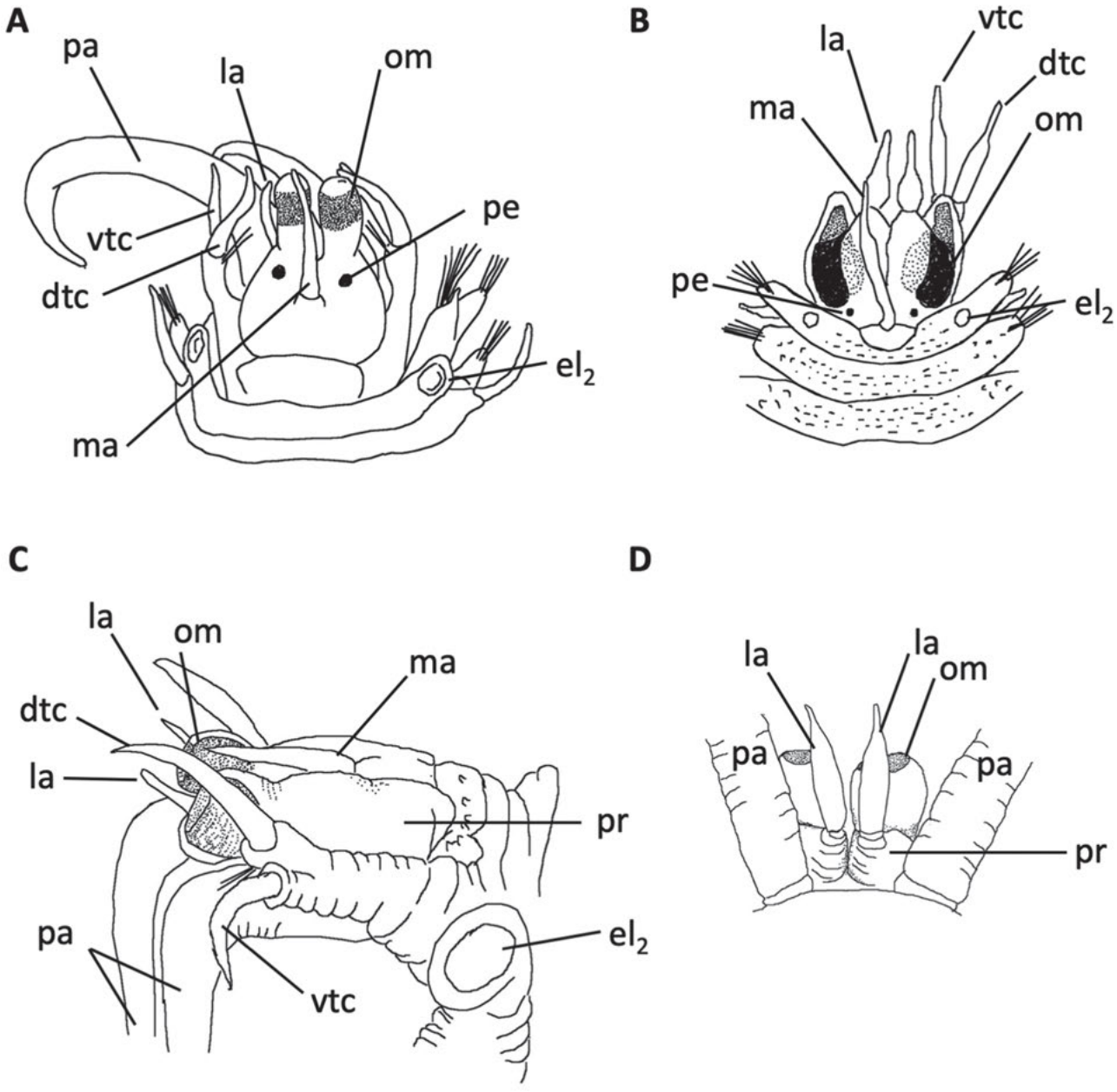


Fig. 7.13.1.2.2: Dorsal view of anterior regions of the different genera of Acoetidae. A, *Polyodontes maxillosus* (Ranzani, 1817). Prostomial type 3. Redrawn after Barnich and Fiege (2003). B, *Zachsiella nigromaculata* (Grube, 1878). Prostomial type 2. Redrawn after Buzhinskaja (1982). *Acoetes jogasimae* (Izuka, 1912), lateral (C) and ventral views (D). Redrawn after Imajima (1997). Prostomial type 3. Images not drawn to scale. dtc, dorsal tentacular cirrus; el_2, elytrophore segment 2; la, lateral antenna; ma, median antenna; om, ommatophore; pa, palp; pe, posterior eyes; pr, prostomium; vtc, ventral tentacular cirrus.

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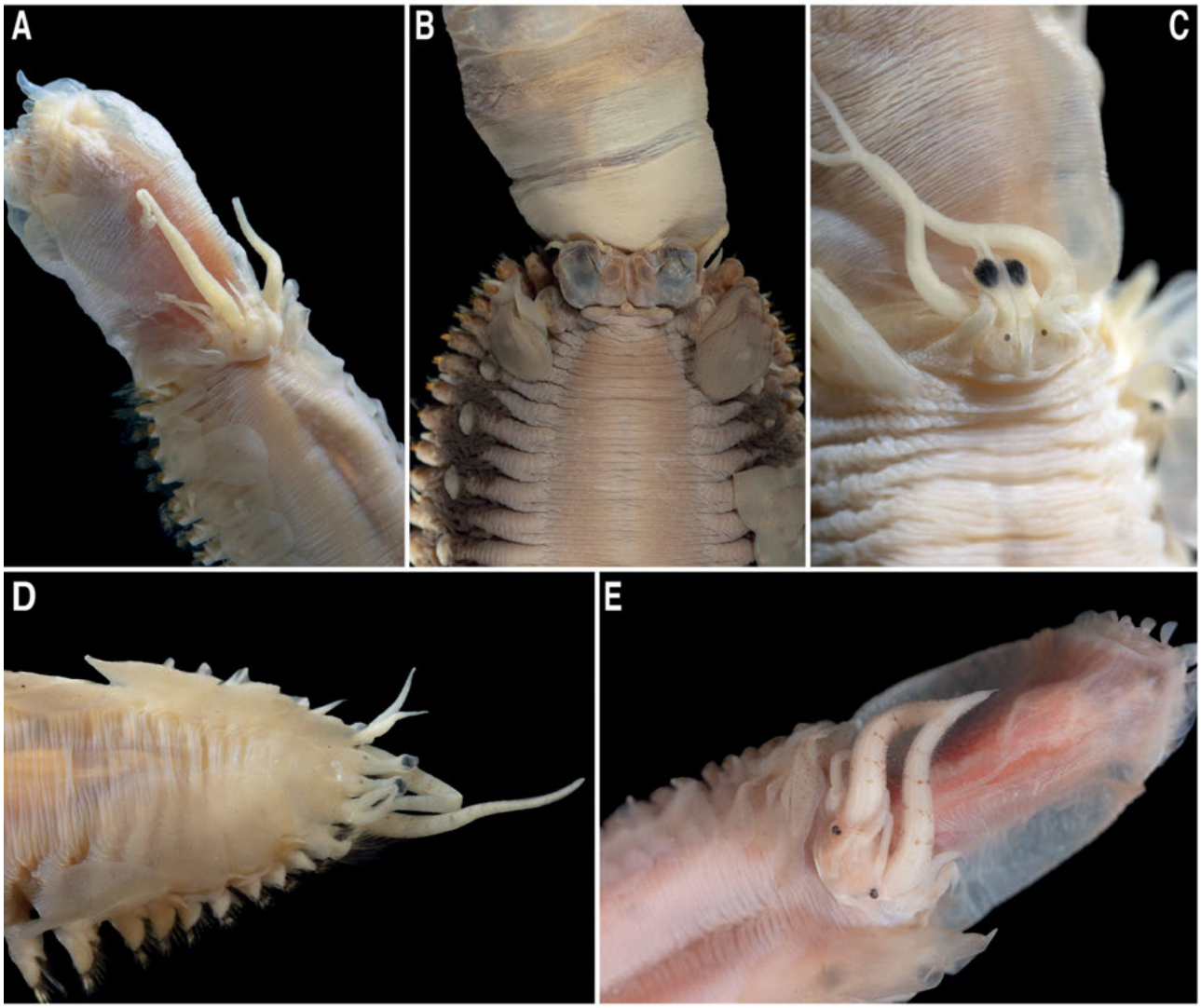


Fig. 7.13.1.2.3: Prostomial and eye variations across Acoetidae. A, *Euarche tubifex* Ehlers, 1887 (USNM 71456). Type 1 prostomia. B, *Eupolyodontes batabanoensis* Ibarzábal, 1988 (USNM 98809). Type 2 prostomia. C, *Polyodontes frons* Hartman, 1939 (USNM 50730). Type 3 prostomia. D, *Acoetes melanonota* (Grube, 1876) (USNM 98809). Type 3 prostomia. E, *Eupanthalis kinbergi* McIntosh, 1876 (USNM 1184294). Type 1 prostomia.

Nearly all described Acoetidae are from partial specimens; however, in general, acoetids have a considerable size range, being up to 1 m or more in length and over 40 mm wide. Because acoetids are rarely collected whole, maximums and minimums in size and segment number are often unknown. *Polyodontes maxillosus* (Ranzani, 1817) is considered one of the largest acoetids, reportedly reaching a length of 2 m (Saint-Loup 1889), whereas *Eupolyodontes batabanoensis* Ibarzábal, 1988 is known to have upward of 400 or more segments.

Body coloration is minimal in acoetids, often stated as being "without" (Fig. 7.13.1.2.4D). However, dark transverse bands along the dorsum are common throughout Acoetidae and hues of brown and yellow are reported from several species of *Polyodontes*. Pigmentation is most noticeable on the elytra, often exhibiting bright colors and patterns (e.g., *Polyodontes kuroshio* Jimi, Tomioka, Orita, & Kajihara, 2019; Fig. 7.13.1.2.4D). Both the dorsum and the venter are smooth and lacking papillae. Papillae may be present on the prostomium and prostomial appendages, including tentaculophores, ceratophore of the median antenna, and nuchal regions. The dorsal body surface is often transversely grooved and may obscure segmental boundaries. The ventral nerve cord is protected by a median longitudinal ridge.

Similar to other scale worms, elytra in Acoetidae are attached to bulbous elytrophores on segments 2, 4, 5, and 7 and then alternate until segment 23. Beyond that point,

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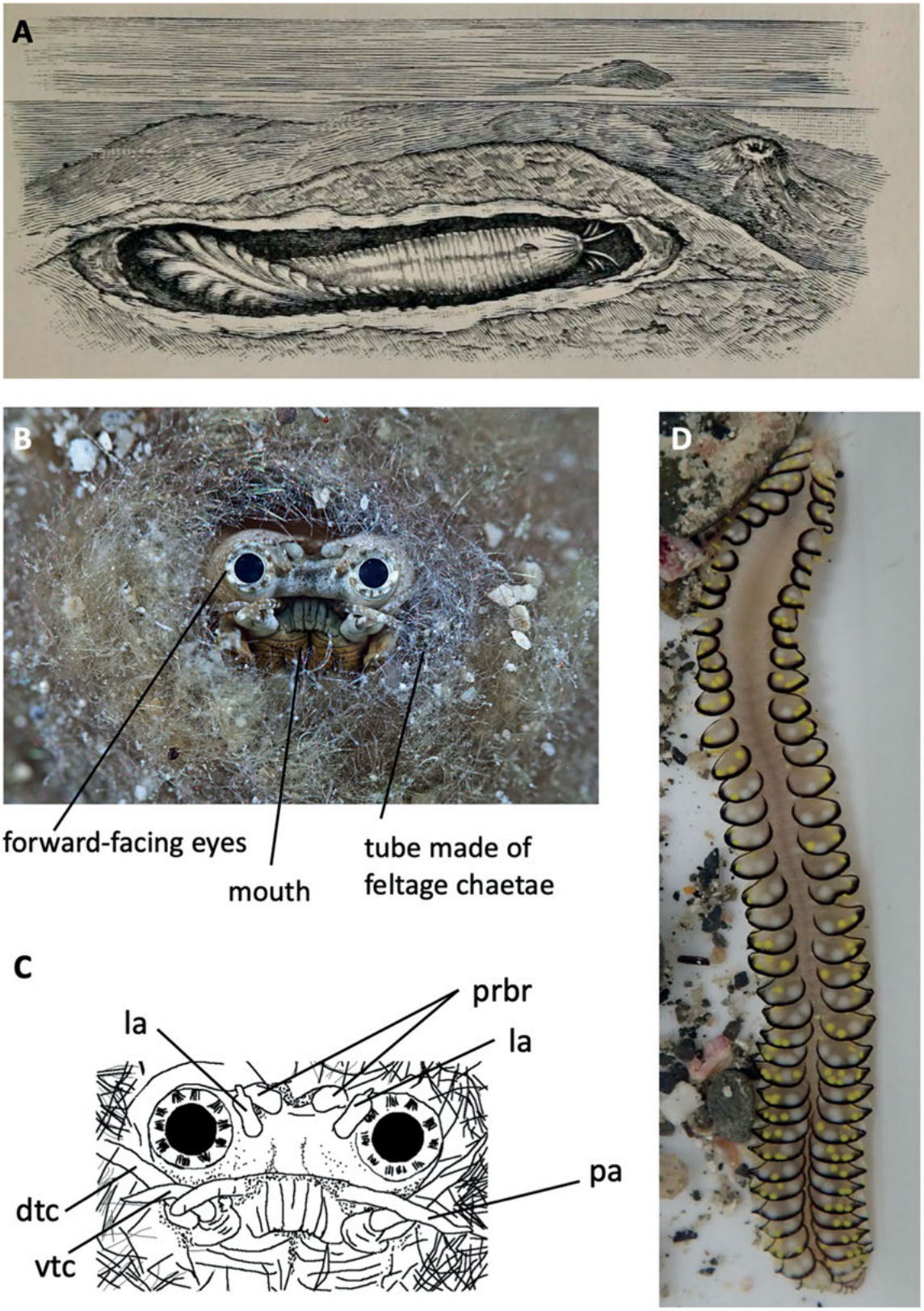


Fig. 7.13.1.2.4: Acoetids in their natural settings. A, Drawing of *Panthalis oerstedi* Kinberg, 1856 in its burrow (British Museum (Natural History) 1901). B, *Eupolyodontes* sp. at the opening of its tube. Photo by Cedric Paul, with permission. C, Annotated drawing of B. D, *Polyodontes kuroshio* Jimi, Tomioka, Orita, & Kajihara, 2019. Photo by Naoto Jimi, with permission. Images not drawn to scale. dtc, dorsal tentacular cirrus; la, lateral antenna; pa, palps; prbr, prostomial branchiae; vtc, ventral tentacular cirrus.

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the pattern can be variable among families (see Aphroditiformia chapter). In acoetids, elytra and dorsal cirri usually alternate until the end of the body (Fig. 7.13.1.2.4D). Jimi et al. (2019), however, reported changes to this pattern in *Polyodontes kuroshio* where the alternating pattern stopped on segment 23, followed by consecutive elytra being present on segments 23–26, then returning to an alternating pattern posteriorly to the end, but on every other even segment. On segments without elytra, indistinct dorsal tubercles are present.

Generally, the head and prostomial region in Acoetidae is highly developed and contains well-developed sense organs (Figs. 7.13.1.2.1–7.13.1.2.3). The tentacular segment (segment 1) is directed anteriorly, fused to the prostomium (Fig. 7.13.1.2.C). The palps are ventral in all acoetids and are often long and tapered, being smooth, papillate, or a combination of both. In *Eupolyodontes*, palps are much smaller than in other genera and rarely longer than the ommatophores.

Prostomium. According to Pettibone (1989), there are four distinct types of prostomia, each correlated to the degree of ommatophore development. The simplest prostomial type (type 1) is found in species of *Euarche* (Figs. 7.13.1.2.1B and 7.13.1.2.3A) and *Eupanthalis* (Figs. 7.13.1.2.1C and 7.13.1.2.3E), being oval or bilobed and having two pairs of sessile eyes. At a quick glance, members of this form resemble Polynoidae. The sessile eyes may be lacking (e.g., *Euarche mexicana* Pettibone, 1989) or with the anterior pair slightly larger (e.g., *Eupanthalis aena* (Moore, 1903)). The second prostomial type (type 2) is found in *Zachsiella* (Fig. 7.13.1.2.2B) and *Eupolyodontes* (Figs. 7.13.1.2.1D and 7.13.1.2.3B), being wide and bilobed with large anteriorly projecting ommatophores that occupy most of the prostomium. Sessile eyes are lacking in *Eupolyodontes* but are present in *Zachsiella*. The third prostomial type (type 3) is present in *Acoetes* (Figs. 7.13.1.2.1A and 7.13.1.2.3D), *Panthalis* (Fig. 7.13.1.2.1F), and *Polyodontes* (Figs. 7.13.1.2.2A and 7.13.1.2.3C). Within these genera, the prostomium is bilobed, bearing a pair of bulbous ommatophores that extend anteriorly. The ommatophores may have a narrow neck like in *Acoetes* and *Polyodontes* (e.g., *Acoetes melanonota* (Grube, 1876)) or, as in *Panthalis*, lack a narrow neck completely (e.g., *Panthalis alaminosae* Pettibone, 1989). Ommatophores lack color in *Panthalis*, but are colored in *Acoetes* and *Polyodontes*. Sessile eyes are present in *Acoetes* and *Polyodontes* but absent in *Panthalis*. The most peculiar type of prostomium (type 4) is represented by *Neopanthalis* (Fig. 7.13.1.2.1E), having anteriorly extended ommatophores that are fused along their midline. Sessile eyes are absent.

Most acoetids have three prostomial antennae: a pair of lateral antennae and a median antenna. The position of the lateral antennae corresponds to the prostomial type: type 1, lateral antennae are visible and anteriorly positioned (Fig. 7.13.1.2.1C); type 2, lateral antennae are anteriorly positioned between the ommatophores (Fig. 7.13.1.2.1D); type 3, lateral antennae are attached ventrally on the ommatophores, barely visible dorsally (Fig. 7.13.1.2.2A); and type 4, lateral antennae are attached on the distal tip of the fused ommatophores (Fig. 7.13.1.2.1E). Lateral antennae may be hidden completely from dorsal view in some species (e.g., *Acoetes congoensis* Pettibone, 1989). The median antenna in Acoetidae consists of a basal ceratophore and a distal ceratostyle, often referred to as the median occipital antenna. All genera except *Eupanthalis* have a well-developed median antenna (Fig. 7.13.1.2.1C). In some species of *Eupolyodontes*, the median antenna is small or even absent (e.g., *Eupolyodontes thomassini* Pettibone, 1989). Prostomial branchiae (fleshy appendages) may be present in some species of *Eupolyodontes* (e.g., *Eupolyodontes amboinensis* Malaquin & Dehorne, 1907); however, the true function of these structures is unknown (Figs. 7.13.1.2.4B, C).

Nuchal organs in Acoetidae are referred to as nuchal lobes, presumed to be present in some form in all acoetids. These lobes are positioned between the posterior region of the prostomium and the dorsal surface of segment 2. In most genera, only a single nuchal lobe is present, but in *Eupolyodontes* it can be bilobed (Figs. 7.13.1.2.1D and 7.13.1.2.3B). Nuchal lobes may be papillate and often are the attachment point for the occipital antenna.

Segment 1 envelopes the prostomium laterally. The tentaculophores of the dorsal and ventral tentacular cirri are positioned lateral or ventral to the prostomium (Figs. 7.13.1.2.2C and 7.13.1.2.6A) and are supported by one or two aciculae (e.g., *Panthalis*). If present, notochaetae may be found in single or multiple groups along the tentacularphores (e.g., *Neopanthalis, Panthalis, Acoetes,* and *Polyodontes*). Acicular lobes may be present (e.g., *Eupolyodontes amboinensis*) as well as papillae. The ventral tentacular cirrus is usually longer than the dorsal tentacular cirrus, but it is variable, as is the case in *Eupolyodontes cornishii* Buchanan, 1894 where the dorsal tentacular cirrus is longer. In *Acoetes southcarolinensis* Pettibone, 1989, the tentacular cirri are bulbous with filamentous tips. Pigment along the tentacular cirri may be present as either spots or bands.

Peristomium. Acoetids have a ventrally positioned mouth, posterior to any prostomial appendage. Like other scale worms, the lips are the only vestige of the peristomium (Rouse and Pleijel 2001). The anterior, lateral, and

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posterior lips of the mouth are formed by the first three segments. Radial folds are often present. All acoetids have an eversible large muscular pharynx that greatly extends beyond the palps or tentacular cirri (Fig. 7.13.1.2.5). The distal border of the pharynx is crowned by a circle of terminal papillae: 13 pairs in *Euarche* and *Eupanthalis*, 15 pairs in *Panthalis* and *Acoetes* with middorsal and midventral papillae longer and situated on lobulated bases, 19 pairs in *Polyodontes* with middorsal and midventral papillae longer and situated on lobulated bases, and up to 39 pairs of closely set papillae in *Eupolyodontes* with both middorsal and midventral papillae long and tapered.

Jaws. As in most scale worms, acoetids have four strongly hooked jaws (Fig. 7.13.1.2.5C, D), presented as one dorsal and one ventral pair, positioned just inside the lumen of the everted pharynx. Each jaw has 7–17 lateral teeth but may be as little as two depending on the size of the animal. *Acoetes mohammadi* Pettibone, 1989 is reported to lack lateral teeth, but it was noted in the description that it may be due to wear. In his study of jaws, Wolf (1986) noted that acoetid (referred to as polyodontid) jaws differ from Polynoidae and Sigalionidae in that the ventrolateral plate is fused to the concave margin of the fang, being dentate along the outer edge.

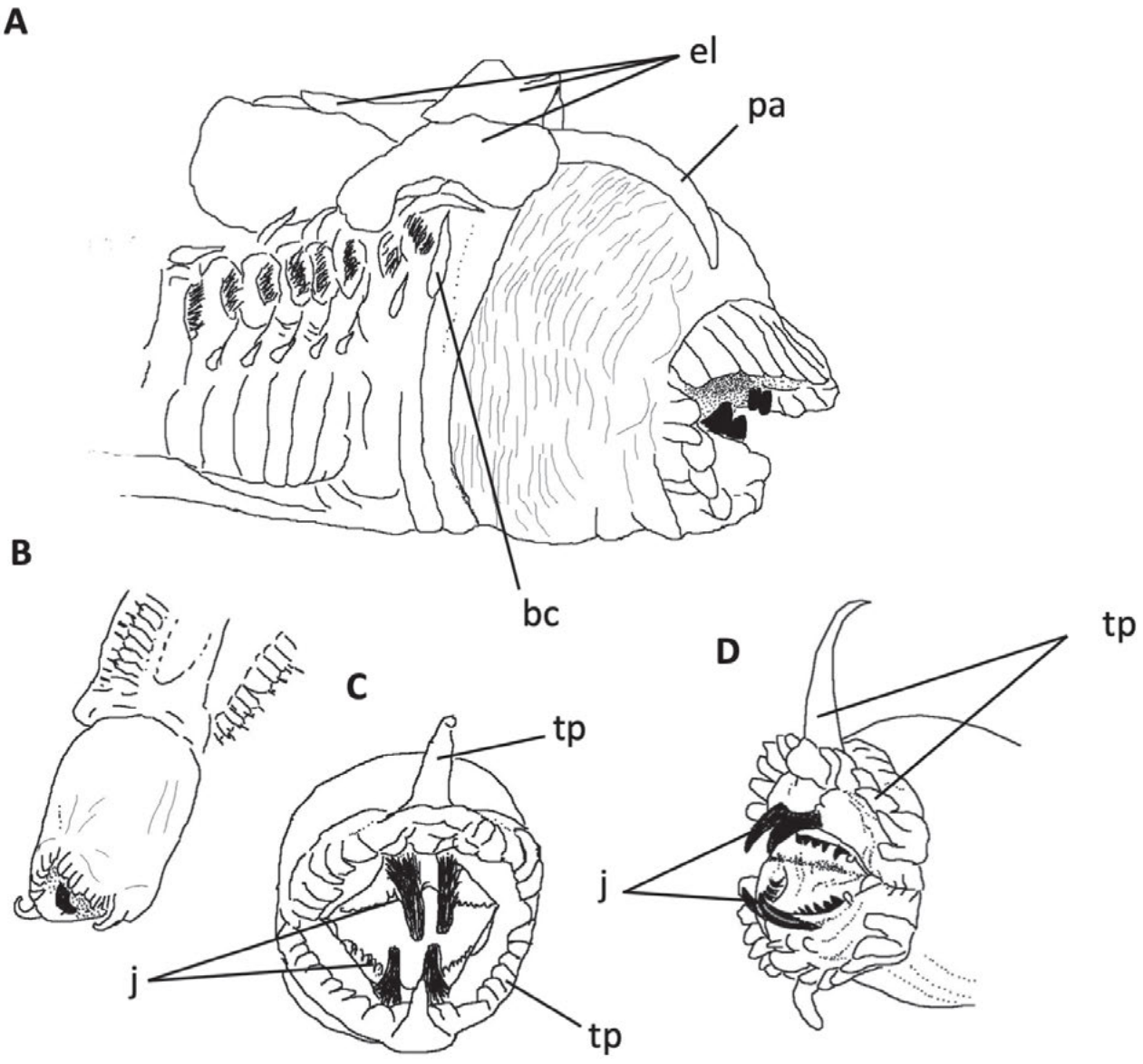


Fig. 7.13.1.2.5: Everted pharynx showing terminal mouth papillae and jaws. A, Lateral view of everted pharynx and prostomial appendages in *Euarche rudipalpa* (Amaral & Nonato, 1984). B and C, Pharynx of *Polyodontes maxillosus* (Ranzani, 1817) in ventral (B) and frontal views (C). D, Terminal mouth papillae and jaws of *Acoetes jogasimae* (Izuka, 1912). Redrawn after Imajima (1997). Images not drawn to scale. bc, buccal cirrus (segment 2); el, elytra; j, jaw; pa, palp; tp, terminal papillae.

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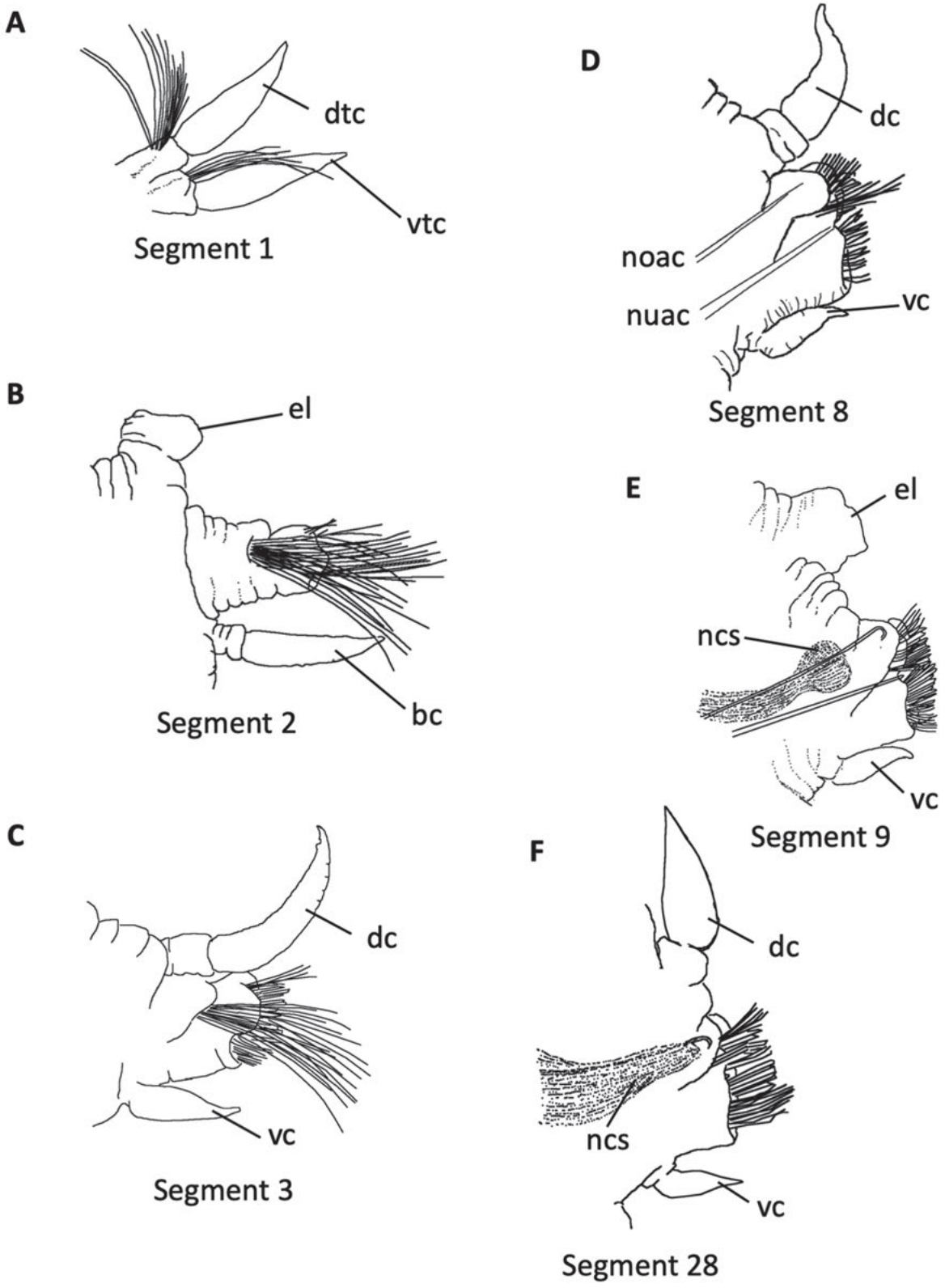


Fig. 7.13.1.2.6: Variation in segment morphology in *Euarche tubifex* Ehlers, 1887. Redrawn after Imajima (1997). A, Segment 1, tentacular segment. B, Segment 2, buccal segment and first elytragerous segment. C, Segment 3, first cirrigerous segment. D, Segment 8. E, Segment 9, first segment with notopodial chaetal sacs. F, Segment 28. Images not drawn to scale. bc, buccal cirrus; dc, dorsal cirrus; dtc, dorsal tentacular cirrus; el, elytrophore; ncs, notopodial chaetal sac; noac, notopodial acicula; nuac, neuropodial acicula; vc, ventral cirrus; vtc, ventral tentacular cirrus.

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Segment morphology. Segment 2, or buccal segment (Fig. 7.13.1.2.6B), is modified similarly as in other scale worms and is the first elytragerous segment. The ventral buccal cirri are enlarged, anteriorly directed, and lateral to the mouth. Resembling the tentacular cirri, both the cirrophore and style are thicker and longer than the ventral cirri of the following segments. The parapodia are biramous or subbiramous and are oriented laterally. Watson (1895) noted that segment 2 parapodia were quite important in the manipulation of feltage chaetae for tube construction (see Anatomy section for terminology), referring to them as "weaving feet." The notopodium is supported by a thin acicula, and notochaetae may be present (Fig. 7.13.1.2.8A). The neuropodium has a stout acicula, and neurochaetae are often lanceolate and slender. Various prechaetal and postchaetal lobes may be present. Pettibone (1989) referred to these structures as anteroventral bracts, but "bract" is a botany term referencing leaf structures. In an attempt to remove confusion, the term "neuropodial lobe" (*sensu* Aungtonya 2005) should be implemented for any structure covering the base of the chaetae, similar to what has been implemented in Sigalionidae genera.

Acoetid elytra generally have a simple oval or round shape that is occasionally elongated transversely (Fig. 7.13.1.2.4D). The elytra are small in comparison to the size of the worms, attached to bulbous, sometimes papillated, elytrophores positioned on the lateral borders of the body (Fig. 7.13.1.2.6C, E). Their position often leaves the midline of the dorsum uncovered. The elytra do overlap anteriorly to protect the prostomial appendages and are often found overlapping in the narrowed, posteriormost segments. Most acoetids have thin transparent elytra that are smooth and flexible, but thick opaque elytra occur in *Eupolyodontes thomassini* Pettibone, 1989, and *Eupanthalis edriophthalma* (Potts, 1910) is reported to have slightly inflated elytra. Similar to the deep incisions found throughout the Pelogeniinae (Sigalionidae), acoetids bear lateral pouches on their posterior elytra. These pouches (=pockets) may begin as early as the third elytral pair (e.g., *Eupolyodontes hartmanae* Pettibone, 1989) or may be absent completely (e.g., *Acoetes congoensis*). Surface ornamentation is rarely documented, but microtubercles were identified in *Euarche tubifex* Ehlers, 1887 (Salazar-Vallejo et al. 2014) and surface areolae are common throughout species of *Acoetes* and *Polyodontes*. Color is highly variable on acoetid elytra and may be restricted to the lateral and posterior margins or throughout the surface of the elytra. Color patterns are also present in some species and may be a single repeating pigment spot or colored crescent shape along the interior elytron border as in *Zachsiella nigromaculata* (Grube, 1878), yellow margins as in *Polyodontes lupinus* (Stimpson, 1856), or completely bright orange with light spots as in *Polyodontes vanderloosi* Barnich & Steene, 2003.

In addition to the dorsal (tentacular) cirri of segment 1, dorsal cirri are located on all non-elytragerous segments (Fig. 7.13.1.2.6C, D, F), generally consisting of a short cirrophore and styles that do not project beyond the tips of the neurochaetae. An exception to this exists on segments 3, 6, and 8, where styles may extend beyond the neurochaetae as the parapodia become modified. From segment 9 posteriorly (Fig. 7.13.1.2.6E), cirrophores are wide and appear inflated, having short subulate or wide conical styles. Aside from the buccal cirri (segment 2), the ventral cirri are all short and subulate, most often attached near the base of the parapodia (Fig. 7.13.1.2.6).

Parapodial branchiae are common throughout Acoetidae, forming on the anterior, dorsal, and posterior sides of the parapodia and the base of the elytrophores/cirrophores (Fig. 7.13.1.2.7A, B). In *Polyodontes vanderloosi*, these branchiae can also be found ventrally. Acoetid branchiae have a thick cuticle and are extensions of the coelom, similar to the branchiae found in *Branchipolynoe* (Polynoidae) (see Hourdez and Jouin-Toulmond 1998). Not all segments bear branchiae, and their presence may be restricted to specific body regions or segments. Their appearance is variable, appearing as digitiform, bulbous, filamentous, or arborescent projections, and species may exhibit more than one form throughout their body. Larger species of *Eupolyodontes* and *Polyodontes* exhibit well-developed branchiae, whereas smaller species (e.g., *Euarcche*, *Eupanthalis*, *Zachsiella*, *Neopanthalis*, and *Panthalis*) may have few to no branchia.

Segments 3–8 in Acoetidae can be considered as transitional segments (Fig. 7.13.1.2.6C, D). Moving posteriorly from segment 3, the parapodia gradually modify their appearance; the notopodium becomes smaller and less pronounced, whereas the neuropodium becomes larger, often with the development of neuropodial lobes. If present, capillary notochaetae become shorter and fewer in number. Pettibone (1989) divided the neurochaetae of these segments into three distinct groups (groups 1, 2, and 3) based on their position (lower, middle, and upper), respectively (Figs. 7.13.1.2.8 and 7.13.1.2.9). The phylogenetic significance of these groups remains to be tested, but recent acoetid descriptions continue to reference these groupings (see Jimi et al. 2019). Neurochaetae of group 1 (lower; i.e., infraacicular) are slender with gently curving tapered tips and large basal spinules, becoming tightly arranged distally; group 2 (middle; i.e., acicular) neurochaetae are stout, acicular with rounded or hooked tips, generally smooth and with aristae; and group 3

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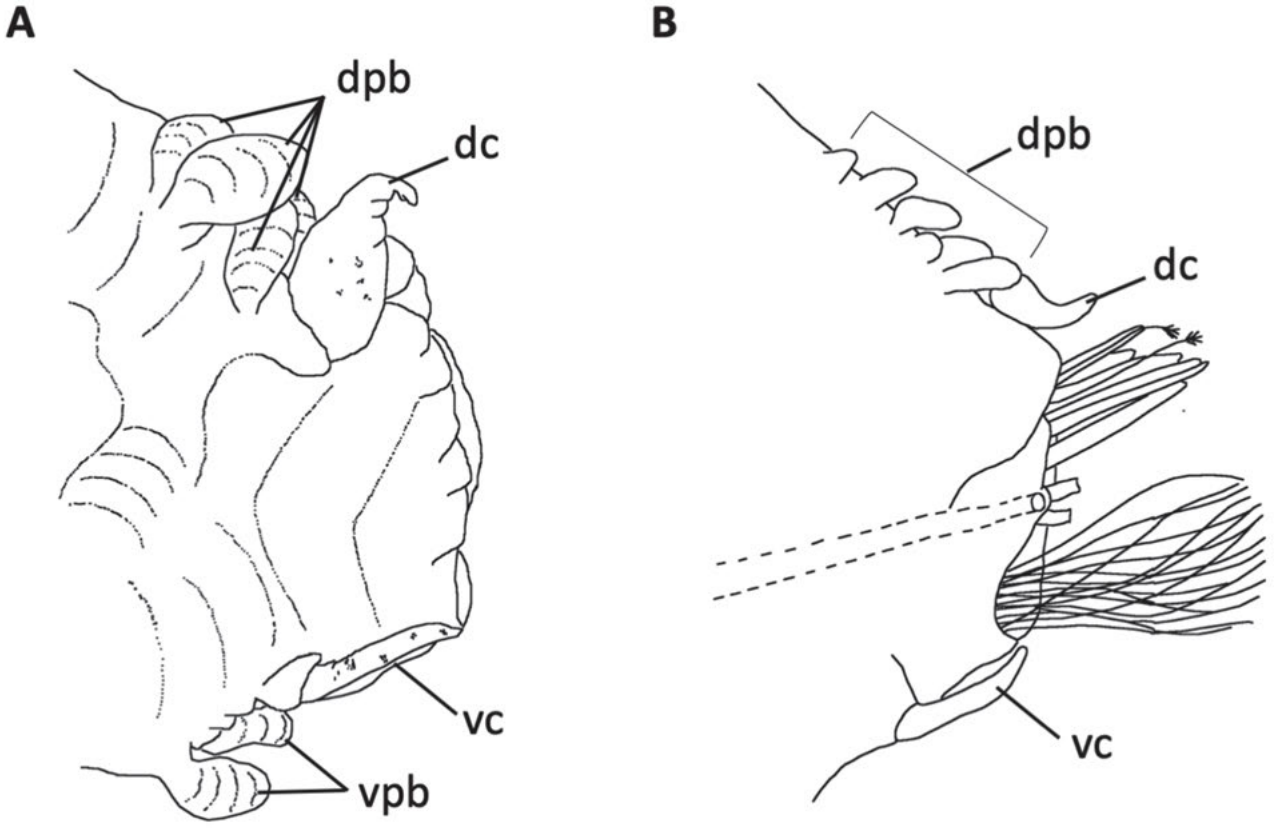


Fig. 7.13.1.2.7: Examples of parapodial branchiae in Acoetidae. A, *Polyodontes vanderloosi* Barnich & Steene, 2003. Chaetae not shown. Redrawn after Barnich and Steene (2003). B, *Eupolyodontes gulo* (Grube, 1855). Redrawn after Barnich and Fiege (2003). Images not drawn to scale. Neuropodial acicula demarked by dashed lines. dc, dorsal cirrus; dpb, dorsal parapodial branchiae; vc, ventral cirrus; vpb, ventral parapodial branchiae.

(upper; i.e., supraacicular) neurochaetae are lanceolate with spinules, tapering distally (Fig. 7.13.1.2.8B). Upper neurochaetae (group 3) may be completely absent in these segments.

From segment 9 posteriorly, the parapodia go through another major transformation, marking the start of the notopodial feltage chaetae ("spinning glands" (Fig. 7.13.1.2.6E, F); see below). To accommodate these spinning fibers, the notopodium enlarges to about half the size of the neuropodium, supported by a thin notoacicula and a stout neuroacicula. Feltage chaetae may be absent in the posteriormost segments. Internally, the feltage notochaetae appear rope-like or coiled, extending inward toward the middle of the body cavity. The feltage chaetae exit via a slit on the underside of the notopodium. Capillary notochaetae may also be present in some species of *Euarche, Eupanthalis, Acoetes,* and *Polyodontes*. The neurochaetae continue to be identified as the before mentioned three groups; however, group 3 (upper) neurochaetae are further divided from segment 9 posteriorly into "type a" and "type b" (Pettibone 1989). Neurochaetal morphology of the group 3 subdivisions are genera specific (Figs. 7.13.1.2.8B, C and 7.13.1.2.9). In general, the appearance of type a (group 3a) is long and stout, resembling a combination of aristate and penicillate, whereas the appearance of type b (group 3b) is short and slender. Specifically, type "a" neurochaetae in *Euarche, Eupanthalis, Neopanthalis,* and *Polyodontes* are long and lanceolate, tapering distally to fine tips; in *Zachsiella*, they are long, acicular, and aristate with spinules; in *Eupolyodontes*, they are long and penicillate with a double brush; in *Panthalis*, they are long, penicillate with short rows of spinules subdistally; and in *Acoetes*, they abruptly taper to slender tips with long spinules (pseudopenicillate) as well as rows of spinules subdistally. Group 3a neurochaetae emerge from an anterodorsal neuropodial lobe opposite the exit slit for the feltage notochaetae, allowing them to assist in manipulating the feltage fibers. Type b neurochaetae are typically shorter and may be hidden by the notopodium. Their appearance is variable, tapering to sharp tips with whorls of spinules along the shaft. Across acoetids, the middle

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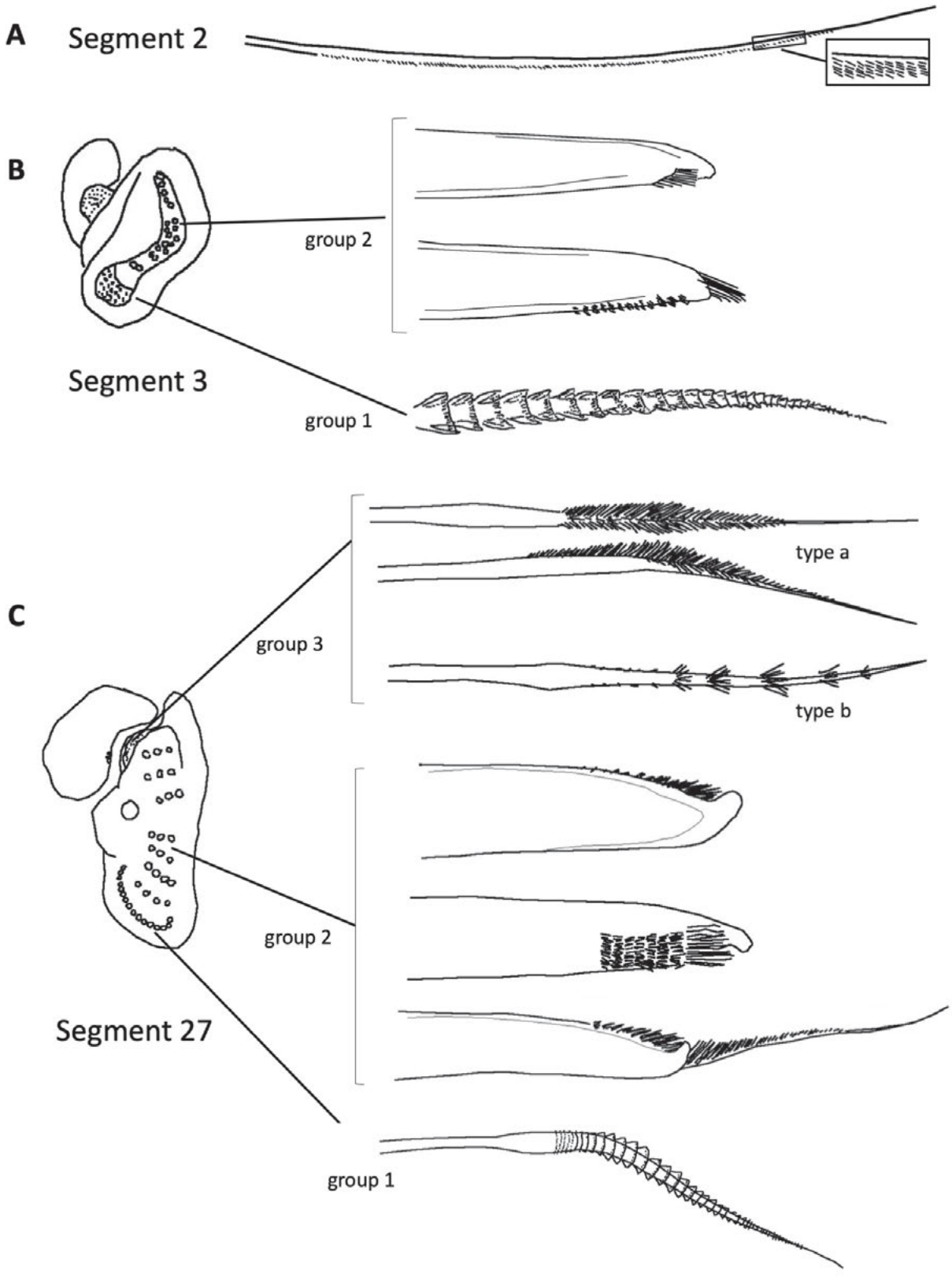


Fig. 7.13.1.2.8: Different chaetal arrangements in *Euarche tubifex* Ehlers, 1887. Chaetal groups, and types, indicated when appropriate. A, Segment 2 notochaetae. Detail of distal spinules shown in insert. B, Segment 3 neurochaetae with detailed drawings of the middle (group 2) acicular neurochaetae (in bracket) and a single lower (group 1) neurochaetae. C, Segment 27 with examples of upper (groups 3a and 3b), middle (group 2), and lower (group 1) neurochaetae. Images not drawn to scale. All images redrawn after Imajima (1997).

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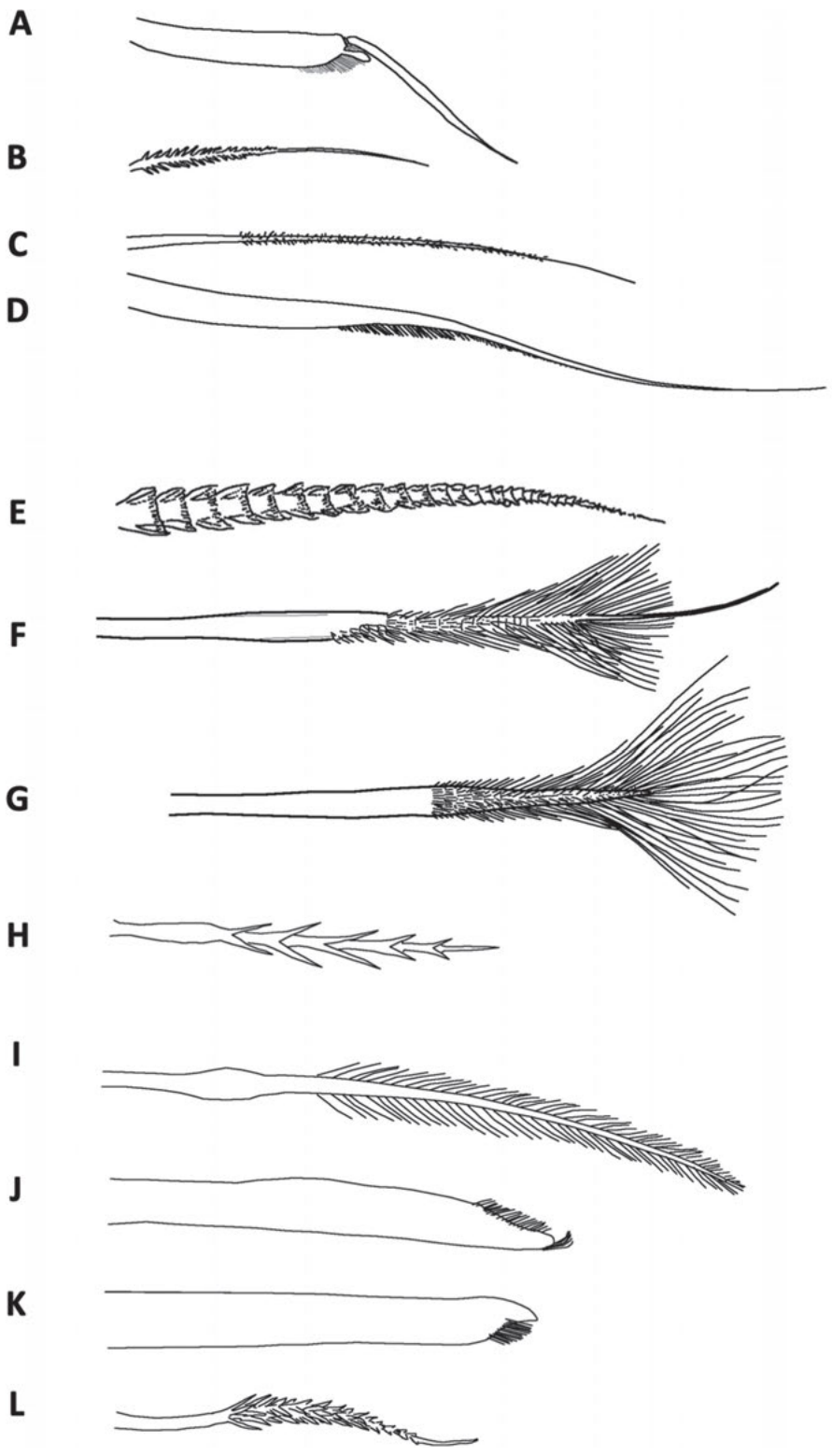


Fig. 7.13.1.2.9: Diversity of chaetal forms across selected Acoetidae. A–D, *Eupanthalis kinbergi* McInstosh, 1876. Aristate acicular neurochaetae from middle of neuropodium (group 2; A), neurochaetae with spines in the lower part (group 1; B), and upper part (group 3b; C and D). Redrawn from Núñez et al. (2015). E, F, *Acoetes jogasimae* (Izuka, 1912). Segment 9 (group 3; F, G) brush-like neurochaetae. Redrawn after Imajima (1997). G–L, *Euarche tubifex* Ehlers, 1887. Segment 3 neurochaetae (group 1). Redrawn after Imajima (1997). Capillary with widely separated spines (group 3b; H), tightly set spines in the upper part (group 3b; I), acicular from middle of parapodium (group 2; J, K), and lower part of parapodium (group 1; L). Redrawn from Núñez et al. (2015).

neurochaetae are all stout and acicular, often aristate or with spinules along the shaft. The lower neurochaetae are numerous, lanceolate, often bearing aristae or other scattered spinules.

External nephridial papillae are absent.

Pygidium. The acoetid body ends with a small pygidium (Fig. 7.13.1.2.4D), although morphological characterization is lacking from most species as the specimens are often incomplete. In *Acoetes pleei* Audouin & Milne Edwards, 1832, the wide or bulbous anus is terminal, but dorsally positioned in

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Polyodontes vanderloosi. Anal cirri are present but typically not longer than the dorsal cirri of earlier segments.

Anatomy

Given that Acoetidae is one of the smaller families within Aphroditiformia, it is of no surprise that little information exists on their overall anatomy. Claparède (1868) provided the first detailed description of the neurochaetal variation and the presence of unusual cord-like structure within the notopodia (Figs. 7.13.1.2.6–7.13.1.2.9). Eisig (1887) provided great detail of the cord-like structure in *Polyodontes maxillosus* and established the term "spinning glands" and "spinning fibers." As mentioned below, the only detailed observations on tube construction (for *Panthalis oerstedi*) were provided by Watson (1895) from small aquaria. More recently, Pflugfelder provided the first histological investigations into the ommatophores (Fig. 7.13.1.2.10), notopodial chaetal sacs, and excretory organs in selected species of *Eupolyodontes* and *Polyodontes* (Pflugfelder 1932, 1934). In 1963, Åkesson described the cerebral and internal morphology of the brain in *Polyodontes oerstedi* (Åkesson 1963). The only other published observations for Acoetidae were by Storch (1968) on the general segmental musculature in *Polyodontes oerstedi*, and by Wolf (1986) on the presence of putative venom glands in piercing jaws across Aphroditiformia.

Nervous system. The most detailed account of the nervous system of an acoetid was given by Åkesson (1963) for *Panthalis oerstedi*, showing a bilobed brain and corpora pedunculata (mushroom bodies) that is similar in architecture found in the aphroditid *Aphrodita aculeata* Linnaeus, 1758, the polynoids *Lepidonotus clava* (Montagu, 1808) and *Harmothoe areolata* (Grube, 1860), and the sigalionid *Sthenelais* cf. *limicola* (Heuer and Loesel 2009, Heuer et al. 2010). In a detailed study, these complex structures are morphologically reminiscent of that of insects and are consistent with their active lifestyle and the important role of the eyes (paired mushroom body neuropils, unpaired midline neuropils and olfactory glomeruli; Heuer and Loesel 2009, Heuer et al. 2010). The large stalked ommatophores of *Panthalis* are partially invaded by the corpora pedunculata, comparable to what was observed in *Polynoe scolopendrina* Savigny, 1822 (Polynoidae; Hanström 1927). The extent of this invasion across other acoetid genera with ommatophores is unknown. A large central neuropil is present and is surrounded by large- to medium-sized neurons. Five mesodermal strands penetrate the cerebral ganglion, corresponding to the medial antennae and the paired lateral antennae and palps. Åkesson (1963) noted that the variable positions of the prostomial appendages (i.e., lateral antennae, palps, and median antenna) complicate their innervation to the brain. Since Åkesson (1963), there have been subsequent evaluations of the nervous system in *Panthalis oerstedi* by Orrhage (1991) and Orrhage and Müller (2005), confirming previous accounts while further elucidating the orientation and innervation of palp and antennal nerves in relation to the brain and the circumesophageal nerve ring.

Eyes. Pflugfelder (1932) characterized the fine structure of the eyes (Fig. 7.13.1.2.10) in *Polyodontes tidemani* Pflugfelder, 1932 and in *Eupolyodontes amboinensis* (as *Eupolyodontes sumatranus*). In his remarks, he noted that acoetids possess unusual stalked eyes with proportions unlike those of other annelids. The simple (Fig. 7.13.1.2.10A) or non-stalked eyes of acoetids are similar to those found in other scale worms, being surrounded by a thin layer of non-pigmented epithelium. The sensory and supporting cells can be distinguished within the retina and are surrounding the crystalline body and connecting fibrils. The supporting cells are uniquely flask shaped under the rhabdoms, and Pflugfelder (1932) noted that these supporting cells provide greater support than those in other scale worms. In comparison, the stalked eyes (Fig. 7.13.1.2.10B) are quite different from the eyes of other annelids, often so large that they distort the prostomium and its appendages. In the center of the eye, there is an iris-like diaphragm and a pupil clearly visible. This diaphragm in Pflugfelder's illustrations for *Eupolyodontes amboinensis* clearly subdivides the ommatophore into anterior and posterior sections. The anterior refractive body is dome-shaped above the pupil. Both the cornea and the anterior chamber of the eye are crystal clear. The posterior refractive body (below the diaphragm) makes up the bulk of the ommatophore, with the retina and pigment cells lying distally. Surprisingly, the pedunculate eyes of *Polyodontes* and *Panthalis* are similar to that of *Eupolyodontes*; however, their proportions are more elongate (Fig. 7.13.1.2.10C). The fine structures of the ommatophores are very similar to the simple eyes, with flask-shaped sensory cells and well-defined rhabdoms. A strong optic nerve is present and leads into the central neuropil (Pflugfelder 1932, Åkesson 1963). Åkesson (1963) noted that the second pair of eyes (=simple eyes) are likely rudimentary and nonfunctional in *Panthalis oerstedi*, with their nerve fibers seemingly not connected. It is unclear if these eyes lack function in all species of *Panthalis* or across other acoetid genera with simple eyes. Surprisingly, if the large ommatophores are damaged in *Panthalis*, they do not regenerate but are replaced by the smaller rudimentary pair that migrates and forms a misshaped ommatophore with a large transparent cornea and well-defined optic nerve (Åkesson 1963).

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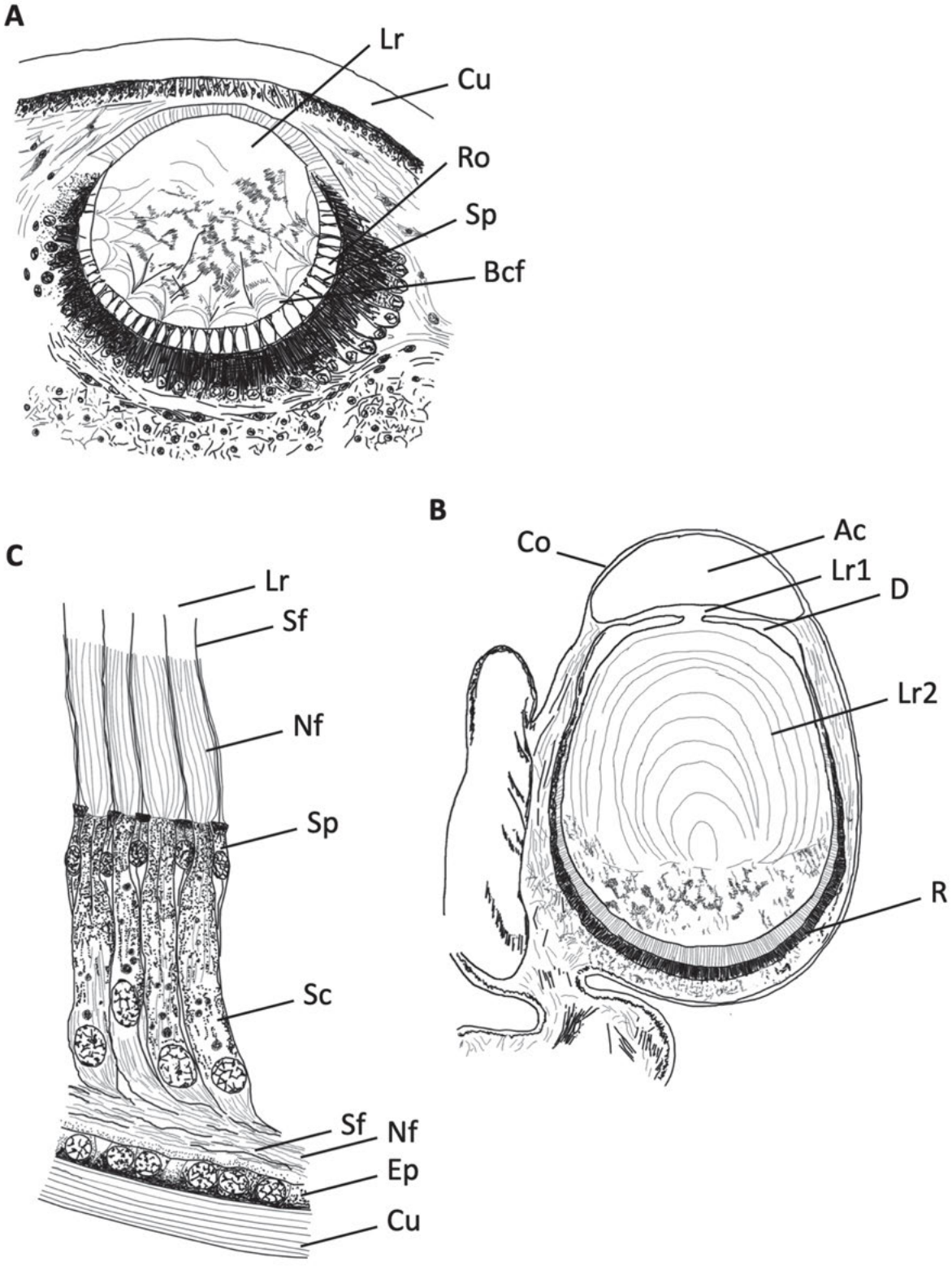


Fig. 7.13.1.2.10: Internal eye morphology of Acoetidae. Redrawn after Pflugfelder (1932). A, Cross section through a sessile eye of *Polyodontes tidemani* Pflugfelder, 1932. B, Frontal section through the ommatophore of *Eupolyodontes amboinensis* Malaquin & Dehorne, 1907 (as *Eupolyodontes sumatranus* Pflugfelder, 1932). C, Median section through the stalked eye of *P. tidemani*. Images not drawn to scale. Ac, anterior chamber; Bcf, bow-shaped connecting fibrils; Co, cornea; Cu, cuticle; D, diaphragm; Ep, epidermis; Lr, light-refractive body; Lr1 and Lr2, anterior and posterior refractive body, respectively; Nf, neurofibrils; R, retina; Ro, rhabdoms; Sc, sensory cell; Sf, support fibers; Sp, support cells.

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Musculature. Storch's (1968) comparative studies on segmental muscles in annelids is the most detailed myoanatomical description for Acoetidae. In general, the musculature appears simplified or less developed than those of nontubiculous scale worms. Circular muscles are absent as in other scale worms, but consistency in body wall and parapodial muscles from segment to segment is absent (Storch 1968, Tzetlin et al. 2002, Tzetlin and Filippova 2005). When compared to the myoanatomy of *Aphrodita* (Aphroditidae), *Panthalis oerstedi* lacks several muscle groups from both, the body wall (e.g., longitudinal and ventral oblique muscles) and from the parapodia (e.g., acicular muscles). In general, the parapodial musculature is most notably different in acoetids when compared to other scale worms, being modified to accommodate the notopodial chaetal sacs. In turn, these changes have also modified the degree of intestinal caecum within the parapodial space.

Nephridia. There is relatively little known about the excretory organs in Acoetidae. Pflugfelder (1934) remains one of the few studies to examine both the excretory system and the feltage chaetae in detail. In general, the nephridia are extremely small given the large size of acoetids, questioning their overall function. Based on his accounts, the nephridia are closed blindly to the coelom, composed of follicles that contained golden granules that are enveloped in a chitin-like sheath. Pflugfelder (1934) noted that their color contributes to the coloration of the internal notopodial chaetal sacs, offering up the hypothesis that the two structures are closely tied together. Further studies are needed to characterize what, if any, association exists between these two structures. Excretory granules can also be found throughout the caecum and elsewhere, suggesting that excretion is largely carried out by body epithelium.

Feltage chaetae. As early as 1868, Claparède noted a distinct morphological feature that appeared as a sinuous cord trailing off into the body cavity from the parapodia in *Polyodontes maxillosus*. In a later and more thorough examination, Eisig (1887) referred to these unusual structures as "segmented spinning glands," comprised of bundles of fine golden threads that exited through a notopodial slit. Pflugfelder (1934) showed that these fine golden threads were in fact chaetae formed by chaetogenesis but continued to use the term "spinning gland" although his histological investigations proved otherwise. Since then, the term "spinning gland" has also been applied to any felt-like covering in species of *Aphrodita* (Aphroditidae), and for species of *Sthenelanella* (Sigalionidae) (Pettibone 1969, Tilic et al. 2021). In her revision of Acoetidae, Pettibone (1989) explicitly states that this term is a misnomer but its use continues regardless. In an attempt to rectify the prolonged use of inaccurate terminology, we have instilled the terms "feltage chaetae" and "notopodial chaetal sacs" based on Tilic et al. (2021) for *Sthenelanella* when describing the golden notopodial fibers of Acoetidae. Briefly, the notopodial chaetal sacs of Acoetidae are covered by peritoneum (= coelomic epithelium) and have a metallic sheen with tightly packed golden yellow to green fibers. On the smaller closed end, loose connective tissue and excretory cells are present, further contributing to the hypothesis that excretion and notopodial chaetal sacs are interconnected (Pflugfelder 1934). The notopodial chaetal sacs lie nearly parallel to the notopodium when within them, then turn perpendicularly, becoming free within the coelom. The sacs are longer and more prominently coiled in the anterior segments, while being shorter with fewer coils in the posteriormost segments. Pflugfelder (1934) noted internal glandular tubes proximal to the notopodial slit where the feltage chaetae exit, suggesting that secretions enable the feltage chaetae to be separated into individual fibers during tube construction. All acoetids possess notopodial chaetal sacs from segment 9. In the description of *Acoetes jogasimae* (Izuka, 1912), it was noted that feltage chaetae was not observed, but the original drawings show large oocytes that likely obscured them.

Regeneration. Aphroditiformids have remarkable regenerative abilities across their external morphological features (e.g., elytra, dorsal cirri, and antenna), but to what effect anterior or posterior ends are capable of regenerating is unknown across the families. In Acoetidae, several specimens have been caught exhibiting posterior regeneration. Because most species are only known by anterior portions, it is largely presumed that acoetids are capable of regenerating an entirely new anterior region after the posterior region retreats within their tubes to regenerate (Pettibone 1989).

Reproduction and development

Reproduction and development in Acoetidae are unknown and largely assumptive from our knowledge of closely related Aphroditiformia. In general, acoetids can be considered gonochoristic with external fertilization. Sexes are separate, as both sperm and large yolky oocytes have been observed within the posterior body cavities (Hartman 1951, Pettibone 1989). Like other scale worms, gametes likely exit the coelom through a ciliated coelomostome and continue out through a narrow ciliated duct (Christie 1982). This reproductive morphology is common among errant annelids.

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Larval development in Acoetidae has not yet been described (Rouse and Pleijel 2001). Similar to other Aphroditiformia, acoetids likely have trochophore larvae present in the water column 1–2 days after fertilization. Distinctive structures, such as eyespots or rudimentary appendages needed for familial identification, likely develop in the metatrochophore and nectochaete larval stage. Juvenile acoetids were mentioned by Pettibone (1989) for the genera *Acoetes* and *Panthalis*, stating a close resemblance to the adults but differing in their chaetal morphology and degree of eye development and position.

Biology and ecology

Acoetids have a distribution that is effectively worldwide, common between intertidal zones and 1500 m. Most species are described from warm temperate and tropical regions, with no record from Antarctic waters. Soft sands and mud are preferred substrates, but *Eupanthalis tubifex* is known to inhabit shell gravel and *Polyodontes kuroshio* is described from rocky substrates.

All acoetids inhabit self-constructed tubes (Fig. 7.13.1.2.4A, B), reaching up to a meter or more in length for larger species (e.g., *Polyodontes lupines*). In *Euarche maculosa* (Treadwell, 1931), the posterior portion of the body is firmly attached to the tube and may explain why most acoetids are only represented by fragments during collection (Willey 1905). Unlike most other annelids, acoetids construct their tubes using feltage chaetae (chitinous silken fibers) and not membranous linings. Each tube is carefully constructed by weaving the feltage chaetae into crisscross patterns, which they cement together using the surrounding substrate (Pettibone 1989, Jumars et al. 2015). These tubes may have a parchment-like appearance but are tough and fibrous. Acoetid tubes are slightly larger than the worm and may be flush with (e.g., *Polyodontes lupinus*) or rise above the sediment (e.g., *Eupolyodontes batabanoensis*). Tubes are often repaired rather than abandoned. Barnich and Steene (2003) reported that *Polyodontes vanderloosi* repaired a damaged portion of a tube within 24 hours after being removed for *in situ* underwater photography. *Acoetes pleei* has been reported to build Y-shaped tubes, shared between two individuals. Overall tube construction varies between species and may be open or closed posteriorly. Tubes may exhibit mucus or cobweb-like extensions concealing the entrance, may be with or without a well-defined external collar, may be annulated, branched, narrowed, or wider in the middle or posterior portions. Numerous commensal organisms are also often associated within Acoetidae tubes, including entoprocts, gastropods, bivalves, and even other scale worms. *Polyodontes lupinus* is often found with the commensal gastropod *Cochliolepis parasitica* Stimpson, 1858, living under their elytra and on their body surface. Only known from these worms, this gastropod feeds off detritus brought into the tube during respiration and feeding. Nielsen (1964) noted that acoetids are often associated with long-lived commensals capable of generating their own water currents. Sponges, algae, bryozoans, or other encrusting organisms may also be present externally on tubes that rise above the sediment surface.

Tube construction itself is an extremely intricate process in Acoetidae. The best *in situ* description of this process is by Watson (1895) on *Panthalis oerstedi* from aquaria. No study has since examined this process for other acoetids; however, their morphology and that of collected tubes suggests that the construction process is highly similar for all. In short, Watson (1895) noticed that tube construction (from scratch) begins by weaving their feltage chaetae into what looks like small cobwebs where mud or sediment can be attached. From within, additional layers of feltage chaetae are added parallel to each other but transverse to the tube. These layers are not consistent for the entire length of the tube, and often, no consistent pattern was found along the tube. As the interior dimensions decrease with the added layers, the worm will expand its anterior segments and burst through the anterior portion of the tube. Once burst, the entire process starts over, with the free ends of the internal tube splayed outward. According to Watson (1895), the tubes are a series of hollow truncated cones stacked up one inside the other.

Because acoetid tubes are not secretions, their construction requires both morphological and behavioral modification. Parapodia of segment 2 (buccal segment), so-called weaving feet (Watson 1895), are used in conjunction with their buccal cirri to manipulate the feltage chaetae and the in-swept mud and sediment. As the tube enlarges, the body and elytra will be pressed against the tube for support, allowing the weaving feet, and occasionally dorsal cirri of segment 3, to further assist with construction. Unlike normal parapodial paddling motion, in acoetids, parapodia from segment 2 are brought together near the midline of the body to perform the weaving action (Fig. 7.13.1.2.6B). During this process, the curved chaetae of segment 2 direct the feltage chaetae toward the buccal region. In Acoetidae, segment 9 (Fig. 7.13.1.2.6E) marks the start of the production and storage of feltage chaetae and the beginning of the aristate — penicillate neurochaetae (type a, sensu Pettibone 1989). Resembling bottlebrushes, these neurochaetae are directed anteriorly and guide the feltage chaetae toward the weaving feet. Watson (1895) noted that the spinules of these brush-shaped

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neurochaetae appear to open and close when manipulating the feltage chaetae.

Acoetids possess parapodial- and sometimes prostomial branchiae (Fig. 7.13.1.2.7), but the dynamics of respiration or tube ventilation is largely unknown. Water in the tube is likely renewed by carefully orientating their prostomial appendages and their first few segments, directing water flow inward similar to that of tube dwelling sigalionids (Eibye-Jacobsen et al. 2019). Additionally, respiration is likely further aided by their mutualistic association with commensals capable of generating their own water currents (Pettibone 1989). Watson (1895) observed that the elytra in *Panthalis oerstedi* (in aquaria) do not lie flat but are held above the body and exhibit a constant rise and fall, indicative of facilitating water exchange for the purpose of respiration. Polynoids also carefully position their elytra to direct water posteriorly over their bodies, but circulating water currents are generated by ciliated regions along their parapodia and the surface of their dorsum (Lwebuga-Mukasa 1970). Interestingly, ciliation across the dorsal body surface and along the parapodia is not reported in Acoetidae, suggesting that acoetids rely on other means to generate respirational water currents.

Acoetids are discretely mobile, reluctant to leave their tubes entirely (Jumars et al. 2015). If disturbed, acoetids will retreat within or, as in the case of *Polyodontes lupinus*, will position themselves head down. Watson (1895) noted that *Panthalis oerstedi* was capable of awkwardly swimming (in aquaria), but to what extent this is utilized in the wild is unknown. Acoetids are strategic ambush (sit and wait) predators that lure prey by protruding the tips of their palps, or their elongated mouth papillae, from their tube, seizing unsuspecting passers (Fig. 7.13.1.2.3B). Acoetids grasp or pierce their prey with their beak-like jaws (Fig. 7.13.1.2.5) then engulf it with their highly expandable pharynx. Using *Polyodontes lupinus* and *Euarche tubifex* (as *Eupanthalis*), Wolf (1986) identified that the piercing jaws of these two acoetids similarly had an internal canal and organ assumed to be a venom gland, but the canal did not open at the tip of the jaws. The venom gland of acoetids is smaller and less developed compared to the size of the animal and to the other scale worm families. The functionality of the venom delivery system requires verification, as well presence of venom glands across all acoetid genera. Occasionally, the voraciousness of acoetids is on display, as anterior portions of *Polyodontes maxillosus* have been caught on fishing lines, specifically an extended pharynx (wider than body) with fluorescent ultramarine-blue granules on the tips and four denticulate jaws. These fluorescent tips are likely used to attract prey at night; however, it is unknown how many acoetids have this feature (Pettibone 1989).

Phylogeny and taxonomy

The original family designation for Acoetidae was "Acoetea" by Kinberg (1856) and included species descriptions for *Panthalis oerstedi* and *Acoetes grubei* (Kinberg, 1856). However, Ranzani (1817) for *Polyodontes maxillosa* is the earliest reference to any acoetid. The taxonomic nomenclature of Acoetidae has varied significantly over time, most notably being referred to by "Acoetinae," "Polyodontidae," or "Polyodontinae" (Pettibone 1989). Using a number of morphological characters, Muir (1982) suggested that Acoetidae (as "Polyodontidae") be treated as a subfamily of Polynoidae (as "Polyodontinae") given that he found them to only differ by the presence of feltage chaetae (putative synapomorphy). Rouse and Fauchauld (1997) using cladistic analyses of morphological characters recovered Acoetidae and Aphroditidae as sister groups because of the shared presence of feltage chaetae. Eventually, those scale worm groups having only simple chaetae were lumped together in what was referred to as the "Aphroditoidea" and included Acoetidae, Aphroditidae, Eulepethidae, and Polynoidae (Rouse and Pleijel 2001). Although all previous classifications are no longer considered valid, it is interesting to note that the once considered Acoetidae synapomorphies are now all considered shared homologous features: ommatophores (with Aphroditidae and Sigalionidae), "silken" or feltage chaetae (with Aphroditidae and Sigalionidae; Rouse and Fauchald 1997, Tilic et al. 2021), and denticulate jaws (with Iphionidae and Polynoidae; Pettibone 1989).

Recent phylogenetic analyses across Aphroditiformia (Gonzalez et al. 2018, Zhang et al. 2018) has continued to increase representation across all families, with the exception of Acoetidae, where only a single species continues to be available for genetic comparisons. Currently, this is one of the greatest knowledge gaps that remains in Aphroditiformia, as the lack of additional genetic sequences for Acoetidae prevents any further verification of their monophyly and phylogenetic position with respect to Iphionidae and Polynoidae.

Wiklund et al. (2005) provided the first molecular analyses to include a member of Acoetidae (i.e., *Panthalis oerstedi*). Although her dataset was limited, Acoetidae was recovered sister to Polynoidae, rendering "Aphroditoidea" polyphyletic. More recently in a combined approach using molecular and morphological data, Gonzalez et al. (2018) recovered Acoetidae in a clade with Iphionidae, sister to Polynoidae. Although the relationship to Iphionidae was poorly supported by the maximum likelihood analysis, the sister relationship to Polynoidae was highly supported across analyses. Using total evidence approaches (molecular + morphology only terminals), the

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phylogenetic position of Acoetidae remained stable with the inclusion of *Eupanthalis* and *Polyodontes* by morphology only (see Gonzalez et al. 2018), with pseudopenicillate neurochaetae as the apomorphy uniting the family. Zhang et al. (2018) generated the first Acoetidae mitochondrial genome for *Polyodontes oerstedi*; however, recent phylogenetic investigations using mitochondrial genomes (Gonzalez et al. 2021) continue to rely on a single acoetid species. Nevertheless, the implementation of mitogenome analyses continues to recover Acoetidae independent of, and sister to, Polynoidae.

Diagnoses of genera

***Acoetes* Audouin & Milne Edwards, 1832**
Type species: *Acoetes pleei* Audouin & Milne Edward, 1832
13 species
Diagnosis: Acoetids with bulbous, colored, stalked ommatophores and small pair of sessile lateral eyes (type 3). Median antenna well developed, with ceratophore positioned near the middle of the prostomium. Lateral antennae ventrally attached on ommatophores. Palps smooth or papillate. Pharynx with up to 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, tapering to slender tips abruptly; plumose subdistally and spinous rows basally. Type b neurochaetae short but not hidden by notopodia. Parapodial branchiae may be present.

***Euarche* Ehlers, 1887**
Type species: *Euarche tubifex* Ehlers, 1887
5 species
Diagnosis: Acoetids with oval or bilobed prostomium (type 1). Two pairs of sessile eyes, may be absent in some species. Median antenna well developed. Lateral antennae anterior, visible. Pharynx with up to 15 pairs of equally sized papillae. Jaws with eight lateral teeth. Segment 2 with numerous capillary notochaetae. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, long, lanceolate with lateral spinules. Parapodial branchiae absent.

***Eupanthalis* McIntosh, 1876**
Type species: *Eupanthalis kinbergi* McIntosh, 1876
6 species
Diagnosis: Acoetids with oval or bilobed prostomium (type 1). Two pairs of sessile eyes, may be absent in some species. Median antenna absent. Lateral antennae anterior, visible. Pharynx with up to 15 pairs of equally sized papillae. Jaws with eight lateral teeth. Segment 2 with or without notochaetae. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, long, lanceolate with lateral spinules. Parapodial branchiae absent.

***Eupolyodontes* Buchanan, 1894**
Type species: *Eupolyodontes cornishii* Buchanan, 1894
7 species
Diagnosis: Acoetids with bilobed prostomium and large, colored ommatophores (type 2). Median antenna may be absent. Bilobed nuchal organ. Lateral antennae medial to ommatophores. Short palps. May possess prostomial branchiae. Parapodial branchiae present. Pharynx with up to 39 pairs of papillae, middorsal and midventral papillae long. Jaws with up to 17 lateral teeth. Upper neurochaetae (type a) from segment 9 with double brush-shaped tips.

***Neopanthalis* Strelzov, 1968**
Type species: *Neopanthalis pelamida* Strelzov, 1968
1 species
Diagnosis: Acoetids with bilobed prostomium. Ommatophores enlarged and fused (type 4). Median antenna well developed. Lateral antennae dorsally positioned. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, lanceolate with lateral spinules. Parapodial branchiae absent.

***Panthalis* Kinberg, 1856**
Type species: *Panthalis oerstedi* Kinberg, 1856
9 species
Diagnosis: Acoetids with bilobed prostomium, ommatophores mostly lacking color (type 3). Lateral sessile eyes lacking. Well-developed median antenna, ceratophore near middle of prostomium. Lateral antennae attached ventrally on ommatophores. Palps smooth. Pharynx with 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, distally plumose. Type b neurochaetae very short, hidden by notopodium. Parapodial branchiae absent.

***Polyodontes* Blainville, 1828**
Type species: *Polyodontes maxillosus* (Ranzani, 1817)
16 species
Diagnosis: Acoetids with bilobed prostomium and bulbous, colored, stalked ommatophores (type 3). Lateral pair of sessile eyes present. Well-developed median antenna, ceratophore near middle of prostomium. Lateral

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antennae attached ventrally on ommatophores. Palps smooth or papillate. Pharynx with 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, spinous. Type b neurochaetae shorter than type a but not completely hidden by notopodia. With or without parapodial branchiae.

Zachsiella Buzhinskaja, 1982

Type species: *Zachsiella nigromaculata* (Grube, 1878)
1 species

Diagnosis: Acoetids with bilobed prostomium and large, colored ommatophores (type 2). Median antenna well developed. Lateral antennae medial to ommatophores. Parapodial branchia absent. Pharynx with 13 pairs of papillae, middorsal and midventral papillae longer. Jaws with up to seven lateral teeth. Upper neurochaetae (type a) from segment 9 acicular, spinous, aristate. Without parapodial branchiae.

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Stéphane Hourdez

7.13.1.4 Polynoidae Kinberg, 1856

Introduction

The Polynoidae Kinberg, 1856 is, by far, the largest family of Aphroditiformia, with over 900 species. This family is very genus-rich, with 174 currently valid genera, 47% of which are monospecific (Fig. 7.13.1.4.1). Another 32% of genera comprise between two and four species only. The most species-rich genus is *Harmothoe* Kinberg, 1856 with 156 species (16.6% of all species), followed by *Lepidonotus* Leach, 1816 (80 species), *Eunoe* Malmgren, 1865 (49 species), *Polynoe* Lamarck, 1818 (48 species), and *Lepidasthenia* Malmgren, 1867 (42 species). They inhabit a very wide range of habitats, from intertidal to abyssal depths, from tropical waters to polar areas (Fig. 7.13.1.4.2). This family has also been very successful in deep-sea hydrothermal vent ecosystems where it is the most species-rich annelid family (over 50 species) and occupies all microhabitats where metazoans are found in this very unusual habitat.

Although they are good swimmers (Fig. 7.13.1.4.2D), only the genera *Drieschia* Michaelsen, 1892 and *Podarmus* Chamberlin, 1919 are holopelagic. The other species only occasionally foray into the water column. *Drieschia*, however, corresponds to a larval form. Similarly, based on a barcode approach, Neal et al. (2014) have shown that *Herdmanella gracilis* Ehlers, 1908 specimens captured in the plankton actually correspond to larval forms of *Austrolaenilla antarctica* Bergström, 1916.

As adults, polynoids usually shelter in small cavities or beneath rocks but can be found inside the tubes of other animals (see Symbiotic relationships section). Sizes usually range between 1 and 5 cm long, but the Antarctic species *Eulagisca gigantea* Monro, 1939 can reach about 30 cm in length and 12 cm width.

The relationship of Polynoidae with other families of Aphroditiformia remains unclear. There is not any recognized synapomorphy in Polynoidae. Recent molecular studies, however, suggest that Iphioninae should be considered a distinct family from Polynoidae (Gonzalez et al. 2018; Norlinder et al. 2012; Zhang et al. 2018). These studies included a single Acoetidae (*Panthalis oerstedi* Kinberg, 1856) that separated species of Iphioninae from the other species of Polynoidae. In addition to the use of a single species to represent Acoetidae, support for this topology is relatively limited (see relevant section on phylogeny for further discussion). In this chapter, Iphionidae are considered as part of the family Polynoidae,

https://doi.org/10.1515/9783110647167-005

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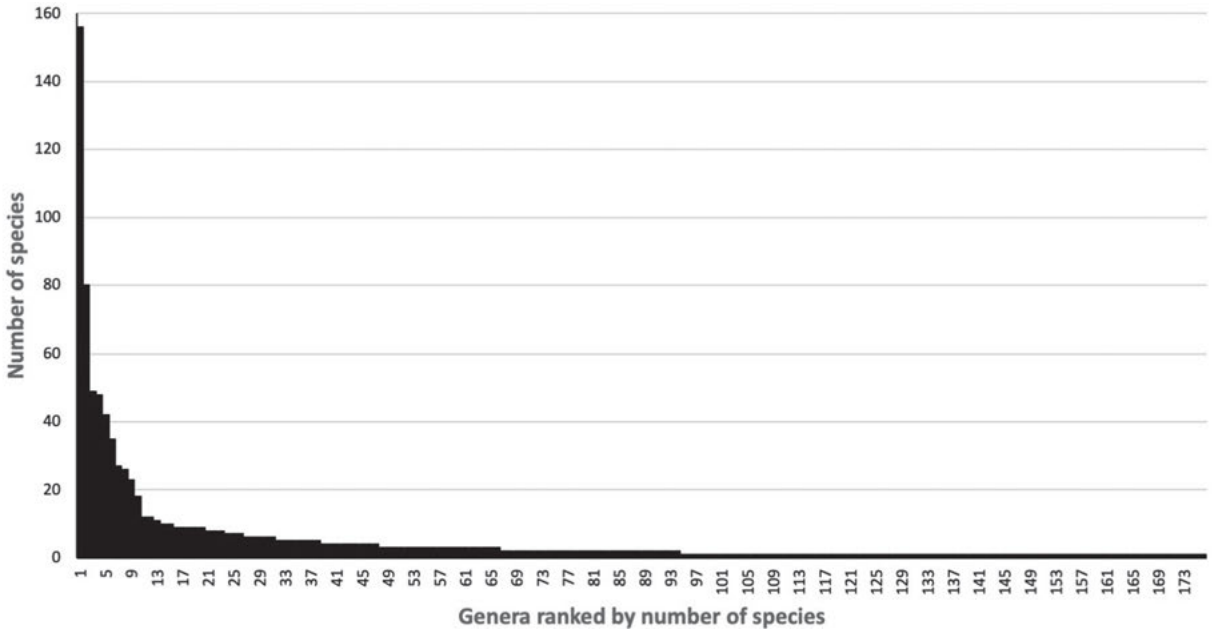


Fig. 7.13.1.4.1: Distribution of the number of species per genus.

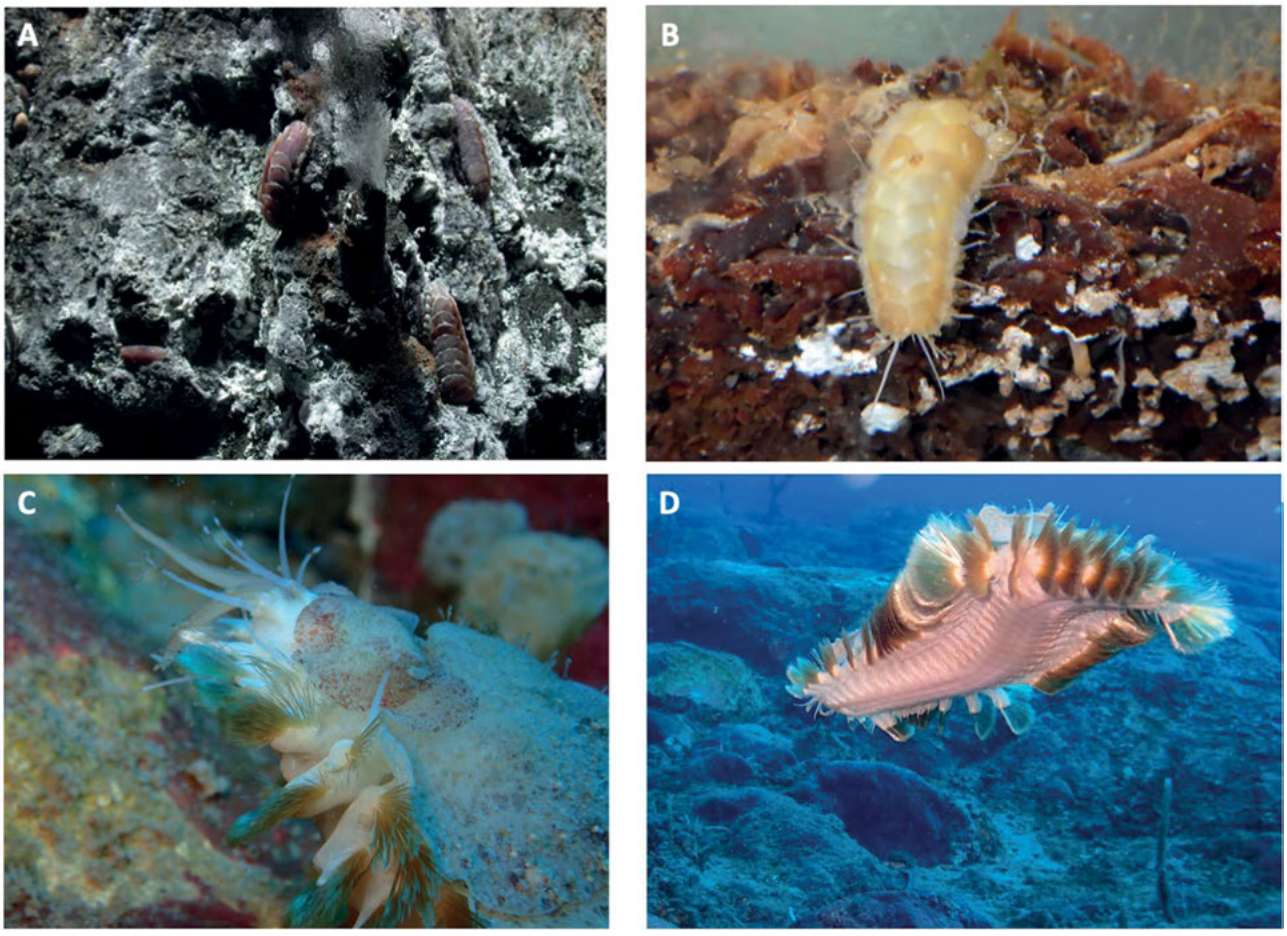


Fig. 7.13.1.4.2: Polynoidae in their habitat. A, *Branchinotogluma segonzaci* (Miura & Desbruyères, 1995). Lau Basin, Copyright WHOI-Lau 2009. B, *Harmothoe fuligineum* (Baird, 1865) on the holdfast of *Himantothallus grandifolia* (A. Gepp & E.S. Gepp) Zinova, 1959. C and D, *Eulagisca uschakovi* Pettibone, 1997. Close-up of the anterior on the bottom (C) and swimming (D). Copyright Pierre Chevaldonné (IMBE, France). B–D, Antarctica, Adélie Land. POLARIS summer campaign series.

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and referred to as the subfamily Iphioninae. Similarly, the revision of subfamilies proposed by Bonifácio and Menot (2019) will not be used here and the formerly accepted subfamily names will be used.

Morphology and taxonomically important characters

Polynoids possess numerous characters that are used in their taxonomy. This section offers an overview of these characters and their diversity in Polynoidae.

General appearance

The body can be linear or elliptical. The number of segments can be as small as 15 and reach well over 100. The numbering of segments in the past has not been consistent, and modern researchers agree to count the tentacular segment as the first segment.

Prostomium and anterior area

The prostomium is usually bilobed and can bear 0, 1, 2, or 3 antennae (Fig. 7.13.1.4.3). The subfamilies Bathyedithinae and Polaruschakovinae are completely devoid of antennae. The median antenna is always absent in the subfamily Iphioninae. The presence and position of the insertion of the lateral antennae is a key character in the higher-level taxonomy, in particular at the subfamily level (Fig. 7.13.1.4.3). In Lepidastheniinae and Lepidonotinae, the lateral antennae are inserted terminally on the prostomium (Fig. 7.13.1.4.3B and D). In Polynoinae, the lateral antennae are inserted ventrally or terminoventrally (Figs. 7.13.1.4.3A and 7.13.1.4.4A–C). In Iphioninae, lateral antennae can be missing as well (e.g., *Thermiphione*; Fig. 7.13.1.4.3E) or inserted terminally on the prostomium (e.g., *Iphione*; Fig. 7.13.1.4.3F). In Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonotopodinae (Fig. 7.13.1.4.3C), Macellicephalinae, Macellicephaloidinae, and Macelloidinae, the lateral antennae are absent. However, some species in these subfamilies possess frontal filaments attached to the anterior of the prostomium where lateral antennae are attached in Lepidonotinae and Lepidastheniinae (Fig. 7.13.1.4.4D). The styles of the antennae can be smooth or papillated (Figs. 7.13.1.4.3 and 7.13.1.4.4C), tapering regularly, or be subulate.

On either side of the prostomium, the palps are directed forward and can sometimes display linearly disposed tufts of cilia. Their overall proportions (length compared to the prostomium) can be used to distinguish species. Next to the palps, the cirrophores of the two pairs of tentacular (= buccal) cirri can either bear short, stout chaetae (Fig. 7.13.1.4.3A and B) or be smooth (achaetous; Fig. 7.13.1.4.3C–F). For a species, the cirri resemble those of the antennae (i.e., smooth or papillated; Figs. 7.13.1.4.3 and 7.13.1.4.4).

When eyes are present, they are always sessile. Deep-sea species are usually devoid of eyes (Fig. 7.13.1.4.3C and E). The eyes appear dorsally on the prostomium; the posterior pair is usually located on the posterior edge of the prostomium. The anterior pair can be located where the prostomium is widest (Fig. 7.13.1.4.3A, B, D, F) or sometimes on the ventral side of the prostomium (Fig. 7.13.1.4.3C).

Pharynx

The pharynx is eversible and can be projected forward (Fig. 7.13.1.4.10A). When fully extended, the opening is surrounded by papillae whose number, relative sizes, and shapes can be used to distinguish species. The pharynx is usually equipped with two pairs of jaws. Characteristics of these jaws (smooth or bearing teeth and the number of these teeth) are also used to distinguish species. In *Vampiropolynoe embleyi* Marcus & Hourdez, 2002, the jaws are lacking and only small plates remain at the opening of the pharynx (Fig. 7.13.1.4.10C). In this species, the inner surface of the pharynx is covered in keratinized teeth (Fig. 7.13.1.4.10D).

Parapodia

Parapodia can bear elytra (elytrophorous) or dorsal cirri (cirrigerous) (Fig. 7.13.1.4.5). In *Gesiella jameensis* (Hartmann-Schröder, 1974), an additional filamentous structure (called "accessory filamentous sensory organ" by Pettibone (1976)) is attached to the distal part of the cirrophores, in addition to the dorsal cirrus. The dorsal cirri can be smooth or papillated and can taper gradually to a fine tip or be slightly swollen close to the tip. A ventral cirrus, digitiform and usually small, is inserted near the middle of the neuropodium.

The parapodia are usually biramous (Fig. 7.13.1.4.5A, B), but the notopodium can be reduced or absent in some genera (Fig. 7.13.1.4.5C–F). The aciculae can sometimes protrude from the soft tissues (Figs. 7.13.1.4.5 and 7.13.1.4.6). The neuropodium also possesses characteristics that are used for taxonomy at different levels. The neuropodial acicular lobe (= prechaetal lobe) can be terminated by a terminal papilla (Fig. 7.13.1.4.6A), a fleshy extension above the protruding acicula (= supra-acicular process; Fig. 7.13.1.4.6B), or not have any extension. The neuropodium can be deeply incised (e.g., Lepidastheniinae; Fig. 7.13.1.4.6E), or the acicular lobe and postchaetal lobes can be short (e.g., Lepidonotinae; Fig. 7.13.1.4.6D). The ventral side of the neuropodium can also bear papillae (e.g., Lepidastheniinae; Fig. 7.13.1.4.6E).

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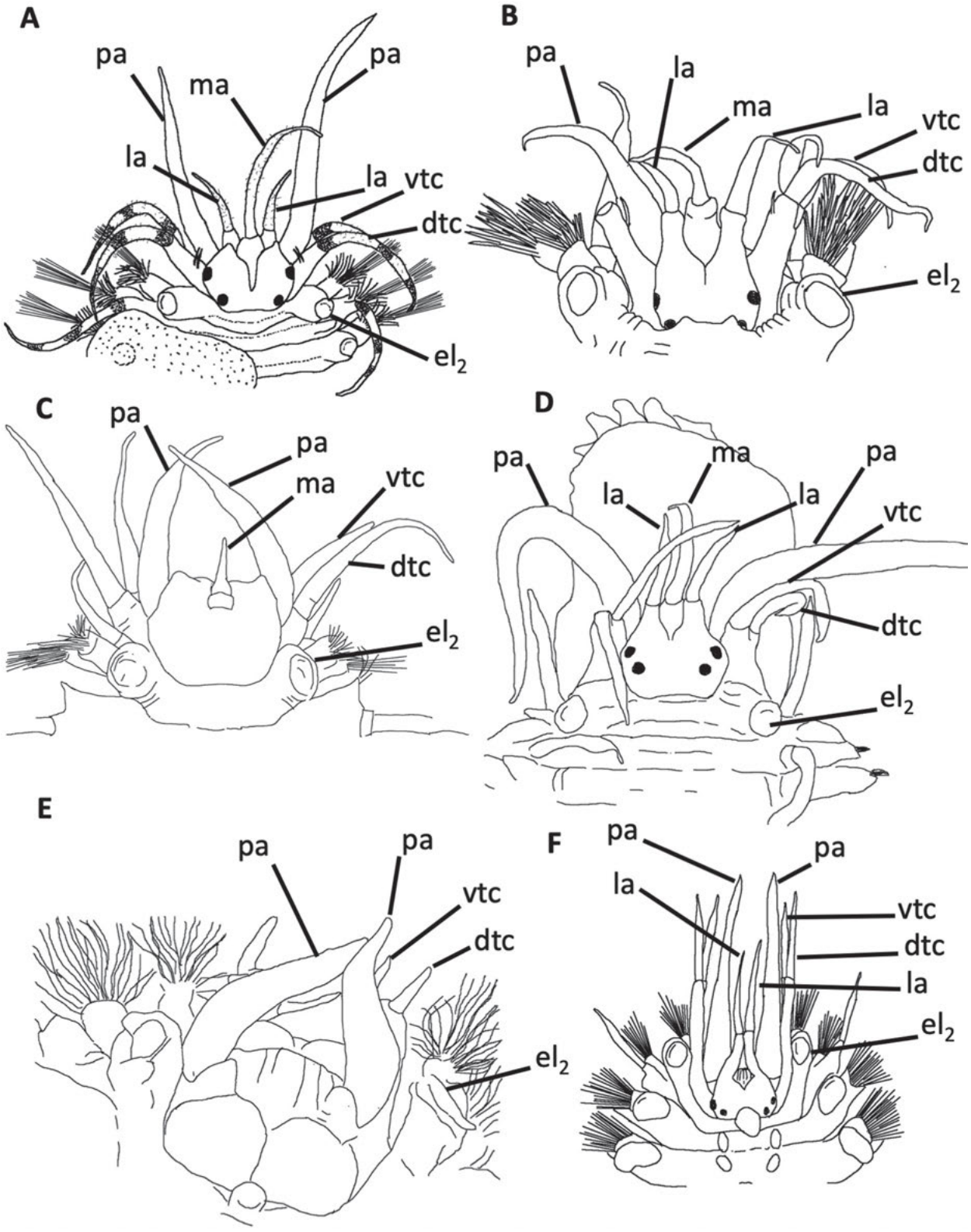


Fig. 7.13.1.4.3: Anterior regions of Polynoidae with different numbers of antennae. A, *Harmothoe extenuata* (Grube, 1840); redrawn after Barnich & Fiege (2003). B, *Lepidonotus carinulatus* (Grube, 1869); redrawn after Imajima (1997). C, *Lepidonotopodium atalantae* Desbruyeres & Hourdez, 2000. D, *Lepidasthenia loboi* Salazar-Vallejo, González & Salazar-Silva, 2015. E, *Thermiphione risensis* (Pettibone, 1986). F, *Iphione ovata* Kinberg, 1856; redrawn after Pettibone (1976). dtc, dorsal tentacular cirrus; el_2, elytrophore segment 2; la, lateral antenna; ma, median antenna; pa; palp; vtc; ventral tentacular cirrus.

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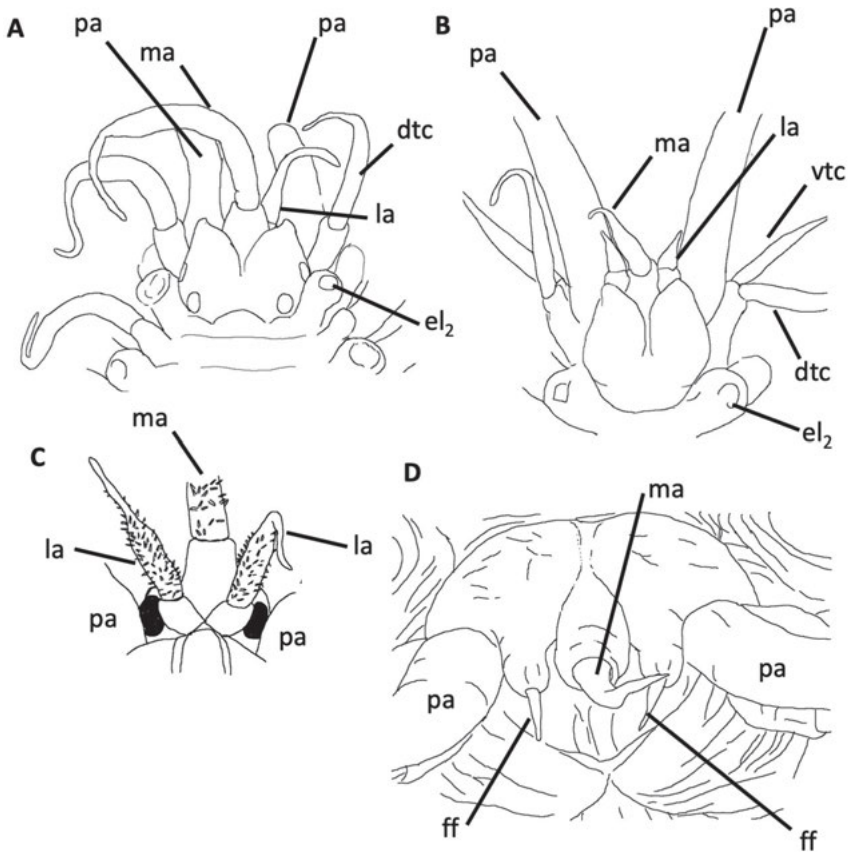


Fig. 7.13.1.4.4: Insertion of lateral antennae (A–C) and of frontal filaments (D).
A, Ventral insertion (e.g., *Harmothoe* sp.). B, Terminoventral insertion (e.g., *Malmgrenia* sp.). C, Ventral view of ventral insertion in *Harmothoe spinifera* (Ehlers, 1864). Redrawn after Imajima (1997). D, Frontal filaments occupy the position of lateral antennae. *Branchinotogluma sandersi* Pettibone, 1985. Frontal view. dtc, dorsal tentacular cirrus; el_2, elytrophore segment 2; ff, frontal filament; la, lateral antenna; ma, median antenna; pa, palp; vtc, ventral tentacular cirrus.

There are no compound chaetae. Notopodial and neuropodial chaetae are usually morphologically different. There is a great diversity of chaetal morphologies (Figs. 7.13.1.4.7 and 7.13.1.4.8) that are used as a key taxonomic character defining some genera. Notochaetae can be of different types in a single bundle. They can be smooth or with rows of spines. Notochaetae are often blunt tipped or capillaries, but in Iphioninae, they usually are feather capillaries (Fig. 7.13.1.4.7). Penicillate notochaetae are encountered in *Barrukia* Bergström, 1916.

The neurochaetae are very diverse (Fig. 7.13.1.4.8). Supra-acicular and subacicular neurochaetae are often of different types. Generic neurochaetae have a long shaft and a head beyond a swollen part (= shoulder). The proportion of the head and the presence of a semilunar pocket on the shoulder (e.g., *Subadyte* Pettibone, 1969) can be used in taxonomy. *Australaugeneria* Pettibone, 1969 and *Uncopolynoe* Wehe, 2006 bear hooks (Fig. 7.13.1.4.8) on the anterior neuropodia. The shoulder can also bear strong teeth (e.g., Lepidonotinae), and their number and robustness are useful at the species level.

Elytra

The elytra are found on chaetigers 2, 4, and 5 and every other segment until segment 23. The segments that do not bear elytra bear dorsal cirri instead. Their pattern beyond segment 23 is variable, and some species are devoid of elytra beyond segment 23 (e.g., *Polynoe scolopendrina* Savigny, 1822). Exceptions to the canonical elytral pattern exist. In Branchinotogluminae and Branchipolynoinae, the number of segments is 21, and segments 20 and 21 bear dorsal cirri only. In Macellicephalinae *Bathykurila guaymasensis* Pettibone, 1989, there are only 15 segments, and the two last ones also only bear dorsal cirri. The first pair of elytra is often distinctly different from the following ones: they accommodate the palps and tentacular cirri that project forward while covering the prostomium. In *Gorgoniapolynoe* Pettibone, 1991, the first pair of elytra is translucent. The elytra can completely cover the dorsum or they can be very small and leave most of the dorsum uncovered (e.g., *Branchipolynoe symmytilida* Pettibone, 1984).

The ornamentation of the elytra is also a very important character to distinguish species (Fig. 7.13.1.4.9). The species of Iphioninae have a very distinctive polygonal surface with spines or tubercles (Fig. 7.13.1.4.9A). The surface can be completely smooth (e.g., Branchipolynoinae and most Branchinotogluminae) or bear different structures. In particular, the presence and distribution of micro- and macrotubercles, as well as border and surface papillae (Fig. 7.13.1.4.9), are characters used. These are

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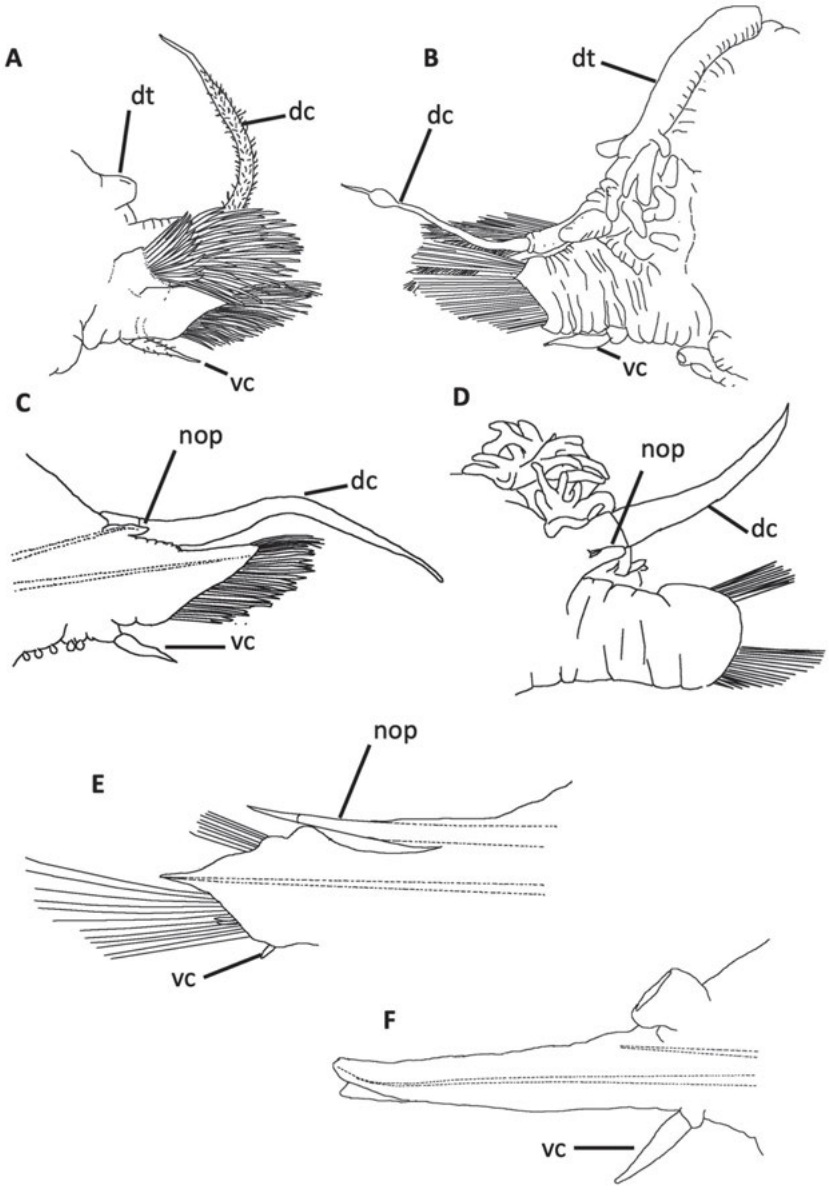


Fig. 7.13.1.4.5: Parapodia of Polynoidae. Biramous parapodia of *Harmothoe imbricata* (Linnaeus, 1767) (A) and *Euphione chitoniformis* (Moore, 1903) (B). Subbiramous parapodia from *Lepidasthenia interrupta* (Marenzeller, 1902) (C) and *Branchipolynoe tjiasmantoi* Lindgren, Hatch, Hourdez, Seid & Rouse, 2019 (D). Notopodium reduced to acicula. *Macellicephaloides uschakovi* Levenstein, 1971 (E). Uniramous parapodium from *Macelloides antarctica* Uschakov, 1957. Chaetae not represented (F). A, B, and C redrawn from Imajima (1997). E and F redrawn from Pettibone (1976). dc, dorsal cirrus; dt, dorsal tubercle; nop, notopodium; vc, ventral cirrus. Dotted lines are outlines of aciculae.

especially useful at the species level, allowing the distinction between closely related species (e.g., *Harmothoe*; Fig. 7.13.1.4.9B–G).

In most species, the elytra detach easily and are lost at the time of preservation. Their importance in identifying species requires that specimens be preserved in individual tubes.

Posterior segments

The pygidium bears a pair of anal cirri, but these are often lost when the animals are preserved. The anus can be terminal or dorsal. In male Branchinotogluminae and Branchipolynoinae, the posterior segments can be greatly modified. In association with sexually dimorphic ventral papillae, this led Marian Pettibone to initially describe different species for males and even a different genus (*Opisthotrochopodus* Pettibone, 1985).

Biology and ecology

Symbiotic relationships

Polynoidae are, by far, the polychaete family in which most of the commensal species are found (about half of the polychaetes known to be commensal). They are more often associated with echinoderms or with tube- and burrow-producing species from several phyla, including other polychaetes (Martin and Britayev 1998, 2018). Overall, about 20% of the Polynoidae species are commensal (Martin and Britayev 1998, 2018).

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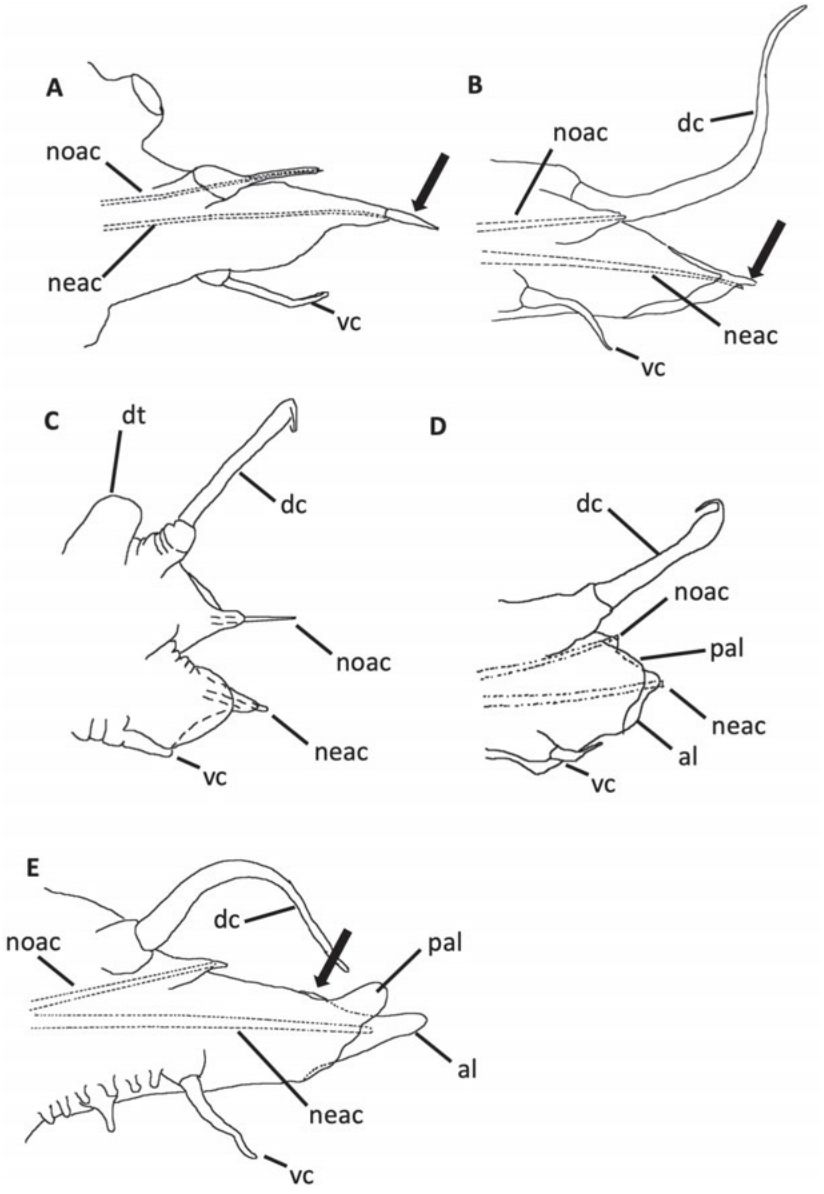


Fig. 7.13.1.4.6: Parapodial features (simplified drawings, chaetae omitted). A, Parapodium with terminal papilla (arrow). *Neobylgides scotiensis* Pettibone, 1993. B, Parapodium with supra-acicular process (arrow). *Malmgrenia lunulata* (Delle Chiaje, 1830). C, Parapodium without terminal processes. Only the aciculae protrude. D, Parapodium with a shallow incision between the presetal (= acicular) lobe and the postacicular lobe (e.g., Lepidonotinae). *Lepidonotus clava* (Montagu, 1808). E, Parapodium with a deeply incised neuropodium (e.g., Lepidastheniinae). *Lepidasthenia brunnea* Day, 1960. al, acicular lobe; dc, dorsal cirrus; dt, dorsal tubercle; neac, neuropodial acicula; noac, notopodial acicula; pal, postacicular lobe; vc, ventral cirrus. Dotted lines are outlines of aciculae. A, Redrawn from Pettibone (1993). B, D, E, Redrawn after Barnich and Fiege (2003). C, Redrawn after Bock et al. (2010).

A symbiotic relationship can be accompanied by morphological modifications of both partners (Martin and Britayev 1998, 2018). A reduction of parapodia and elytra is commonly observed in the genera *Branchipolynoe* Pettibone, 1984 and *Arctonoe* Chamberlin, 1910. The host can also exhibit morphological modifications; in particular, "worm paths" have been reported in various species of cnidaria with hard skeletons (De Assis et al. 2019, Martin and Britayev 2018).

Bioluminescence

Some Polynoidae display bioluminescence in epidermal cells of the elytra. The phenomenon was discovered in the family in late nineteenth century and has so far been observed in 17 distinct species (one Lepidastheniinae and 16 Polynoinae) (see Moraes et al. 2021 for a review). The luminescence is produced by a membrane photoprotein, called polynoidin, which reacts to the presence of superoxide radicals (Bassot and Nicolas 1995). These authors suggest that the tubercles on the elytra may act as lenses that focus the light emitted by special organelles, called photosomes, that are found in the cells of the basal layer of the elytra (Plyuscheva and Martin 2009). Although bioluminescence was not observed in the Lepidonotinae *Lepidonotus clava* (Montagu, 1808) and *Lepidonotus squamatus* (Linnaeus, 1758), an active polynoidin was purified from their scales, and the authors suggest it could be a superoxide radical scavenger (Plyuscheva and Martin 2009).

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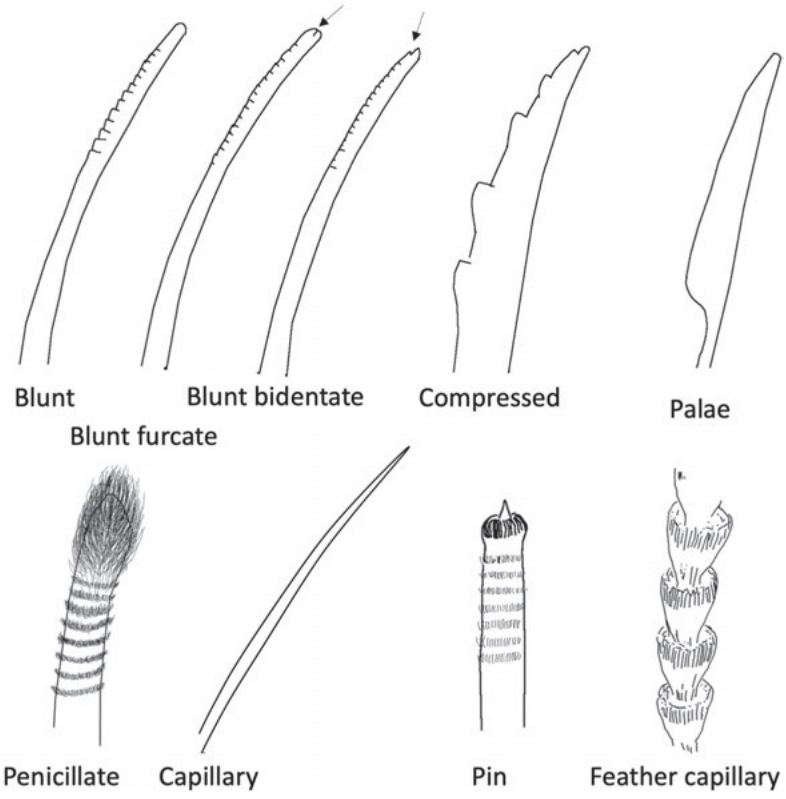


Fig. 7.13.1.4.7: Diversity of notochaetae. Top row redrawn after Muir (1982).

Feeding

Polynoidae are generally predators (Jumars et al. 2015), but some vent and seep species may feed on bacterial mats (e.g., *Vampiropolynoe embleyi* Marcus & Hourdez, 2002). Many Polynoidae include algal fragments in their diet. Some commensals take advantage of their host's diet, feeding either as kleptoparasites or by coprophagy (Jumars et al. 2015). Polynoidae are usually active predators, and they capture their preys by projecting their muscular pharynx forward. The pharynx is usually armed with two pairs of jaws that can be smooth or can bear teeth (Fig. 7.13.1.4.10). At the base of the jaws, a structure that may be a venom gland has been reported by Wolf (1986). In the species *Vampiropolynoe embleyi*, the jaws are missing and replaced by small sclerotinized plates (Fig. 7.13.1.4.10D; Marcus and Hourdez 2002). This species was collected in bacterial mats on which they likely feed. Digestion takes place all along the digestive system, from the pharynx lining to the gut and the segmental caeca (Fig. 7.13.1.4.10E; for further details, see chapter 7.13.1).

Respiratory exchange and respiratory pigments

Polynoids from different habitats (deep-sea, hydrothermal vents, shallow temperate) have similar oxygen consumption rates, and these rates are similar to those of other annelids (Le Layec and Hourdez 2021).

Most of the Polynoidae are devoid of true gills (branchiae), although some small appendages are referred to as gills in a variety of species (e.g., *Euphione* McIntosh, 1885; Fig. 7.13.1.4.5B). True gills are however found in some deep-sea hydrothermal vent species, in the subfamilies Branchiplicatinae, Branchinotogluminae, and Branchipolynoinae and in the species *Thermopolynoe branchiata* Miura, 1994 (subfamily Lepidonotopodinae) (Fig. 7.13.1.4.11). The gills in the species *Branchipolynoe symmytilida* Pettibone, 1984 and *Branchipolynoe* aff. *seepensis* Pettibone, 1986 (Branchipolynoinae) correspond to thin lateral expansions of the body wall and are not perfused by blood vessels (Fig. 7.13.1.4.11). Instead, the coelomic fluid circulates inside the gills, moved by patches of cilia (Hourdez and Jouin-Toulmond 1998).

For the species devoid of gills, gas exchange likely occurs by diffusion through the body wall. In shallow-water polynoids, water is renewed at the surface of the body by cilia located on the body wall (Lwebuga-Mukasa, 1970). This water flow is not produced by the movement of the elytra. In the Antarctic species *Eulagisca uschakovi* Pettibone, 1997, the posterior elytra form a funnel (Fig. 7.13.1.4.11A) from which water flows out, probably moved by rows of cilia found on the dorsum (personal observation).

The respiratory pigments found in the Polynoidae are all heme-containing pigments. Although a small vascular system is present, most Polynoidae are devoid

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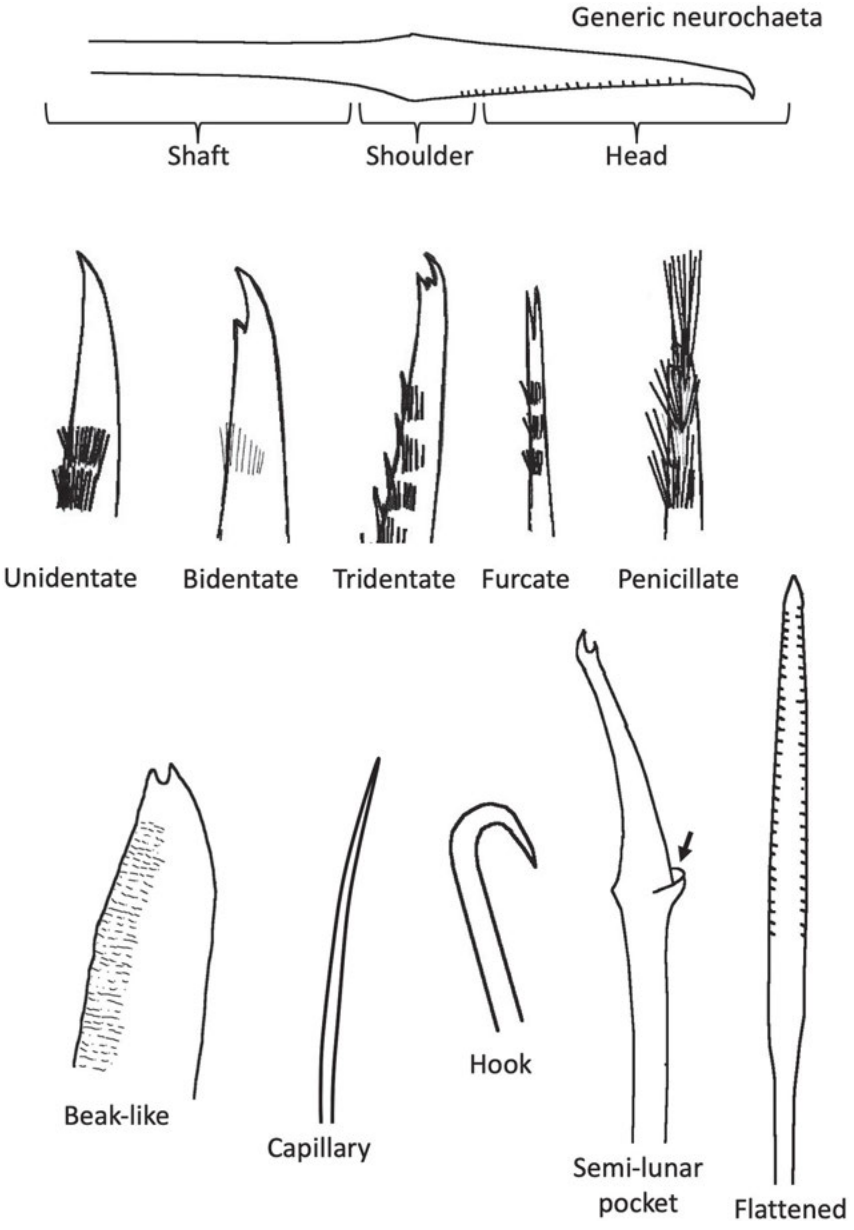


Fig. 7.13.1.4.8: Diversity of neurochaetae. Middle row and left of lower row: tip diversity.

of true hemoglobin circulating in the body. A specific globin is however expressed the nervous system, clearly visible in the ventral nerve cord and in the cerebral ganglia (Fig. 7.13.1.4.12A and B; Weber 1978, Weber and Vinogradov 2001). In some deep-sea hydrothermal vent species, large amounts of hemoglobin (i.e., globins circulating the body) are found in the coelomic cavity (Fig. 7.13.1.4.12). In the two species studied so far, *Branchipolynoe symmytilida* and *Branchipolynoe seepensis*, these hemoglobins exhibit a very high affinity for oxygen, and limited cooperativity (Hourdez et al. 1999a, b). The respiratory pigments contained in the body of hydrothermal vent species represent a very significant storage of oxygen for these species that experience chronic hypoxia. In the vent species *Branchipolynoe* aff. *seepensis*, assuming fully oxygenated hemoglobins, the total bound oxygen represents a quantity sufficient to meet the metabolic needs for about 90 minutes (Hourdez and Lallier 2007).

The hemoglobins are extracellular and, in *Branchipolynoe*, the globins have a unique structure for annelids, with tetradomain subunits arranged into dimers and trimers (Hourdez et al. 1999a, b, Weber and Vinogradov 2001). Molecular studies indicate that this circulating globin is the result of tandem gene duplications from an intracellular single-domain globin (Projecto-Garcia et al. 2010).

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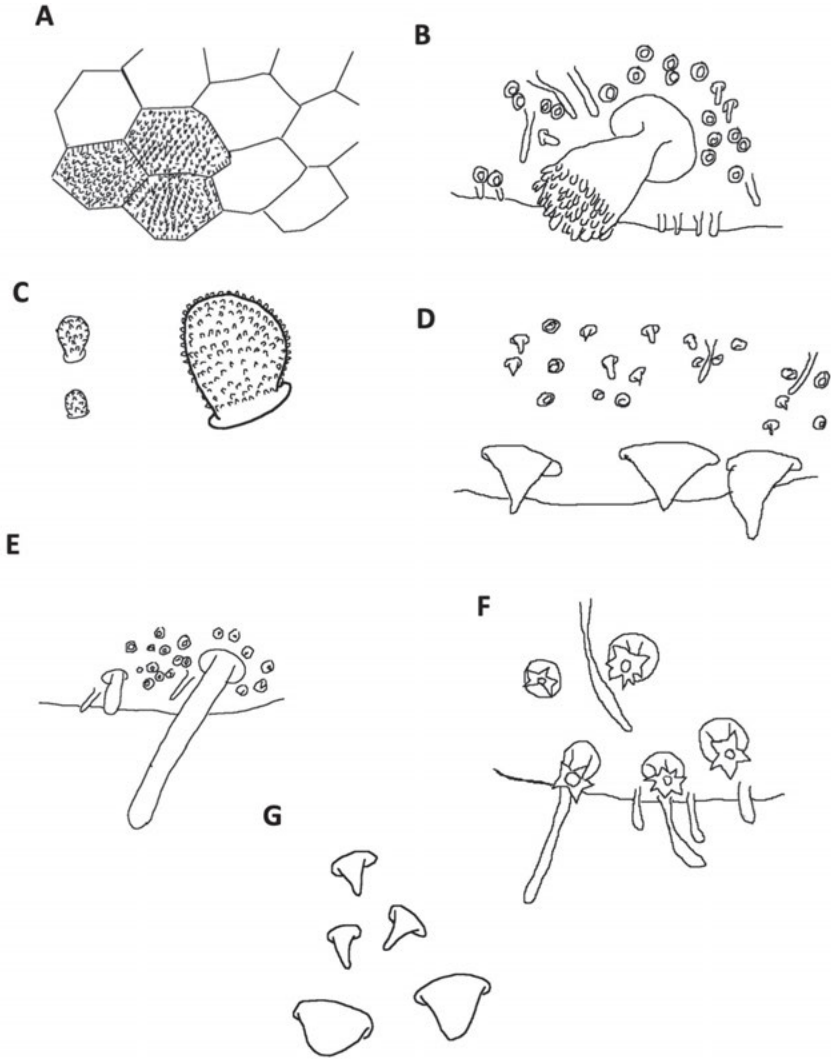


Fig. 7.13.1.4.9: Diversity of elytra surface ornamentation. A, Polygonal pattern typical of Iphioninae. Fine ornamentation only represented in three of the polygones. B–G, Macrotubercles from different species of *Harmothoe*. Redrawn after Barnich and Fiege (2003). B, Macrotubercle, border papillae, surface papillae, and microtubercles from *Harmothoe clavigera* (M. Sars, 1863). C, Macrotubercles from *Harmothoe globifera* (Sars G. O., 1873). D, Macrotubercles, surface papillae, and microtubercles from *Harmothoe aspera* (Hansen, 1878). E, Large finger-like macrotubercle, surface papillae, and microtubercles in *Harmothoe rarispina* (M. Sars, 1861). F, Surface papillae and star-tipped macrotubercles from *Harmothoe antilopes* McIntosh, 1876. G, Macrotubercles from *Harmothoe abyssicola* Bidenkap, 1895.

Reproduction and development

As for other Aphroditiformia, sexes are separate in Polynoidae (Wilson 1991). The gametes develop in the epithelium that lines the coelomic cavity, and nearly mature gametes are released into the coelomic cavity where their maturation progresses (Daly 1974). Mature oocytes found in the coelomic cavity usually cannot be directly fertilized, and a maturation factor seems to be necessary (Bentley and Pacey 1992, Howie 1961). In *Lepidonotus sublevis* Verrill, 1873, however, the oocytes are fertilizable after a brief incubation in seawater (Simon, 1965). In the deep-sea hydrothermal vent species, *Branchipolynoe* aff. *seepensis* Pettibone 1986 (Jollivet et al. 2000) also report the presence of ovaries with oocytes at different stages of maturation and ovisacs to store the large mature oocytes. These ovisacs have not been reported in any other polynoid species. The oocytes are usually 80–150 µm in diameter for non-hydrothermal vent species and 400–500 µm for vent species (Table 7.13.1.4.1 and references therein).

The reproduction and the development of at least 18 species of Polynoidae have been studied (Giangrande 1997, Phillips and Pernet 1996, Van Dover et al. 1999, Wilson 1991). Most of these species free-spawn their gametes into the surrounding water, where fertilization occurs and development takes place. For a few species, however, sperm is transferred by pseudocopulation (e.g., *Harmothoe imbricata* (Linnaeus, 1767), *Branchipolynoe* spp.; Daly 1972, Jollivet et al. 2000, Van Dover et al. 1999). The shallow-water species *H. imbricata* broods its embryos under the maternal elytra until they are released as larvae. The produced larvae usually feed in the plankton, but the large size of the oocytes found in *Branchipolynoe* aff. *seepensis* suggests that the larvae are lecitotrophic and disperse over long distances (Daguin and Jollivet 2005, Jollivet et al. 2000, Plouviez et al. 2008). These studies

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Tab. 7.13.1.4.1: Oocyte diameters for species from various habitats and lifestyles.

Genus	Species	Environment/lifestyle	Oocyte diameter (µm)	Reference
Branchipolynoe	*seepensis*	Hydrothermal commensal	400–500[1]	Jollivet et al. (2000), Van Dover et al. (1999)
Branchinotogluma	sp. MAR	Hydrothermal, free-living	420[1]	Van Dover et al. (1999)
Alentia	*gelatinosa*	Temperate coastal, free-living	100	Bhaud and Cazaud (1987)
Gattyana	*cirrosa*	Temperate coastal, free-living	90–120	Rasmussen (1973), Curtis (1977)
Gorgoniapolynoe	*caeciliae*	Deep-sea, symbiotic	80–90	Eckelbarger et al. (2005)
Halosydna	*brevisetosa*	Temperate coastal, free-living	100–120	Blake (1975), Buzhinkakaya (1982)
Harmothoe	*derjugini*	Temperate coastal, free-living	150	Britayev and Ivanova (1985)
Harmothoe	*extenuata*	Temperate coastal, free-living	95	Bhaud and Cazaud (1987), Pettibone (1963), Cazaux (1972)
Harmothoe	*imbricata*	Temperate coastal, free-living	120–150	Blake (1975), Cazaux (1968), Daly (1972, 1973, 1974), Rasmussen (1973), Garwood (1981)
Harmothoe	*lunulata*	Temperate coastal, free-living	75–80	Bhaud and Cazaud (1987)
Lepidonotus	*clava*	Temperate coastal, free-living	78–100	Bhaud and Cazaud (1987)
Lepidonotus	*squamatus*	Temperate coastal, free-living	100–120	Bhaud and Cazaud (1987), Rasmussen (1973), Franzén (1956), Strathmann (1987)

[1] Values reported for mature oocytes only for hydrothermal vent species, in which oocytes at different stages of maturation are found in the ovaries.

also indicated that the juveniles sometimes found with a large *B.* aff. *seepensis* female in the mantle cavity of the vent mussels are not genetically related to that female (Plouviez et al. 2008).

The most detailed recent study of larval development of an Aphroditiformia is probably that of Pernet (2005) who worked on the three closely related symbiotic Polynoidae *Arctonoe vittata* (Grube, 1855), *Arctonoe pulchra* (Johnson, 1897), and *Arctonoe fragilis* (Baird, 1863) (see chapter 7.13.1). The development is essentially the same for all Aphroditiformia that have been studied to date. These species produce planktotrophic larvae with a prototroch but no metatroch or food groove cilia. Feeding starts after the development of episphere cilia. After 6–12 weeks, metamorphosis occurs, with the development of anterior appendages (palps, antennae, and tentacular cirri) and the beginning formation of elytra and dorsal cirri. The morphology of the larvae at different stages for eight other European species was also reported (Bhaud and Cazaux 1987).

Growth

Very few studies of the growth and longevity of the Polynoidae have been published so far. A possible tool for such studies in the Polynoidae is the use of growth rings on the jaw base (Fig. 7.13.1.4.10B) as a proxy of the age of animals (Britayev and Belov 1994). The authors established a correlation between these growth rings and duration since the beginning of a colonization experiment in the White Sea. This can in turn be used to estimate the age of the animals in population dynamics studies (e.g., Plyuscheva et al. 2004). Based on these data, the life expectancy of the polynoid species studied probably does not exceed 2–3 years.

Phylogeny and taxonomy

Fossil record

Fossilization of soft-bodied animals is rare, and very few fossils of Aphroditiformia are available (for further details, see chapter 7.13.1; pp.71–72). Among these fossils, the lack of distinctive characters (either too small or not well preserved) does not allow the classification to lower taxonomic levels.

Morphology-based taxonomy

Despite all the morphological characters available, the phylogenetic importance of these characters is difficult to evaluate. As a result, a very large number of genera have been created to accommodate characters that may not be of importance at this taxonomic level.

The study of deep-sea species with unusual morphologies that showed no clear affinities to known shallow-water polynoids led to the definition of seven subfamilies Admetellinae Uschakov, 1977; Bathyedithinae Pettibone, 1976; Bathymacellinae Pettibone, 1976; Macellicephalinae Hartmann-Schröder, 1971; Macellicephaloidinae Pettibone, 1976; Macelloidinae Pettibone, 1976; and

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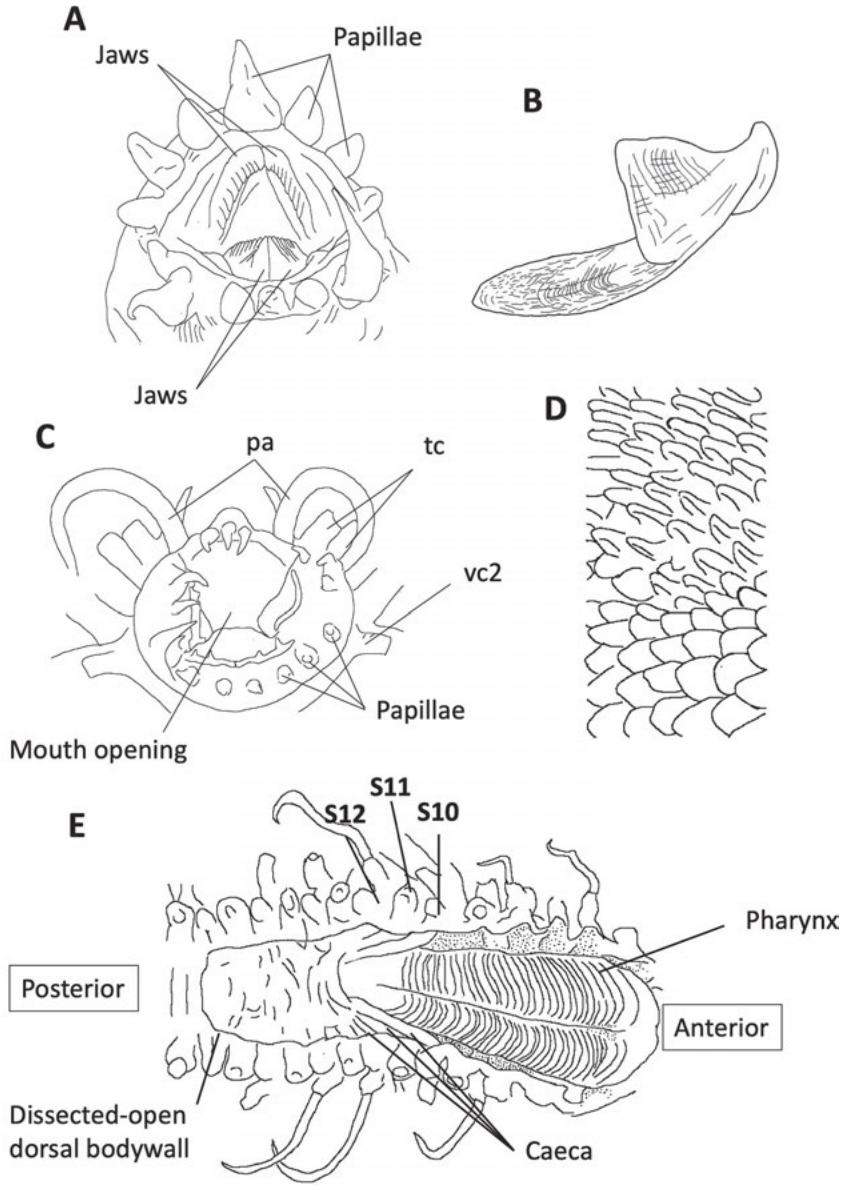


Fig. 7.13.1.4.10: A, Pharynx opening of *Lepidonotopodium piscesae* Pettibone, 1988. B, Jaw from *Harmothoe* sp. Note the growth rings on the shaft. C, Mouth opening of *Vampiropolynoe embleyi* Marcus & Hourdez, 2002. Note the lack of jaws and presence of keratinized plates. D, Keratinized teeth on the inner lining of the same species. E, Dissection of the anterior of *Harmothoe fuligineum* (Baird, 1865). Dorsal view showing the pharynx and bases of the first three pairs of caeca. S10, S11, and S12, segments 10, 11, and 12. pa, palp; tc, tentacular cirrophores; vc2, ventral cirrophore of segment 2.

Polaruschakovinae Pettibone, 1976. Similarly, the discovery of unusual species that inhabit hydrothermal vent ecosystems has led to the description of five new subfamilies (Branchinotogluminae Pettibone, 1985; Branchiplicatinae Pettibone, 1985; Branchipolynoinae Pettibone, 1984; Lepidonotopodinae Pettibone, 1983; and Vampiropolynoinae Marcus & Hourdez, 2002). As the exploration of these understudied environments led to the discovery of new species, some subfamilies have seen new species added (Table 7.13.1.4.1). Some subfamilies, however, still remain very small, comprising a single genus, and sometimes a single species. It is possible that some lineages are not greatly diversified, but it is also possible that these subfamilies were established on characters that do not hold significance at this taxonomic level. Conversely, convergent adaptation could lead to groupings that are based on adaptive characters. The use of molecular data can help shed light on these hypotheses.

Muir (1982) used morphological characters to study affinities within Polynoidae and in respect to other Aphroditiformia. Although this study was published before the description of the first hydrothermal vent species, Muir (1982) validated the existence of the subfamilies described at that point. In this work, Muir also suggested that Acoetidae should be a subfamily of Polynoidae ("Polyodontinae" in the article), as the only synapomorphy of the species belonging to Acoetidae is the presence of spinning glands in their parapodia.

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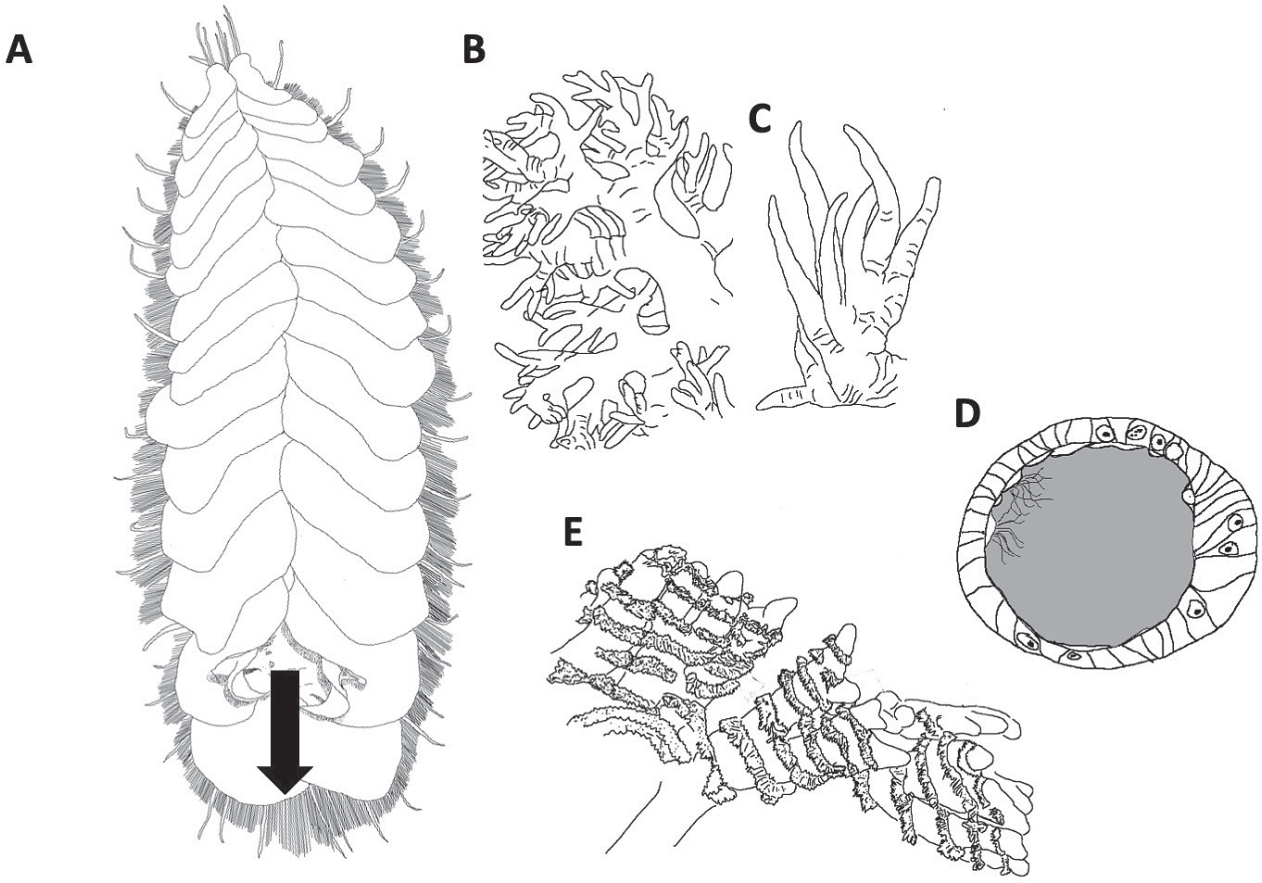


Fig. 7.13.1.4.11: A, Dorsal view of a live specimen of *Eulagisca uschakovi* Pettibone, 1997. Arrow indicates flow of water exiting from space between dorsal body wall and elytra. Gills from *Branchipolynoe symmytilida* Pettibone, 1984 (B), *Branchipolynoe* aff. *seepensis* Pettibone, 1986 (C, D), and (E) *Thermopolynoe branchiata* Miura, 1994. D, Cross section through a filament. Gray area corresponds to coelomic fluid in the central space, surrounded by a single layer of epidermal cells.

Phylogenetic studies

Based on recent molecular studies, Polynoidae firmly belong to Aphroditiformia (e.g., Weigert and Bleidorn 2016). Polynoidae form a monophyletic group in combined molecular and morphological studies (Norlinder et al. 2012, Gonzalez et al. 2018). Based on the position of the species of Acoetidae used, Norlinder et al. (2012) elevated the polynoid subfamily Iphioninae to family level (= Iphionidae). However, the branch support for this grouping is very weak (posterior probability 0.53, bootstrap 51% for maximum likelihood and below 50% for parsimony). This topology (placing the Acoetidae between the Iphioninae lineage and the remainder of the polynoids) has also been recovered by Gonzalez et al. (2018) using a combination of molecular and morphological data and by Zhang et al. (2018) using exclusively molecular data. Both of these latter studies recovered the same topology with better confidence. However, issues remain as the family Acoetidae was represented by a single species (*Panthalis oerstedi*), which is assumed to represent the whole family. Furthermore, for a family as diverse as the Polynoidae, the choice of species requires a careful selection of species based on subfamily affiliations, multiple species in a given genus if possible, and accessibility (in collections or in the environment).

As the number of species was relatively limited in Norlinder et al. (2012), Zhang et al. (2018), and Gonzalez et al. (2018), establishing a phylogeny for the 900 species of Polynoidae is not possible in the foreseeable future. Bonifácio and Menot (2019) took advantage of the rare sampling on deep-sea nodules and the diversity of species belonging to various typically deep-sea subfamilies to explore their relationships with other polynoid subfamilies. They based their interpretations on

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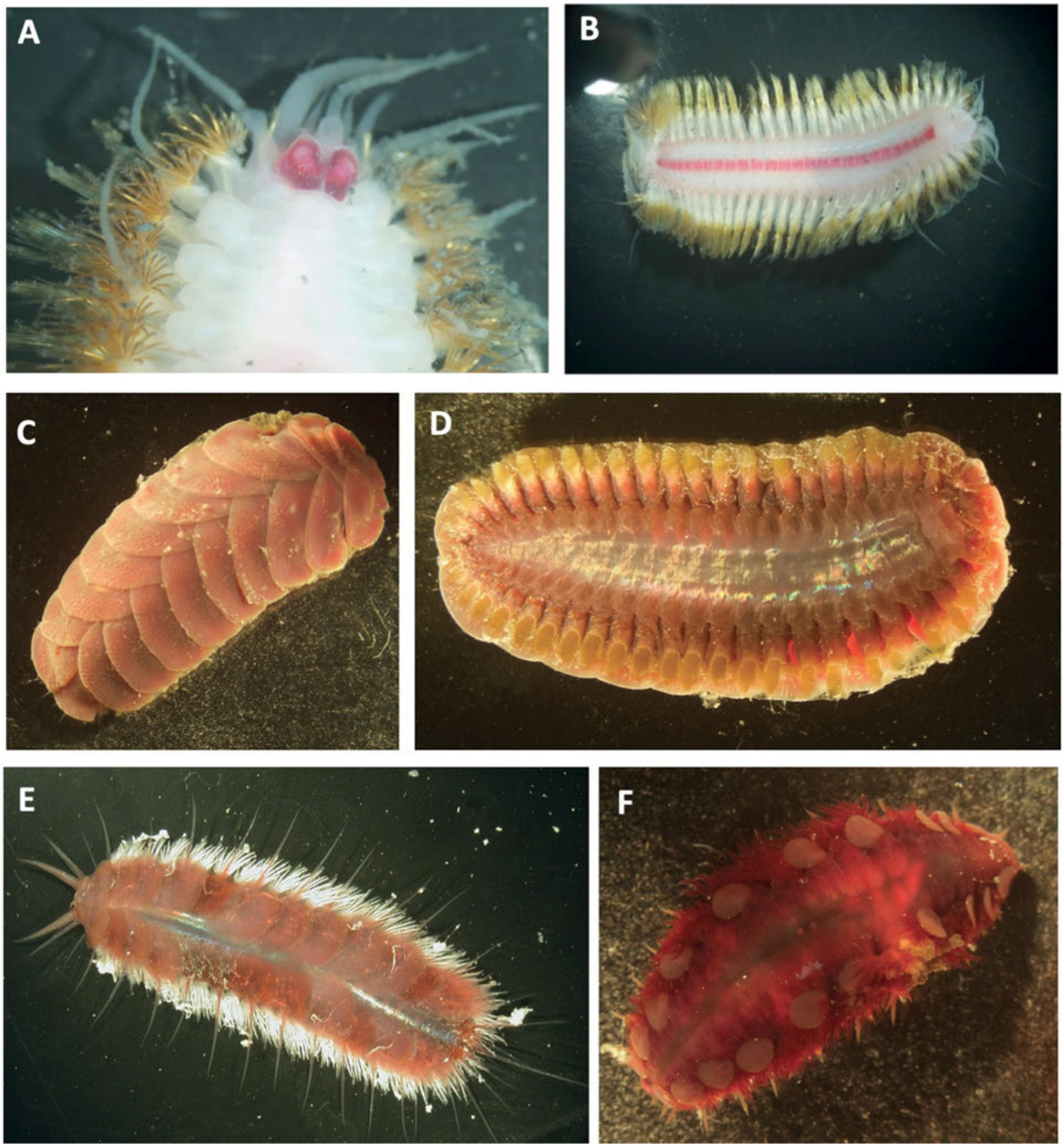


Fig. 7.13.1.4.12: Globin in Polynoidae. *Harmothoe* sp. Anterior, dorsal view (A). Ventral side, whole body (B). *Lepidonotopodium williamsae* Pettibone, 1984. Dorsal view (C) and ventral view (D). E. *Branchiplicatus cupreus* Pettibone, 1985. F. *Branchipolynoe symmytilida* Pettibone, 1984.

molecular data (COI, 18S and 16S markers) and extended their species sampling by using morphological data for species for which no molecular data were available. They suggest combining the typically hydrothermal vent subfamilies (Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Vampiropolynoinae, and Lepidonotopodinae) and species of the genus *Levensteiniella* Pettibone, 1985 (Macellicephalinae) into a single subfamily (Lepidonotopodinae). Similarly, Bonifácio and Menot (2019) suggest combining Bathyedithinae,

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Tab. 7.13.1.4.2: Polynoid subfamilies, authority, depth range, and known habitat. Sublittoral (0–200 m), bathyal (200–2000 m), abyssal (2000–6000 m), and hadal (deeper than 6000 m).

Subfamily	Authority	Habitat	Number of genera	Number of species
Admetellinae	Uschakov, 1977	Bathyal	2	4
Arctonoinae	Hanley, 1989	Sublittoral	15	19
Bathyedithinae	Pettibone, 1976	Abyssal	2	3
Bathymacellinae	Pettibone, 1976	Abyssal	2	4
Branchinotogluminae	Pettibone, 1985	Bathyal, abyssal (hydrothermal vents and organic matter)	2	18
Branchiplicatinae	Pettibone, 1985	Bathyal, abyssal (hydrothermal vents)	1	1
Branchipolynoinae	Pettibone, 1984	Bathyal, abyssal (hydrothermal vents, cold seeps)	1	9
Eulagiscinae	Pettibone, 1997	Sublittoral, bathyal, abyssal	3	8
Gesiellinae	Muir, 1982	Sublittoral (anchialine caves)	1	1
Iphioninae	Baird, 1865	Sublittoral, bathyal, abyssal (hydrothermal vents and organic matter)	3	13
Lepidastheniinae	Pettibone, 1989	Sublittoral	12	65
Lepidonotinae	Willey, 1902	Sublittoral	26	175
Lepidonotopodinae	Pettibone, 1983	Bathyal, abyssal (hydrothermal vents)	2	9
Macellicephalinae	Hartmann-Schröder, 1971	Sublittoral, bathyal, abyssal (hydrothermal vents anchialine caves)	18	65
Macellicephaloidinae	Pettibone, 1976	Abyssal, hadal	1	9
Macelloidinae	Pettibone, 1976	Bathyal, abyssal	1	1
Polaruschakovinae	Pettibone, 1976	Abyssal	5	9
Polynoinae	Kinberg, 1856	Sublittoral, bathyal, abyssal	58	487
Uncopolynoinae	Wehe, 2006	Sublittoral	1	1
Vampiropolynoinae	Marcus & Hourdez, 2002	Bathyal, abyssal (hydrothermal vents)	1	1

Bathymacellinae, Gesiellinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, and Polaruschakovinae into the Macellicephalinae (genus *Levensteiniella* excluded). Molecular data were however missing for Branchiplicatinae, Vampiropolynoinae, Admetellinae, Macelloidinae, and Uncopolynoinae, and the Lepidonotopodinae were represented by a single species and a single marker (16S). Furthermore, the confidence values for some of the deep branches were not very high. Because of these limitations, all 19 "classical" subfamilies are maintained here (Table 7.13.1.4.2).

The large number of genera (47% of which monospecific) and the numerous subfamilies, four of which are also monospecific (Table 7.13.1.4.2), call for a systematic revision, and an effort for phylogenetic reconstruction could help greatly to that end.

Taxonomic account

The following taxonomic list is based on the current status in the World Record of Marine Species (WoRMS) (Read and Fauchald 2021). Because of the issues on the basis of synonymizing some deep-sea subfamilies by Bonifácio and Menot (2019) as mentioned earlier in this chapter, the following list does not completely follow the current status in WoRMS and maintains the subfamilies recognized before (Table 7.13.1.4.1; Bonifácio and Menot 2019).

Admetellinae Uschakov, 1977

Currently valid genera: 2

Admetella McIntosh, 1885

Number of currently valid species: 3

Bathyadmetella Pettibone, 1967

Number of currently valid species: 1

Arctonoinae Hanley, 1989

Currently valid genera: 15

Adyte Saint-Joseph, 1899

Number of currently valid species: 1

Arctonoe Chamberlin, 1920

Number of currently valid species: 3

Asterophilia Hanley, 1989

Number of currently valid species: 2

Australaugeneria Pettibone, 1969

Number of currently valid species: 4

Bathynoe Ditlevsen, 1917

Number of currently valid species: 6

Capitulatinoe Hanley & Burke, 1989

Number of currently valid species: 1

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Disconatis Hanley & Burke, 1988
Number of currently valid species: 2
Gastrolepidia Schmarda, 1861
Number of currently valid species: 1
Medioantenna Imajima, 1997
Number of currently valid species: 2
Minusculisquama Pettibone, 1983
Number of currently valid species: 1
Neohololepidella Pettibone, 1969
Number of currently valid species: 2
Parabathynoe Pettibone, 1990
Number of currently valid species: 1
Parahololepidella Pettibone, 1969
Number of currently valid species: 1
Pottsiscalisetosus Pettibone, 1969
Number of currently valid species: 1
Showascalisetosus Imajima, 1997
Number of currently valid species: 1

Bathyedithinae Pettibone, 1976
Currently valid genera: 2
Bathyedithia Pettibone, 1976
Number of currently valid species: 3
Bathymariana Levenstein, 1978
Number of currently valid species: 1

Branchinotogluminae Pettibone, 1985
Currently valid genera: 2
Branchinotogluma Pettibone, 1985
Number of currently valid species: 12
Peinaleopolynoe Desbruyères & Laubier, 1988
Number of currently valid species: 6

Branchiplicatinae Pettibone, 1985
Currently valid genera: 1
Branchiplicatus Pettibone, 1985
Number of currently valid species: 1

Branchipolynoinae Pettibone, 1984
Currently valid genera: 1
Branchipolynoe Pettibone, 1984
Number of currently valid species: 9

Eulagiscinae Pettibone, 1997
Currently valid genera: 3
Bathymoorea Pettibone, 1967
Number of currently valid species: 2
Eulagisca McIntosh, 1885
Number of currently valid species: 5
Pareulagisca Pettibone, 1997
Number of currently valid species: 1

Subfamily Gesiellinae Muir, 1982
Currently valid genera: 1
Gesiella Pettibone, 1976
Number of currently valid species: 1

Iphioninae Kinberg, 1856
Currently valid genera: 3
Iphione Kinberg, 1856
Number of currently valid species: 7
Iphionella McIntosh, 1885
Number of currently valid species: 1
Iphionides Hartmann-Schröder, 1977
Number of currently valid species: 1
Thermiphione Hartmann-Schröder, 1992
Number of currently valid species: 4

Lepidastheniinae Pettibone, 1989
Currently valid genera: 12
Alentiana Hartman, 1942
Number of currently valid species: 1
Anotochaetonoe Britayev & Martin, 2006
Number of currently valid species: 1
Benhamipolynoe Pettibone, 1970
Number of currently valid species: 2
Hyperhalosydna Augener, 1922
Number of currently valid species: 3
Lepidasthenia Malmgren, 1867
Number of currently valid species: 42
Lepidastheniella Monro, 1924
Number of currently valid species: 4
Lepidofimbria Hartman, 1967
Number of currently valid species: 1
Parahalosydna Horst, 1915
Number of currently valid species: 3
Perolepis Ehlers, 1908
Number of currently valid species: 4
Pseudopolynoe Day, 1962
Number of currently valid species: 1
Showapolynoe Imajima, 1997
Number of currently valid species: 2
Telolepidasthenia Augener & Pettibone, 1970
Number of currently valid species: 1

Lepidonotinae Willey, 1902
Currently valid genera: 26
Alentia Malmgren, 1865
Number of currently valid species: 1
Allmaniella McIntosh, 1885
Number of currently valid species: 2
Augenerilepidonotus Pettibone, 1995
Number of currently valid species: 1

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Cervilia Frickhinger, 1916
Number of currently valid species: 1
Chaetacanthus Seidler, 1922
Number of currently valid species: 3
Dilepidonotus Hartman, 1967
Number of currently valid species: 1
Drieschiopsis Støp-Bowitz, 1991
Number of currently valid species: 1
Euphione McIntosh, 1885
Number of currently valid species: 6
Euphionella Monro, 1936
Number of currently valid species: 4
Halosydna Kinberg, 1856
Number of currently valid species: 35
Halosydnella Hartman, 1938
Number of currently valid species: 6
Halosydnopsis Uschakov & Wu, 1959
Number of currently valid species: 1
Hermenia Grube, 1856
Number of currently valid species: 3
Hermilepidonotus Uschakov, 1974
Number of currently valid species: 2
Heteralentia Hanley & Burke, 1991
Number of currently valid species: 1
Hololepida Moore, 1905
Number of currently valid species: 5
Lepidametria Webster, 1879
Number of currently valid species: 4
Lepidonopsis Pettibone, 1977
Number of currently valid species: 3
Lepidonotus Leach, 1816
Number of currently valid species: 80
Nonparahalosydna Uschakov, 1982
Number of currently valid species: 1
Olgalepidonotus Pettibone, 1995
Number of currently valid species: 1
Parahalosydnopsis Pettibone, 1977
Number of currently valid species: 3
Pseudohalosydna Fauvel, 1913
Number of currently valid species: 1
Sheila Monro, 1930
Number of currently valid species: 1
Telodrieschia Kirkegaard, 1995
Number of currently valid species: 1
Thormora Baird, 1865
Number of currently valid species: 9

Lepidonotopodinae Pettibone, 1983
Currently valid genera: 2
Lepidonotopodium Pettibone, 1983
Number of currently valid species: 8
Thermopolynoe Miura, 1994
Number of currently valid species: 1

Macellicephalinae Hartmann-Schröder, 1971
Currently valid genera: 18
Abyssarya Bonifácio & Menot, 2018
Number of currently valid species: 1
Bathybahamas Pettibone, 1985
Number of currently valid species: 1
Bathycatalina Pettibone, 1976
Number of currently valid species: 1
Bathyeliasona Pettibone, 1976
Number of currently valid species: 4
Bathyfauvelia Pettibone, 1976
Number of currently valid species: 4
Bathykermadeca Pettibone, 1976
Number of currently valid species: 3
Bathykurila Pettibone, 1976
Number of currently valid species: 2
Bathylevensteina Pettibone, 1976
Number of currently valid species: 1
Bathymacella Pettibone, 1976
Number of currently valid species: 1
Bathypolaria Levenstein, 1981
Number of currently valid species: 3
Bathytasmania Levenstein, 1982
Number of currently valid species: 1
Bathyvitiazia Pettibone, 1976
Number of currently valid species: 2
Bruunilla Hartman, 1971
Number of currently valid species: 2
Levensteiniella Pettibone, 1985
Number of currently valid species: 7
Macellicephala McIntosh, 1885
Number of currently valid species: 26
Natopolynoe Pettibone, 1985
Number of currently valid species: 1
Pelagomacellicephala Pettibone, 1985
Number of currently valid species: 1
Yodanoe Bonifácio & Menot, 2018
Number of currently valid species: 1

Macellicephaloidinae Pettibone, 1976
Currently valid genera: 1
Macellicephaloides Uschakov, 1955
Number of currently valid species: 9

Macelloidinae Pettibone, 1976
Macelloides Uschakov, 1957
Number of currently valid species: 1

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Polaruschakovinae Pettibone, 1976
Currently valid genera: 6
Bathycanadia Levenstein, 1981
Number of currently valid species: 1
Bathymiranda Levenstein, 1981
Number of currently valid species: 1
Diplaconotum Loshamn, 1981
Number of currently valid species: 1
Nu Bonifácio & Menot, 2018
Number of currently valid species: 1
Polaruschakov Pettibone, 1976
Number of currently valid species: 5

Polynoinae Kinberg, 1856
Currently valid genera: 58
Acanthicolepis McIntosh, 1900
Number of currently valid species: 2
Acholoe Claparède, 1870
Number of currently valid species: 1
Antarctinoe Barnich, Fiege, Micaletto & Gambi, 2006
Number of currently valid species: 2
Antinoe Kinberg, 1856
Number of currently valid species: 6
Antipathipolyeunoa Pettibone, 1991
Number of currently valid species: 1
Arcteobia Annenkova, 1937
Number of currently valid species: 2
Arctonoella Buzhinskaja, 1967
Number of currently valid species: 1
Australonoe Hanley, 1993
Number of currently valid species: 1
Austrolaenilla Bergström, 1916
Number of currently valid species: 10
Barrukia Bergström, 1916
Number of currently valid species: 2
Bathynotalia Levenstein, 1982
Number of currently valid species: 1
Bayerpolynoe Pettibone, 1991
Number of currently valid species: 1
Brychionoe Hanley & Burke, 1991
Number of currently valid species: 1
Bylgides Chamberlin, 1919
Number of currently valid species: 9
Enipo Malmgren, 1865
Number of currently valid species: 10
Eucranta Malmgren, 1865
Number of currently valid species: 5
Eunoe Malmgren, 1865
Number of currently valid species: 49, including 2 *taxon inquirendum*, which are indeterminable due to holotype in poor condition
Gattyana McIntosh, 1897
Number of currently valid species: 11
Gaudichaudius Pettibone, 1986
Number of currently valid species: 2
Gorekia Bergström, 1916
Number of currently valid species: 1
Gorgoniapolynoe Pettibone, 1991
Number of currently valid species: 9, including one *nomen dubium* (indeterminable juvenile)
Grubeopolynoe Pettibone, 1969
Number of currently valid species: 2
Harmothoe Kinberg, 1856
Number of currently valid species: 156, including 2 *taxon inquirendum* (indeterminable due to insufficient description) and 4 *nomen dubium*
Hartmania Pettibone, 1955
Number of currently valid species: 1
Hemilepidia Schmarda, 1861
Number of currently valid species: 3
Hermadion Kinberg, 1856
Number of currently valid species: 3, including 1 *taxon inquirendum* and 1 *nomen dubium*
Hermadionella Uschakov, 1982
Number of currently valid species: 3
Hesperonoe Chamberlin, 1919
Number of currently valid species: 7
Heteropolynoe Bidenkap, 1907
Number of currently valid species: 1
Hololepidella Willey, 1905
Number of currently valid species: 12
Intoshella Darboux, 1899
Number of currently valid species: 3
Kermadecella Darboux, 1899
Number of currently valid species: 1
Lagisca Malmgren, 1865
Number of currently valid species: 23, including 5 *taxon inquirendum* (indeterminable due to loss or poor condition of type, and insufficient description)
Leucia Malmgren, 1867
Number of currently valid species: 2
Lobopelma Hanley, 1987
Number of currently valid species: 1
Malmgrenia McIntosh, 1874
Number of currently valid species: 18, including 2 *nomen dubium* due to poor condition of type
Malmgreniella Hartman, 1967
Number of currently valid species: 27
Melaenis Malmgren, 1865
Number of currently valid species: 2
Neobylgides Pettibone, 1993
Number of currently valid species: 1

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Neolagisca Barnich & Fiege, 2000
Number of currently valid species: 1
Neopolynoe Loshamn, 1981
Number of currently valid species: 4
Paradyte Pettibone, 1969
Number of currently valid species: 3
Paragattyana Pettibone, 1993
Number of currently valid species: 2
Paralentia Uschakov, 1982
Number of currently valid species: 1
Paralepidonotus Horst, 1915
Number of currently valid species: 5
Pararctonoella Pettibone, 1996
Number of currently valid species: 3
Pettibonesia Nemésio, 2006
Number of currently valid species: 1
Polyeunoa McIntosh, 1885
Number of currently valid species: 2
Polynoe Lamarck, 1818
Number of currently valid species: 48, including 21 *taxa inquirenda* (insufficiently described and loss of types) and 1 nomen dubium and 3 nomen nudum (no associated description and type)
Robertianella McIntosh, 1885
Number of currently valid species: 2
Rullieriella Pettibone, 1993
Number of currently valid species: 1
Russellhanleya Barnich, Sun & Fiege, 2004
Number of currently valid species: 1
Scalisetosus McIntosh, 1885
Number of currently valid species: 5
Subadyte Pettibone, 1969
Number of currently valid species: 8
Tenonia Nichols, 1969
Number of currently valid species: 2
Tottonpolynoe Pettibone, 1991
Number of currently valid species: 1
Verrucapelma Hanley & Burke, 1991
Number of currently valid species: 3
Ysideria Ruff, 1995
Number of currently valid species: 1

Uncopolynoinae Wehe, 2006
Currently valid genera: 1
Uncopolynoe Hartmann-Schröder, 1960
Number of currently valid species: 1

Vampiropolynoinae Marcus &Hourdez, 2002
Currently valid genera: 1
Vampiropolynoe Marcus & Hourdez, 2002
Number of currently valid species: 1

Polynoidae *incertae sedis*
The following genera have not been placed in current subfamilies because their affinities were not clear.
Currently valid genera in this group: 19, including 3 taxon inquirendum based on larval forms, 1 nomen dubium
Bathyhololepidella Buzhinskaya, 1992
Number of currently valid species: 1
Benhamisetosus Averincev, 1978
Number of currently valid species: 1
Drieschella Augener & Pettibone, 1970
Number of currently valid species: 1
Hodor Bonifácio & Menot, 2018
Number of currently valid species: 2
Lepidogyra Hartman, 1967
Number of currently valid species: 1
Ophthalmonoe Petersen & Britayev, 1997
Number of currently valid species: 2
Parapolyeunoa Barnich, Gambi & Fiege, 2012
Number of currently valid species: 1
Phyllantinoe McIntosh, 1876
Number of currently valid species: 1
Phyllohartmania Pettibone, 1961
Number of currently valid species: 1
Phyllosheila Pettibone, 1961
Number of currently valid species: 1
Podarmus Chamberlin, 1919
Number of currently valid species: 1
Polynoella McIntosh, 1885
Number of currently valid species: 3
Polynoina Nolte, 1936
Number of currently valid species: 1
Chaetosphaera Häcker, 1898 (*taxon inquirendum*, based on a larval form)
Number of currently valid species: 1
Drieschia Michaelsen, 1892 (*taxon inquirendum*, based on a larval form)
Number of currently valid species: 5
Eumolphe Risso, 1826 (*taxon inquirendum*, insufficiently described)
Number of currently valid species: 1
Frennia Viguier, 1912 (*taxon inquirendum*, insufficiently described)
Number of currently valid species: 2
Quetieria Viguier, 1911 (*taxon inquirendum*, based on a larval form)
Number of currently valid species: 1
Sinantenna Hartmann-Schröder, 1974 (*taxon inquirendum*)
Number of currently valid species: 1
Herdmanella Darboux, 1899 (*nomen dubium*)
Number of currently valid species: 2

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The following genera have no valid species and should therefore not be considered valid

Eupolynoe McIntosh, 1874

Number of currently valid species: 0

Hylosydna Moore, 1903

Number of currently valid species: 0

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Danny Eibye-Jacobsen, Charatsee Aungtonya, and Brett C. Gonzalez

7.13.1.5.1 Sigalionidae Kinberg, 1856

Introduction

Sigalionidae is the largest scale worm family after Polynoidae, containing 252 species in 32 genera. All scale worms possessing compound chaetae are assembled herein. This family, along with the recently suppressed "Pisionidae" and "Pholoidae," was long presumed to be deeply nested at the base of scale worm systematics given that compound chaetae occur widely in phyllodocidean groups and is considered to be a possible candidate for the sister group to other scale worms. Recent phylogenetic analyses indicate that this is not likely to be the case (e.g., Gonzalez et al. 2018). It thus appears that compound chaetae have reemerged from a scale worm predecessor with only simple chaetae, as the majority of neurochaetae in all sigalionids are compound. Gonzalez et al. (2018) showed that sigalionids have additional apomorphies beyond compound chaetae, including the presence of segmental ctenidia (small ciliated lobes), the absence of dorsal cirri beyond segment 3, and the specific distribution of elytra on the posterior part of the body (see below).

Sigalionids have a worldwide distribution and may be found on both hard and soft substrates from the eulittoral to depths of at least 4000 m. Species of *Sthenelanella* live in long, tough fibrous tubes that may be branched (Pettibone 1969). Other sigalionids live within more temporary mucous tubes or simply hide within the upper layer of the sediment. Sigalionids are rarely seen fully exposed on the substrate. Most species are strictly marine, but several occur in estuarine waters (e.g., *Pholoe baltica* Ørsted, 1843) and some pisionins have even been found in freshwater settings (see Gonzalez et al. 2017).

Based on Gonzalez et al. (2018), we recognize five subfamilies in Sigalionidae: Sigalioninae, Pelogeniinae, Sthenelanellinae, Pholoinae, and Pisioninae. There is strong evidence that four of these subfamilies are monophyletic, but this is not conclusively the case for Sigalioninae, which appears to be paraphyletic given our current taxon sampling. It is our opinion that as long as this caveat is acknowledged, it makes practical sense to treat sigalionins as a separate entity for the purposes of describing morphological variation among sigalionids.

Sigalionidae, as delineated here, includes two groups that until recently were generally treated as separate families, "Pholoidae" and "Pisionidae" (e.g., Hutchings 2000, Rouse and Pleijel 2001). This introduces a high degree of heterogeneity into the family that makes it difficult to provide a cohesive description of the morphology, anatomy, biology, and ecology of its members. In particular, the inclusion of the highly specialized pisionins would result in practically every statement having an exception for that group. For this reason, the subfamily Pisioninae is treated in a separate subchapter (Gonzalez et al. 2017). A similar argument could be made for the pholoins, but their deviations from "classical Sigalionidae" are both less numerous and less radical in nature. Accordingly, the main narrative of this chapter will encompass four subfamilies: Sigalioninae, Pelogeniinae, Sthenelanellinae, and Pholoinae (see Gonzalez et al. 2018). As a consequence of this, general statements in the following on Sigalionidae do not include the Pisioninae unless expressly stated.

Morphology

External morphology

Body shape and size. Sigalionids are generally equally broad along most of the length of their body from about segment 3 (Fig. 7.13.1.5.1.3A–B), with a short posterior region that narrows to the pygidium. In cross section, they often have a rectangular appearance caused by the presence of elytra and well-developed parapodia.

The size range of sigalionids, even excluding pisionins, is considerable, spanning from 1.5 mm in the interstitial *Laubierpholoe swedmarki* (Laubier, 1975) to 150 mm in *Pelogenia antipoda* Schmarda, 1861 and *Pelogenia zeylanica* (Willey, 1905), with records reaching over 200 mm in *Neoleanira tetragona* (Ørsted, 1845). Likewise, the number of segments ranges from 19 in *Taylorpholoe hirsuta* (Rullier & Amoureux, 1979) to almost 300 in *P. antipoda* and *N. tetragona* (see Pettibone 1970c, 1992b, 1997). Most pholoins are less than 1 cm long, whereas sigalionins, sthenelanellins, and pelogeniins are often 3–5 cm long.

Color. Live sigalionids are typically pale white or yellowish, often with red pigmentation on the prostomium and less intensely on the dorsum and parapodia (Fig. 7.13.1.5.1.3B). Dark pigmentation may also occur on the elytra, but typically these are colorless or whitish structures (Fig. 7.13.1.5.1.3A).

Arrangement of elytra and cirri. As in other scale worms, the distribution of elytra on the anterior end of the body follows a very specific pattern; in sigalionids, they occur on segments 2, 4, 5, and 7 and then every other segment

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until segment 23 (Pholoinae) or segment 25 or 27. Continuing posteriorly, all remaining segments bear elytra, which is unique for Sigalionidae. The genus *Pholoides* is a curious exception to this rule in that the initial pattern (elytra on every other segment) continues to the end of the body, which may have up to 48 segments (Pettibone 1992b). Among scale worms, a comparable pattern is only known in Aphroditidae. The interstitial genus *Metaxypsamma*, with up to 24 segments, displays a further anomaly in having the elytra replaced by nodular lobes with 2–4 filiform papillae (Fig. 7.13.1.5.1.2F); these lobes are distributed in the exact same pattern as the elytra, which seems to confirm their homology.

On segments without elytra, a pair of dorsal tubercles is typically found in an equivalent position, occasionally being absent or very weak as in *Leanira* and *Ehlersileanira*. In addition to the dorsal (tentacular) cirri of segment 1, dorsal cirri may occur on segment 3 but are absent on the remainder of the body. If present on segment 3, they appear to replace dorsal tubercles in *Neoleanira* (where they are particularly long and well developed), *Sigalion*, and *Euthalenessa*, whereas they occur together with dorsal tubercles in the pelogeniin genera *Claparedepelogenia*, *Heteropelogenia*, *Pelogenia*, and *Pottsipelogenia* (Fig. 7.13.1.5.1.5A, C).

Scattered papillae may occur on the dorsal and ventral body surfaces, as well as on the parapodia and elytra. Members of Pelogeniinae are remarkable in that the elytra and middorsal surface, as well as the ventral surface in many species, are covered by foreign material such as sand grains, foraminiferan tests, and shell fragments that are held in place by specialized adhesive papillae (Fig. 7.13.1.5.1.5B). A dense covering of nonadhesive papillae is present on the ventral surface in species of *Willeysthenelais* (Fig. 7.13.1.5.1.5F) and some species of *Fimbriosthenelais*.

In all sigalionids, the lateral appendages of most anterior segments (primarily segments 1–3) are directed anteriorly (e.g., Fig. 7.13.1.5.1.1A–B), resulting in the chaetae of segment 1 (if present) pointing straight forward and the prostomium appearing to be placed on top of segment 1 (e.g., Fig. 7.13.1.5.1.1F–G). The anterior edges of segment 1 are apparently fused medially below the prostomium, resulting in the palps emerging ventrolaterally (Pholoinae) or ventrally (other sigalionids) to segment 1 without any external connection to the prostomium (Figs. 7.13.1.5.1.4D, F and 7.13.1.5.1.5B, D).

Prostomium. In pholoins and members of *Sigalion* and *Euthalenessa*, the prostomium is rounded quadrangular or pentagonal in shape (Fig. 7.13.1.5.1.1A, E). In other sigalionids, the prostomium is generally broadly oval (Fig. 7.13.1.5.1.1B).

Most sigalionids have three antennae, the median antenna and a pair of lateral antennae. Some species of *Sigalion*, such as *S. omanensis* Wehe, 2007 and *S. shimodaensis* Imajima, 2006 (Fig. 7.13.1.5.1.1E), seem to genuinely lack a median antenna (Imajima 2006, Wehe 2007), although Mackie and Chambers (1990) pointed out that it is very small and easily detached in this genus. A well-developed median antenna is present in all other sigalionids. Lateral antennae are absent in *Pholoides* (Fig. 7.13.1.5.1.1D) and in all Pholoinae except *Taylorpholoe hirsuta* and some species of *Pholoe* (Figs. 7.13.1.5.1.2D–G and 7.13.1.5.1.3C). They are present in all other sigalionids but may be strongly reduced, as is the case for several species of Pelogeniinae (Figs. 7.13.1.5.1.2A–B and 7.13.1.5.1.5A).

The median antenna usually consists of a basal ceratophore and a distal ceratostyle (a ceratostyle cannot be distinguished in *Sigalion*). In most sigalionids, the median antenna is attached at or near the anterior margin of the prostomium, but in *Sigalion* it is centrally placed, and in the pholoins *Imajimapholoe parva* (Imajima & Hartman, 1964) (Fig. 7.13.1.5.1.2D) and *Taylorpholoe hirsuta* (Fig. 7.13.1.5.1.2H), it is attached occipitally near the posterior margin of the prostomium. The ceratophore of the median antenna is rather strongly developed in members of Pelogeniinae, furthermore with lateral ridges in *Dayipsammolyce* and *Pottsipelogenia*. The style of the median antenna shows considerable variation in its length within the family, and in the genera *Ehlersileanira* and *Leanira*, it is biarticled. Characteristic for many sigalionids is the presence of a pair of more or less fleshy, ear-shaped, nonciliated lobes called auricles at the base of the ceratophore of the median antenna (e.g., Figs. 7.13.1.5.1.1B–C, H and 7.13.1.5.1.4A, C). Auricles are present in all genera of Sigalioninae except *Euthalenessa* (Figs. 7.13.1.5.1.1A and 7.13.1.5.1.4B), *Leanira*, *Pholoides* (Fig. 7.13.1.5.1.1D), and *Sigalion* (Fig. 7.13.1.5.1.1E). In *Sthenelanella*, auricles have the form of semispherical nodules (Figs. 7.13.1.5.1.2C and 7.13.1.5.1.4G). Not to be confused with auricles, several pelogeniin genera, including *Dayipsammolyce*, *Hartmanipsammolyce*, *Heteropelogenia*, and *Pottsipelogenia*, have a pair of small ciliated lobes called ctenidia that are found on or near the base of the ceratophore of the median antenna. The recently described *Ehlersileanira andamanensis* Aungtonya & Eibye-Jacobsen, 2016 is remarkable in having both auricles and a more basal pair of ctenidia (Fig. 7.13.1.5.1.5G; see Aungtonya and Eibye-Jacobsen 2016).

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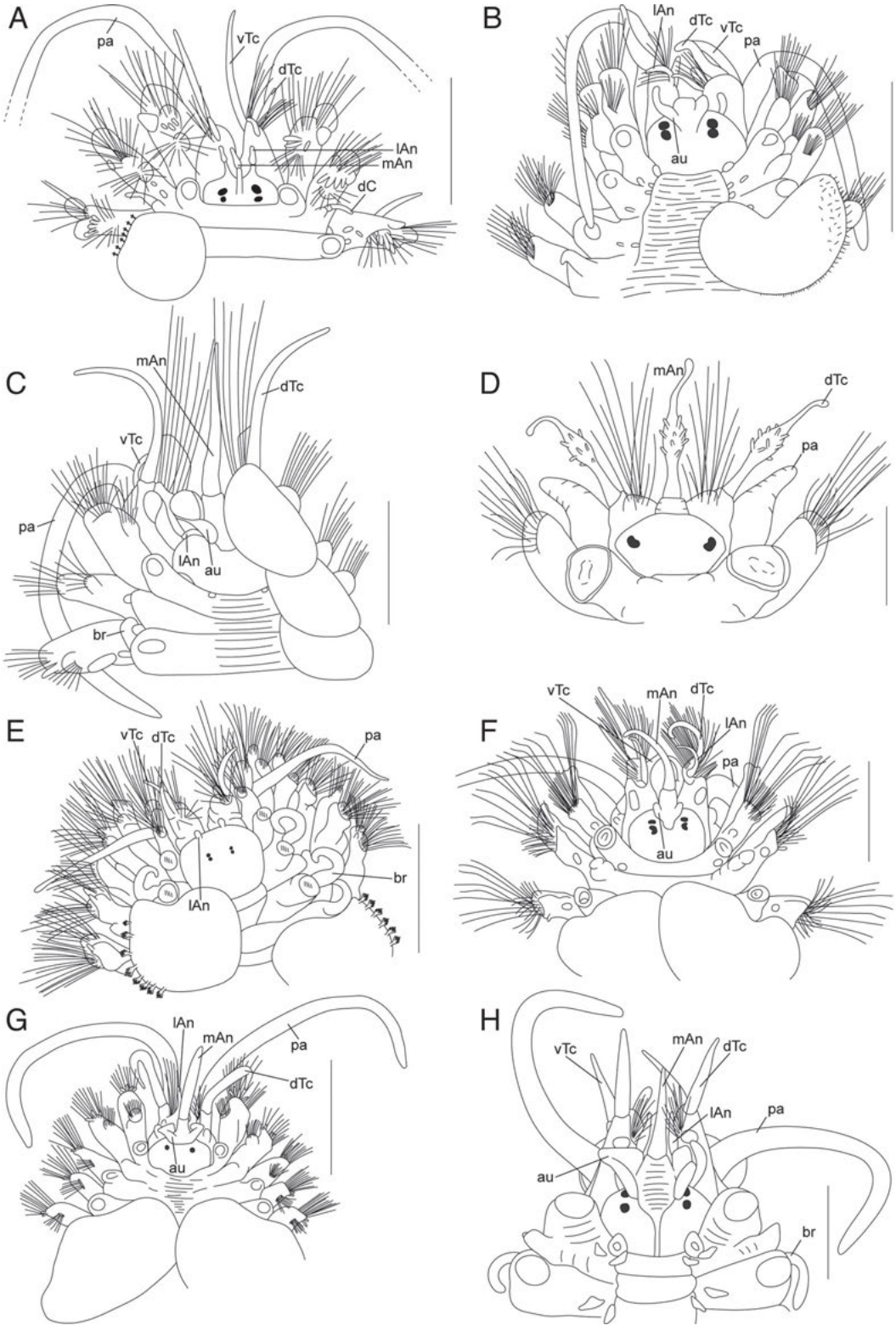


Fig. 7.13.1.5.1.1: Anterior ends in dorsal view: Sigalioninae. A, *Euthalenessa chacei* Pettibone, 1970a. B, *Fimbriosthenelais hirsuta* (Potts, 1910), from Wehe (2007) (style of median antenna missing). C, *Horstileanira crosslandi* Pettibone, 1970. D, *Pholoides brasiliensis* Padovanni & Amaral, 2004. E, *Sigalion shimodaensis* Imajima, 2006. F, *Sthenelais branchiata* Imajima, 2003. G, *Sthenolepis japonica* (McIntosh, 1885), from Wehe (2007). H, *Willeysthenelais diplocirrus* (Grube, 1875), from Pettibone (1971). au, auricle; br, branchia; dC, dorsal cirrus; dTc, dorsal tentacular cirrus; lAn, lateral antenna; mAn, median antenna; pa, palp; vTc, ventral tentacular cirrus. All images redrawn and modified from original descriptions unless otherwise noted. All scale bars, 1 mm; except D, 200 µm.

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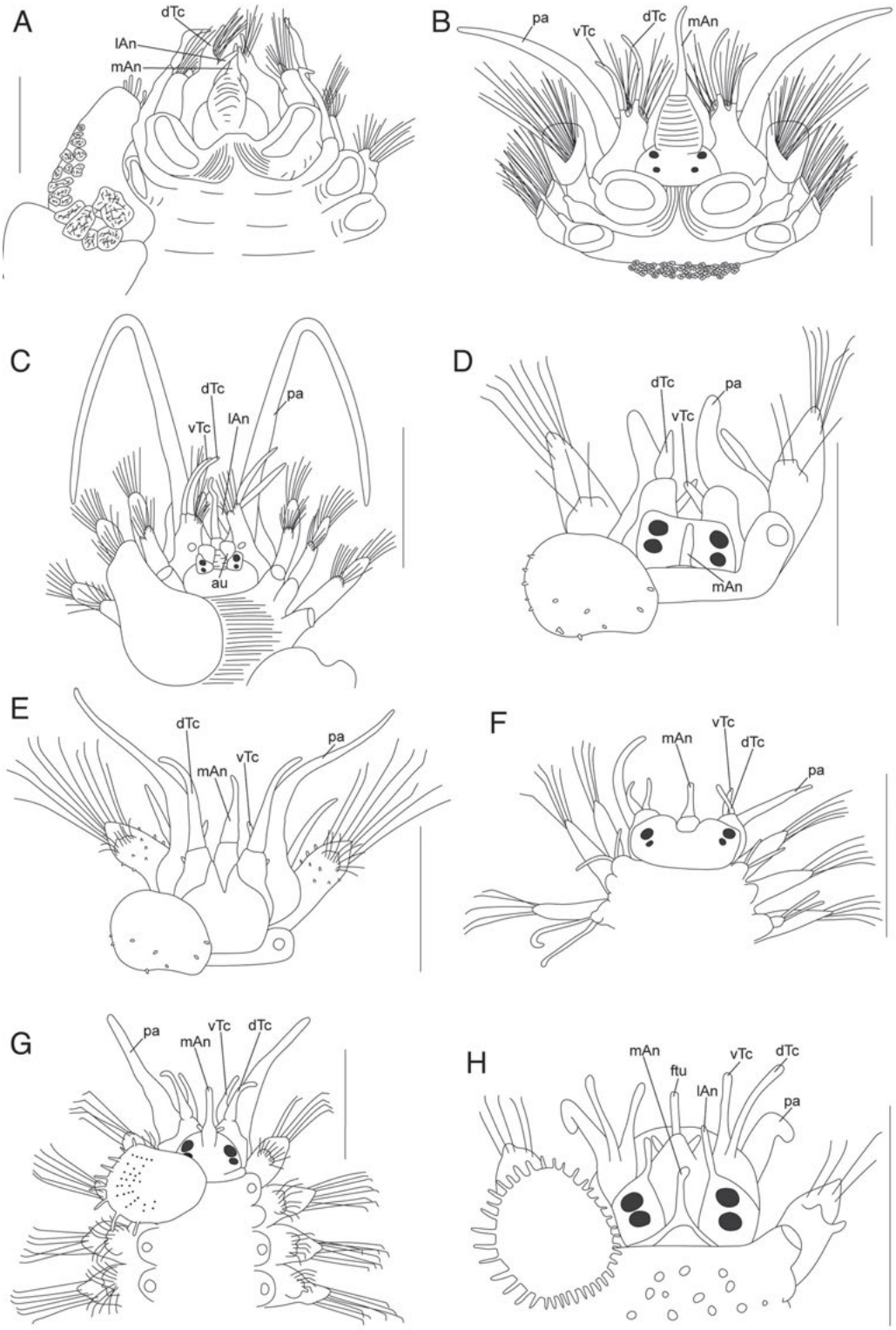


Fig. 7.13.1.5.1.2: Anterior ends in dorsal view: Pelogeniinae (A–B), Sthenelanellinae (C), Pholoinae (D–H). A, *Pelogenia rigida* (Grube, 1868), from Wehe (2007). B, *Neopsammolyce floccifera* (Augener, 1906), from Pettibone (1997). C, *Sthenelanella ehlersi* (Horst, 1916), from Pettibone (1969). D, *Imajimapholoe parva* (Imajima & Hartman, 1964), from Pettibone (1992b). E, *Laubierpholoe maryae* Pettibone, 1992. F, *Metaxypsamma uebelackerae* Wolf, 1986, from Pettibone (1992b). G, *Pholoe chinensis* Wu et al., 1994. H, *Taylorpholoe hirsuta* (Rullier & Amoureux, 1979), from Pettibone (1992b). au, auricle; dTc, dorsal tentacular cirrus; ftu, facial tubercle; lAn, lateral antenna; mAn, median antenna; pa, palp; vTc, ventral tentacular cirrus. All images redrawn and modified from indicated sources (E and G from original descriptions). Scale bars: A–C, 1 mm; all others, 200 µm.

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Lateral antennae in species of *Sigalion* are attached to the anterior margin of the prostomium (Fig. 7.13.1.5.1.1E). In *Euthalenessa*, the lateral antennae also arise from the anterior margin of the prostomium, but most of the length of the ceratophores is fused to the median surface of segment 1 (Fig. 7.13.1.5.1.1A). In all other sigalionids, the lateral antennae, when present, are completely fused with segment 1 (Figs. 7.13.1.5.1.4C and 7.13.1.5.1.5A). Lateral antennae are strongly developed and elongate in *Neoleanira* but are otherwise quite small. Like the median antenna, they are biarticled in *Leanira* and *Ehlersileanira*.

As in most scale worms, two pairs of eyes are usually present on the prostomium (Fig. 7.13.1.5.1.3A–B). A few isolated reports claim that some species possess only one pair, but this needs further confirmation. In some sigalionids, such as species of *Euthalenessa* and *Sthenelanella*, the eyes occur on raised ocular areas. In the interstitial species *Laubierpholoe maryae* Pettibone, 1992, eyes are absent (Fig. 7.13.1.5.1.2E; Pettibone 1992b).

An antenniform or bulbous facial tubercle may be present, positioned below the ceratophore of the median antenna. It is found in the genera *Taylorpholoe* (Fig. 7.13.1.5.1.2H), *Ehlersileanira*, *Euthalenessa*, *Leanira*, *Dayipsammolyce*, *Heteropelogenia*, and *Pottsipelogenia* (Fig. 7.13.1.5.1.5B) and some species of *Pholoe*, *Sigalion*, and *Neopsammolyce*. It is unclear whether the facial tubercle is actually part of the prostomium or is formed by the fused median surface of segment 1.

Nuchal organs are presumed to be present in all sigalionids, placed lateroposteriorly between the prostomium and the dorsal surface of segment 2 (Fig. 7.13.1.5.1.4E). However, reports of their actual occurrence in individual species are very scattered in the literature.

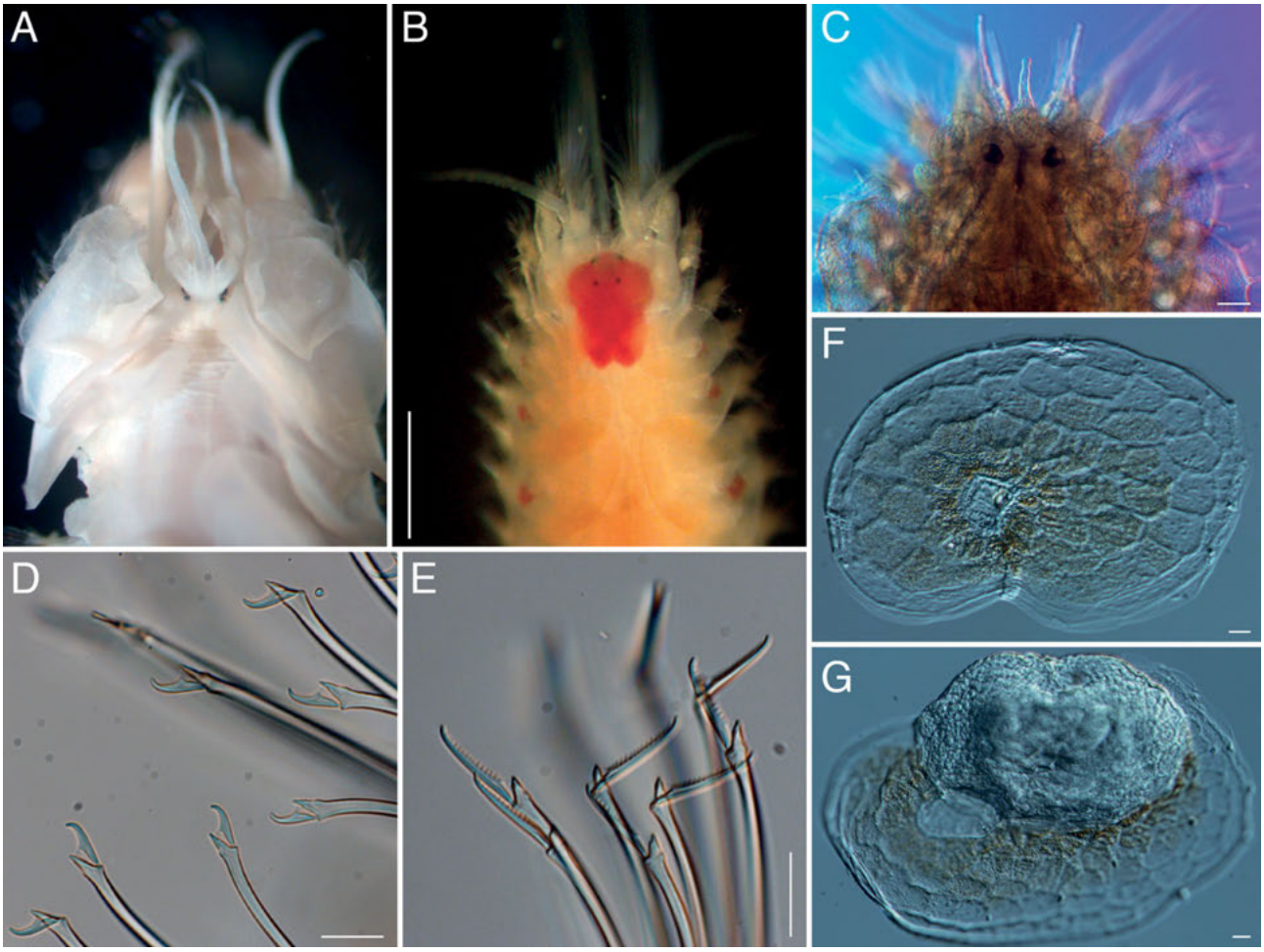


Fig. 7.13.1.5.1.3: Morphology of Sigalionidae: Light micrographs. A, Anterior end, dorsal view of *Mustaquimsthenelais* sp. B, Anterior end, dorsal view of *Labiosthenolepis andamanensis* Aungtonya, 2007. C–E, Anterior end, dorsal view (C) and compound falcigerous neurochaetae (D–E) of *Pholoe* sp. from Eilat, Israel. F–G, Elytra without and with brooding embryo, from *Laubierpholoe* sp. from Miramar, Cuba. Photographs A–B by Charatsee Aungtonya, C–G by Brett C. Gonzalez and the Worsaae Lab, University of Copenhagen. Scale bars: B, 0.5 mm; C, 50 µm; D–G, 20 µm.

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Palps emerge ventrally or ventrolaterally to the prostomium and are usually provided with an inner palpal sheath of variable length (Figs. 7.13.1.5.1.4D and 7.13.1.5.1.5D–E). These inner sheaths are apparently absent in *Sthenelanella* and rudimentary in Pholoinae and *Pholoides*. In addition to this, a short outer palpal sheath is found in all Sigalioninae (Fig. 7.13.1.5.1.4D, F) except members of *Fimbriosthenelais* (Fig. 7.13.1.5.1.5E) and *Pholoides*.

Parapodia and segments. As described above, the left and right sides of segment 1 or the tentacular segment envelop the prostomium laterally. This segment has one (Pelogeniinae and *Euthalenessa*) or two aciculae on each side, as well as two fascicles of chaetae (e.g., Fig. 7.13.1.5.1.1A–B, F). In rare cases, only one fascicle is present, and chaetae are absent on this segment in Pholoinae (Fig. 7.13.1.5.1.2D–H). Because these chaetae are always simple, they are generally regarded as notochaetae. The dorsal and ventral tentacular cirri of segment 1 are elongated to varying degrees. Typically, they are equal in length or the dorsal tentacular cirri are longer than the ventral ones; species of *Euthalenessa* are an exception in having the ventral tentacular cirri longest (Figs. 7.13.1.5.1.1A and 7.13.1.5.1.4B). Only one pair of tentacular cirri is present in *Pholoides* (Fig. 7.13.1.5.1.1D).

On the inner, medial surface of segment 1, dorsal to the palps, most sigalionids have a lobe on each side. In most Sigalioninae, these lobes are elongate and glandular, with a ciliated ridge. They are often characterized as being L-shaped but actually resemble more a boomerang with unequally long arms. In genera such as *Sthenelais* and *Willeysthenelais*, they are fused to the inner palpal sheath. A similar structure is also present in Pelogeniinae. Different terms have been used to describe these organs in various sigalionid subgroups: inner tentacular ridges in *Euthalenessa*, inner tentacular lobes in other Sigalioninae, inner tentacular sheaths in Pelogeniinae, and inner tentacular lamellae in Sthenelanellinae. Despite these different terms, they are probably homologous structures. These lobes are absent in Pholoinae and the sigalionins *Ehlersileanira*, *Labioleanira*, *Leanira*, *Pholoides*, and *Sigalion*.

On the dorsal surface of segment 1, posterior and medial to the dorsal tentacular cirri, a raised elongate structure, anteriorly ending in a free lobe, is found in species of *Horstileanira* (auL on Fig. 7.13.1.5.1.4C). In several other sigalionin genera [*Sthenelais*, *Fimbriosthenelais*, *Mustaquimsthenelais*, *Willeysthenelais* (Fig. 7.13.1.5.1.4A), *Sthenolepis*, *Labiosthenolepis*, and apparently *Neoleanira*] a much shorter, ciliated, cushion-like structure occurs in the same position (ctI on Fig. 7.13.1.5.1.4A). These organs have traditionally been called auricles and ctenidia, respectively, reflecting their resemblance to the similar organs found on the ceratophore of the median antenna (see above). Aungtonya (2003) concluded that the differences between auricles and ctenidia on segment 1 are negligible and combined them under the new term dorsal tentacular crests. However, Wehe (2007) presented convincing evidence that the distinction should be retained, pointing out that the auricles of *Horstileanira* are not ciliated. Nevertheless, further study of a broad range of species is needed in order to determine whether this distinction is reliable at the generic level. A number of small elongate lobes called stylodes may also be found on the dorsal surface of segment 1 in most species of *Ehlersileanira*, *Labioleanira*, *Leanira*, and *Horstileanira*.

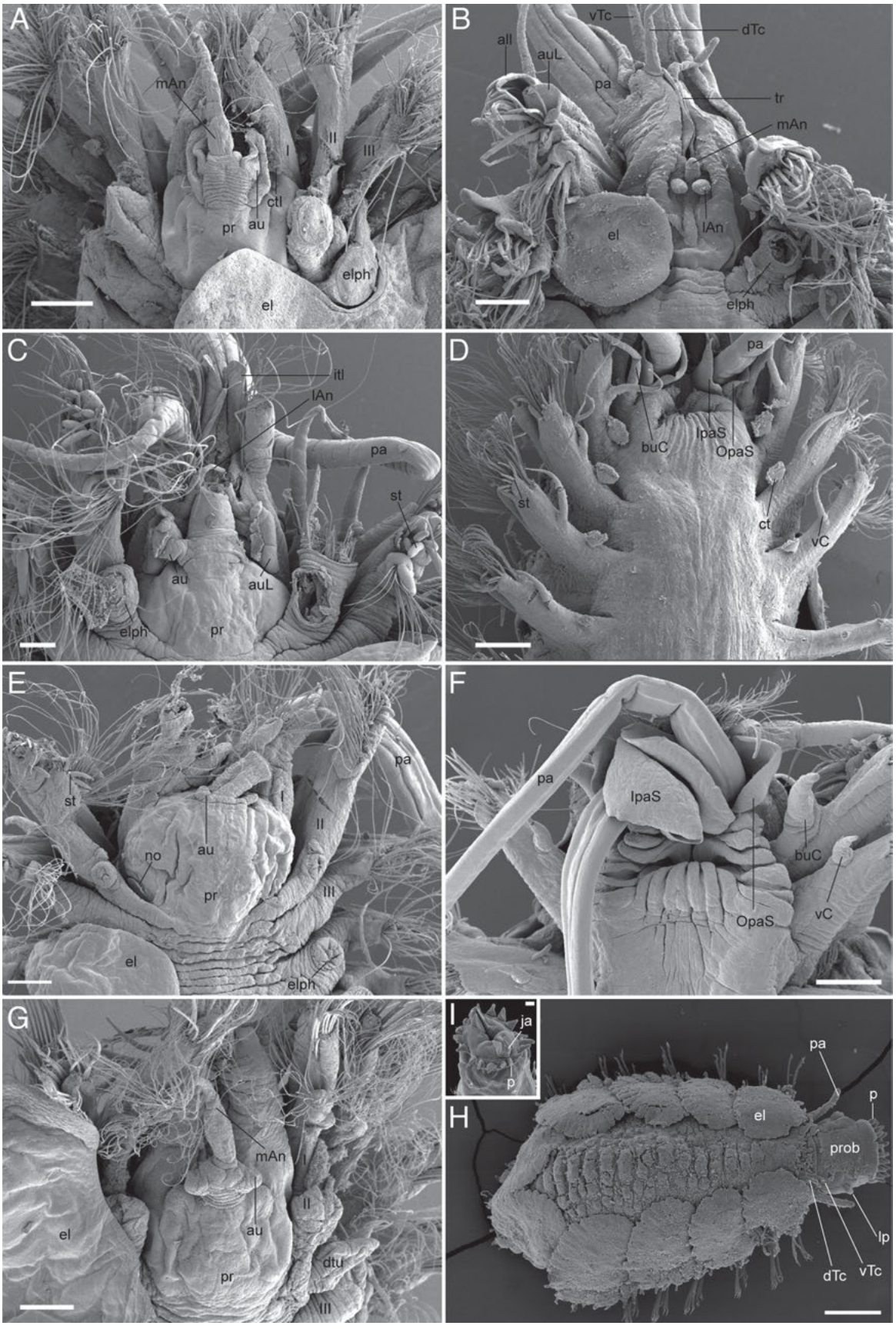
The mouth is positioned ventrally and posterior to the palps (Fig. 7.13.1.5.1.4D, F). According to Hutchings (2000) and Rouse and Pleijel (2001), the lips are the only visible vestige of the peristomium. Anterior and posterior lips are present but the lateral lips are the most strongly developed. Labial lobes, either thin and flattened or thick and fleshy, are found on the lateral lips of *Leanira*, *Labioleanira*, and *Labiosthenolepis* (Fig. 7.13.1.5.1.5D). Labial ctenidia occur on the lateral lips of *Sthenolepis*, *Fimbriosthenelais* (Fig. 7.13.1.5.1.5E), *Sthenelais*, and some species of *Euthalenessa*.

On the rest of the body, each segment typically has a pair of elytra or dorsal tubercles (see above), a pair of biramous parapodia, and a pair of ventral cirri. *Metaxypsamma* is once again an exception in lacking notopodia throughout the body.

To descending degrees, the parapodia of segments 2–4 resemble those of segment 1 in being oriented in a forward direction. They are often modified when compared to those on following segments in having more strongly developed lobes (e.g., in *Euthalenessa*), more numerous and elaborate stylodes, and/or some of the neurochaetae thinner and more elongate. For example, in *Sthenelais branchiata* Imajima, 2003, some of the neuropodial stylodes of segments 2–4 are branched or have papillae (see Imajima 2003), causing them to resemble the stylodes found on all parapodia in *Fimbriosthenelais* (see below). The ventral or "buccal" cirri of segment 2 are enlarged, being both thicker and longer than those of following segments (Figs. 7.13.1.5.1.4D, F and 7.13.1.5.1.5D–E).

Several Pelogeniinae show further specializations on their anterior segments. Segment 2 has a noticeable middorsal hump in *Claparedepelogenia*,

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Hartmanipsammolyce, *Neopsammolyce*, and *Psammolyce*. The acicular lobe of the neuropodium of segment 2 is elongated and filiform in *Claparedepelogenia* and *Psammolyce*. However, in species of *Hartmanipsammolyce* and *Heteropelogenia*, it is the acicular lobe of the neuropodia of segment 3 that is elongated and in the former case resembling a balloon-like lobe.

Sigalionid elytra generally have a simple oval shape. In Sigalioninae, Pelogeniinae, and Sthenelanellinae, the elytra more or less cover the middorsal part of the body (except in *Euthalenessa* and some species of *Horstileanira*), but in Pholoinae, they often leave the midline of the dorsum uncovered (Fig. 7.13.1.5.1.4H). In some species, especially in Pelogeniinae, the elytra bear deep incisions that create lateral or posterior lobes on them. As in other scale worms, the upper surface of the elytron may have papillae and tubercles (Fig. 7.13.1.5.1.6B). Elongated papillae arise along the lateral and posterior margins of the elytron in many species (Fig. 7.13.1.5.1.6D). However, very large surface tubercles, i.e., macrotubercles, are rare. The marginal papillae are unusual in being pinnate (with side branches emerging in two lateral rows from a common stem) in *Sigalion* (Fig. 7.13.1.5.1.6A), palmate (branches emerging from the tip of a common stem) in *Euthalenessa*, and arborescent-branched in *Mustaquimsthenelais* (this also applies to some of the surface papillae). The marginal papillae in *Heteropelogenia* and *Neopsammolyce catenulata* (Amaral & Nonato, 1984) are unique in being multiarticulate, resembling beads on a string (see Amaral and Nonato 1984). Most of the elytral surface papillae of pelogeniins are adhesive and flat-topped, specialized to fasten foreign particles to the surface of the elytron, presumably for protective or camouflage purposes. The elytra of sigalionids are usually quite thin and flexible, but in *Pholoides* they are stiffer and show unique concentric rings on the surface. In the interstitial *Laubierpholoe*, elytra have areolae or a lattice-like ornamentation (Fig. 7.13.1.5.1.3F). Several interstitial Pholoinae also utilize their elytra for reproductive functions, where embryos may be brooded either in brood sacs beneath (*Imajimapholoe* and *Taylorpholoe*) or within (*Laubierpholoe*; Fig. 7.13.1.5.1.3G) their elytra.

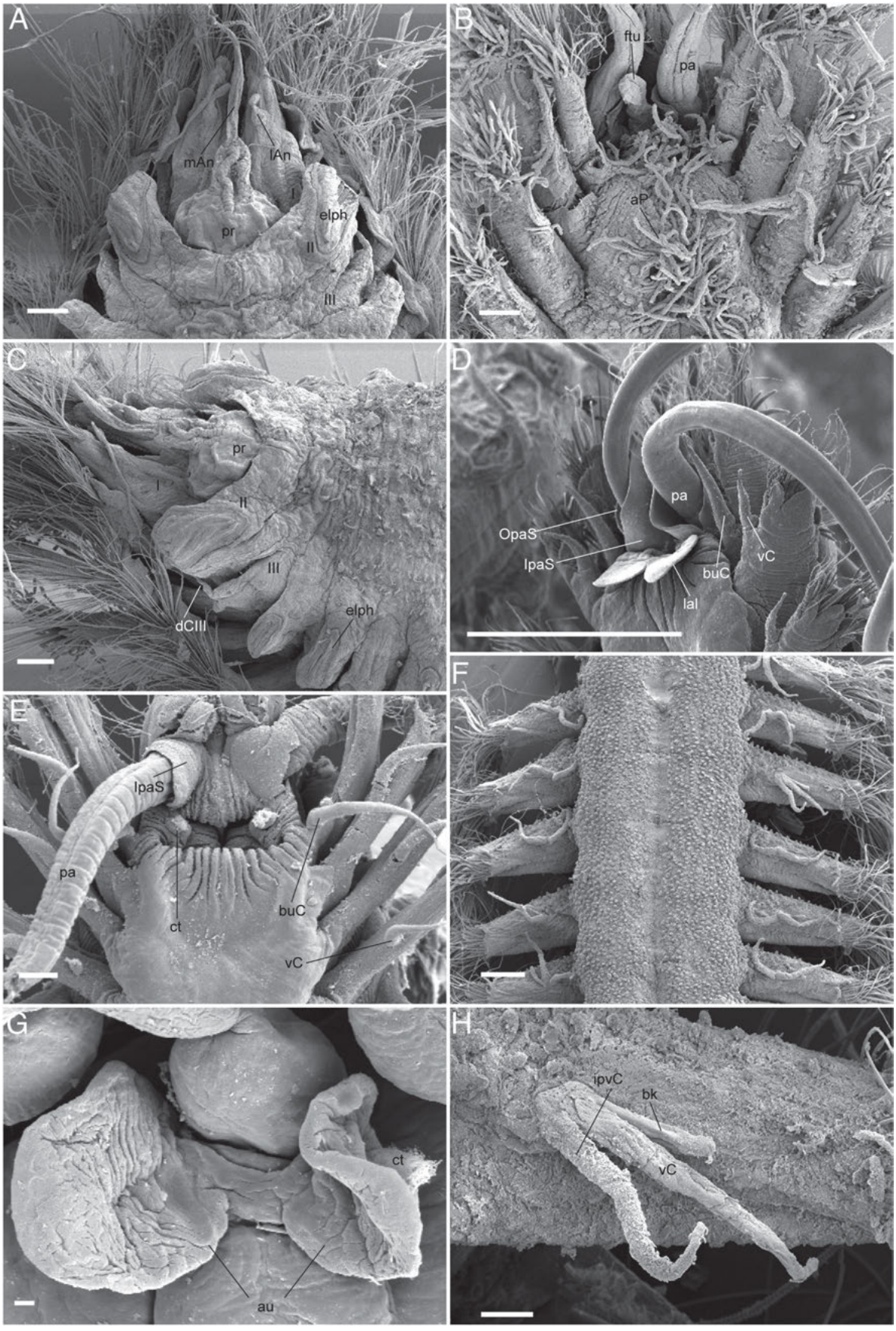
The area of the body wall between the elytron/dorsal tubercle and the notopodium is specialized in sigalionids to serve respirational purposes. The lateral portion of the elytrophore or dorsal tubercle is typically extended and ends in a simple digitiform branchia that points laterally and ventrally (Fig. 7.13.1.5.1.7A–B). Such branchiae are, however, absent in Pholoinae and *Pholoides*. Depending on the species, branchiae begin somewhere between segment 2 and 20 and continue to the end of the body. On the curvature of the body wall between the branchiae and the notopodium, a dorsoventrally arranged series of three ciliated ctenidia usually occurs (Figs. 7.13.1.5.1.7A–B and 7.13.1.5.1.8C). These ctenidia create a current that supplies the branchiae with oxygenated water. Ctenidial pads are often fused as one indistinct pad (e.g., in species of *Leanira* and *Ehlersileanira*) or are very poorly developed (*Pelogenia*, *Psammolyce*, *Neopsammolyce*, and interstitial species of Pholoinae).

Ctenidia may also occur elsewhere on the general body surface, typically on the ventral side of the parapodia, between the ventral cirrus and the main body (Fig. 7.13.1.5.1.4D).

Chaetae. In Sigalionidae, the notopodium has a notoacicula, an acicular lobe, and a fascicle of simple notochaetae. The base of the notochaetae is typically protected by one (dorsal) or two (anterior and posterior) low lobes, often called bracts. In most sigalionids, stylodes occur along the edges of these lobes (Fig. 7.13.1.5.1.7A). A large terminal stylode is found near the tip of the acicular lobe itself in species of *Sigalion* (Fig. 7.13.1.5.1.7B), *Leanira*, *Ehlersileanira*, *Horstileanira*, *Labioleanira*, *Neoleanira*, *Sthenolepis* (Fig. 7.13.1.5.1.7C), *Labiosthenolepis*, and several Pholoinae. The stylodes of *Fimbriosthenelais* are remarkable in having a terminal crown of small papillae, also present on their neuropodial stylodes (Figs. 7.13.1.5.1.6C and 7.13.1.5.1.7A). Notochaetae of sigalionids are generally

◂ **Fig. 7.13.1.5.1.4**: Morphology of Sigalionidae. Scanning electron micrographs: Sigalioninae (A–F), Sthenelanellinae (G), Pholoinae (H–I). A, *Willeysthenelais diplocirrus* (Grube, 1875), anterior end, dorsal view. B, *Euthalenessa digitata* (McIntosh, 1885), anterior end, dorsal view. C, *Horstileanira vanderspoeli* Pettibone, 1970c, anterior end, dorsal view. D, *Sthenelais* sp., anterior end, ventral view. E, *Labioleanira tentaculata* (Horst, 1917), anterior end, dorsal view. F, *Ehlersileanira andamanensis* Aungtonya & Eibye-Jacobsen, 2016 anterior end, ventral view. G, *Sthenelanella* sp., anterior end, dorsal view. H, *Taylorpholoe* sp. from Miramar, Cuba, entire body, dorsal view. I, *Laubierpholoe* sp. from Akumal, México, distal view of everted pharynx showing jaws and 18 terminal papillae. I–III, segments; all, anterior lower lobe; au, auricle; auL, dorsal auricle on segment I; buC, buccal cirrus; ct, ctenidium; ctI, ctenidium on segment I; dTc, dorsal tentacular cirrus; dtu, dorsal tubercle; el, elytron; elph, elytrophore; IpaS, inner palpal sheath; itl, inner tentacular lobe; ja, jaw; lAn, lateral antenna; lp, lateral papilla; mAn, median antenna; no, nuchal organ; OpaS, outer palpal sheath; p, papilla; pa, palp; pr, prostomium; prob, proboscis; st, stylode; tr, tentacular ridge; vTc, ventral tentacular cirrus; vC, ventral cirrus. Photographs A–G by Charatsee Aungtonya, H–I by Brett C. Gonzalez and the Worsaae Lab, University of Copenhagen. Scale bars: A, D, F, 200 µm; B–C, E, G–H, 100 µm; I, 10 µm.

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of the same type, thin, capillary, and with numerous transverse rows of spines (Fig. 7.13.1.5.1.6F). Some of the notochaetae in Pholoinae are characteristic in being geniculate (Figs. 7.13.1.5.1.6F and 7.13.1.5.1.8C). In species of *Sigalion*, notochaetae are distally minutely bifurcated. Uniquely among Sigalionidae, species of *Sthenelanella* have large oval notopodial chaetal sacs, often incorrectly referred to as "spinning glands", in the middle and posterior segments (e.g., in *Sthenolepis japonica* Imajima, 2003 from segment 15, see Imajima 2003), which produce elongate, fiber-like notochaetae (Fig. 7.13.1.5.1.8B) (Tilic et al. 2021). These fibers occur in addition to the normal notochaetae and are used to strengthen the tubes built by these worms, a phenomenon also found in the scale worm family Acoetidae. Species of *Pelogenia* also have thread-like notochaetae, but they arise from the posterior part of each notopodium and do not appear to be produced in specialized sacs.

The neuropodium is usually more strongly developed than the notopodium (Figs. 7.13.1.5.1.7 and 7.13.1.5.1.8), and with the exception of species of *Sigalion* (Fig. 7.13.1.5.1.7B), it is usually also more elongate. The neuroacicula supports a strong acicular lobe, around which the neurochaetae are arranged. As in the notopodia, the bases of the chaetae are protected by variously developed lobes (bracts), typically a dorsoanterior and a ventroanterior lobe as well as either one long posterior lobe (Pelogeniinae, Sthenelanellinae, and *Euthalenessa*) or dorso- and ventroposterior lobes (most Sigalioninae). Numerous stylodes may occur on these lobes, as well as on the acicular lobe. In Pelogeniinae, they are referred to as elongate papillae rather than stylodes (Figs. 7.13.1.5.1.6G and 7.13.1.5.1.8A); in *Heteropelogenia* and *Neopsammolyce catenulata* (Amaral & Nonato, 1984), these papillae are multiarticulate and similar to the marginal papillae on the elytra of these species (see Amaral and Nonato 1984).

Sigalionid neurochaetae show a considerable diversity of form. A small number of the dorsalmost neurochaetae are simple capillaries in several genera of Sigalioninae [*Ehlersileanira*, *Fimbriosthenelais*, *Horstileanira*, *Sigalion* (Fig. 7.13.1.5.1.7B–I), *Sthenelais*, *Sthenolepis*, and *Willeysthenelais*], but otherwise they are all compound, having a single ligament joining the distal article to the basal shaft (Hutchings 2000). Compound neurochaetae are usually referred to as spinigerous (distal article with a sharp, acute tip) or falcigerous (distal tip with a blunt, rounded, often bidentate tip), but the distinction is not always easy to make. A third term, heterocheliger, was proposed by Wehe (2007) for the strange type of neurochaetae that occur in *Mustaquimsthenelais*, resembling a bidentate falciger in which the secondary tooth is greatly elongated and extends beyond the tip of the primary tooth.

The main form of compound spinigers found in Sigalionidae is the canaliculate or camerate type, so called due to its appearance in transmitted light of having a longitudinal series of internal chambers. It is unclear whether this impression is caused by internal or external structures of the distal article. Canaliculate spinigers are found in the sigalionin genera *Ehlersileanira*, *Horstileanira*, *Labioleanira*, *Labiosthenolepis*, *Leanira*, *Neoleanira*, and *Sthenolepis* (Fig. 7.13.1.5.1.7C). Aberrant, noncanaliculate types of spinigers are found in the genera *Sthenelanella* (Figs. 7.13.1.5.1.6H and 7.13.1.5.1.8B) and *Psammolyce*.

Other sigalionids have mainly compound falcigers of varying types, and this was found to be an apomorphic character supporting Sigalionidae by Gonzalez et al. (2018). In Pholoinae and *Pholoides*, the distal article is relatively short, falcate, and unidentate (Figs. 7.13.1.5.1.3D–E, 7.13.1.5.1.6I, and 7.13.1.5.1.8C). In the Pelogeniinae (apart from *Psammolyce*), the distal article of most chaetae is elongated, distally bifid, or

◂ **Fig. 7.13.1.5.1.5**: Morphology of Sigalionidae. Scanning electron micrographs: Pelogeniinae (A–C), Sigalioninae (D–H). A, *Pottsipelogenia* cf. *malayana* (Horst, 1913), anterior end, dorsal view. B, *Pottsipelogenia* cf. *malayana* (Horst, 1913), anterior end, ventral view. C, *Pottsipelogenia* cf. *malayana* (Horst, 1913), anterior end, dorsolateral view. D, *Labiosthenolepis* sp., anterior end, ventrolateral view. E, *Fimbriosthenelais longipinnis* (Grube, 1869), anterior end, ventral view. F, *Willeysthenelais diplocirrus* (Grube, 1875), middle part of body, ventral view. G, *Ehlersileanira andamanensis* Aungtonya & Eibye-Jacobsen, 2016, ceratophore of median antenna. H, *Willeysthenelais diplocirrus* (Grube, 1875), ventral cirrus, ventrolateral view. I–III, segments; aP, adhesive papillae on midventral surface; au, auricle; bk, basal knob at outer lateral base of ventral cirrus; buC, buccal cirrus; ct, ctenidium; dCIII, dorsal cirrus on segment III; elph, elytrophore; ftu, facial tubercle; IpaS, inner palpal sheath; ipvC, papilla on inner lateral base of ventral cirrus; lal, lateral lobe on lateral lip; lAn, lateral antenna; mAn, median antenna; OpaS, outer palpal sheath; pa, palp; pr, prostomium; vC, ventral cirrus. Photographs A–F, H by Charatsee Aungtonya, G from Aungtonya and Eibye-Jacobsen (2016). Scale bars: A–C, E–F, 200 µm; D, 500 µm; H, 50 µm; G, 10 µm.

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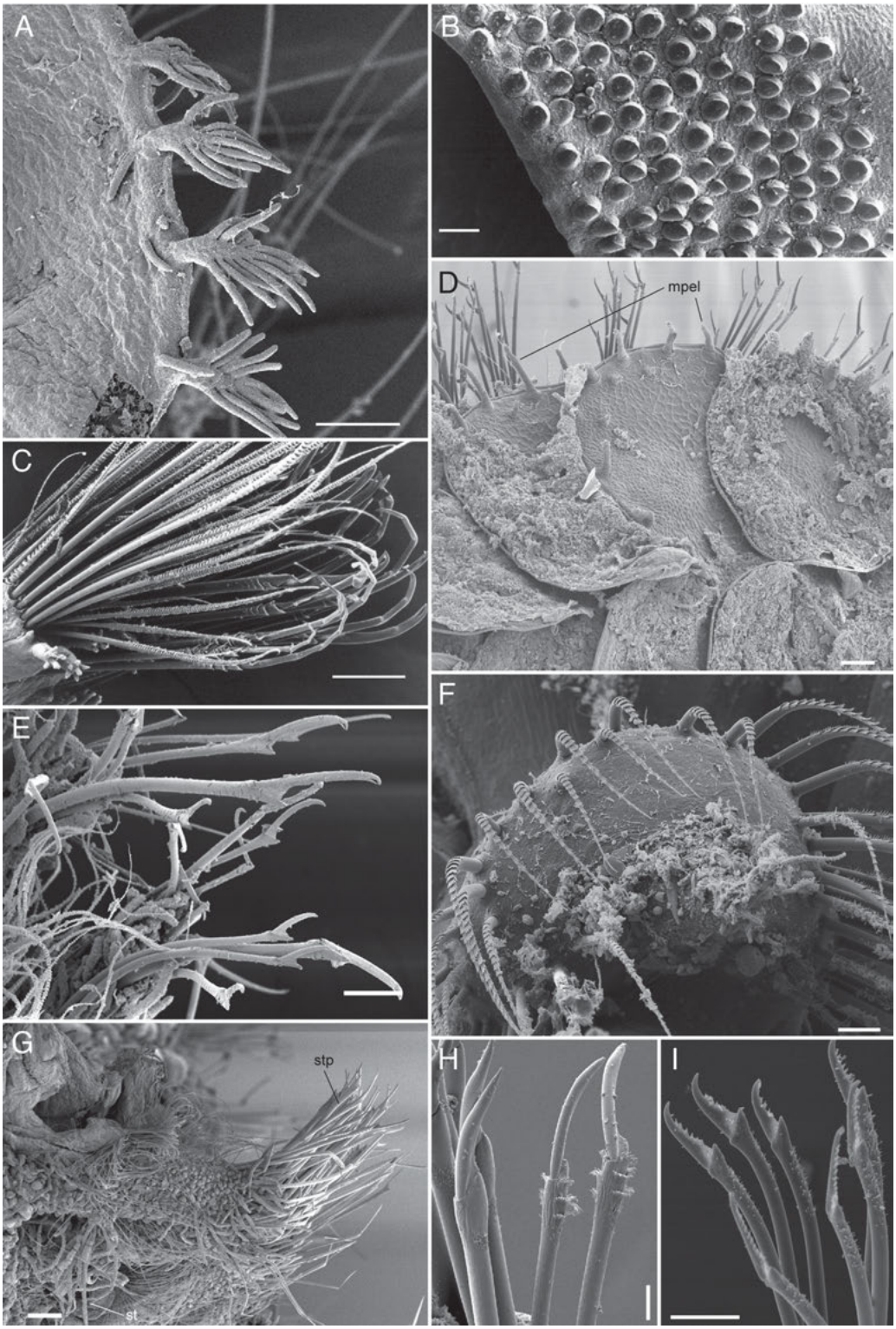


Fig. 7.13.1.5.1.6: Elytra and chaetae. Scanning electron micrographs: Sigalioninae (A–C), Pholoinae (D, F, I), Pelogeniinae (E, G), Sthenelanellinae (H). A, *Sigalion* sp. from the Andaman Sea, Thailand, margin of elytron. B, *Fimbriosthenelais longipinnis* (Grube, 1869), detail of elytron. C, *Fimbriosthenelais longipinnis* (Grube, 1869), multiarticulate falcigerous compound neurochaetae. D, *Pholoe* sp. from Napoli, Italy, elytra from middle of body. E, *Pottsipelogenia* cf. *malayana* (Horst, 1913), falcigerous compound neurochaetae. F, *Pholoe longa* (Müller, 1776), notopodium from middle of body, lateral view. G, *Pelogenia antipoda* Schmarda, 1861, parapodium from middle of body, dorsal view. H, *Sthenelanella* sp. from the Andaman Sea, Thailand, aberrant spinigerous compound neurochaetae. I, *Taylorpholoe* sp. from Mirimar, Cuba, falcigerous compound neurochaetae. mpel, marginal papillae on elytron; st, stylode; stp, stylode-like papillae. Photographs A–C, E, G–H by Charatsee Aungtonya, D, F, I by Brett C. Gonzalez and the Worsaae Lab, University of Copenhagen. Scale bars: A, C, E, 50 µm; B, D, F, H–I, 10 µm; G, 100 µm.

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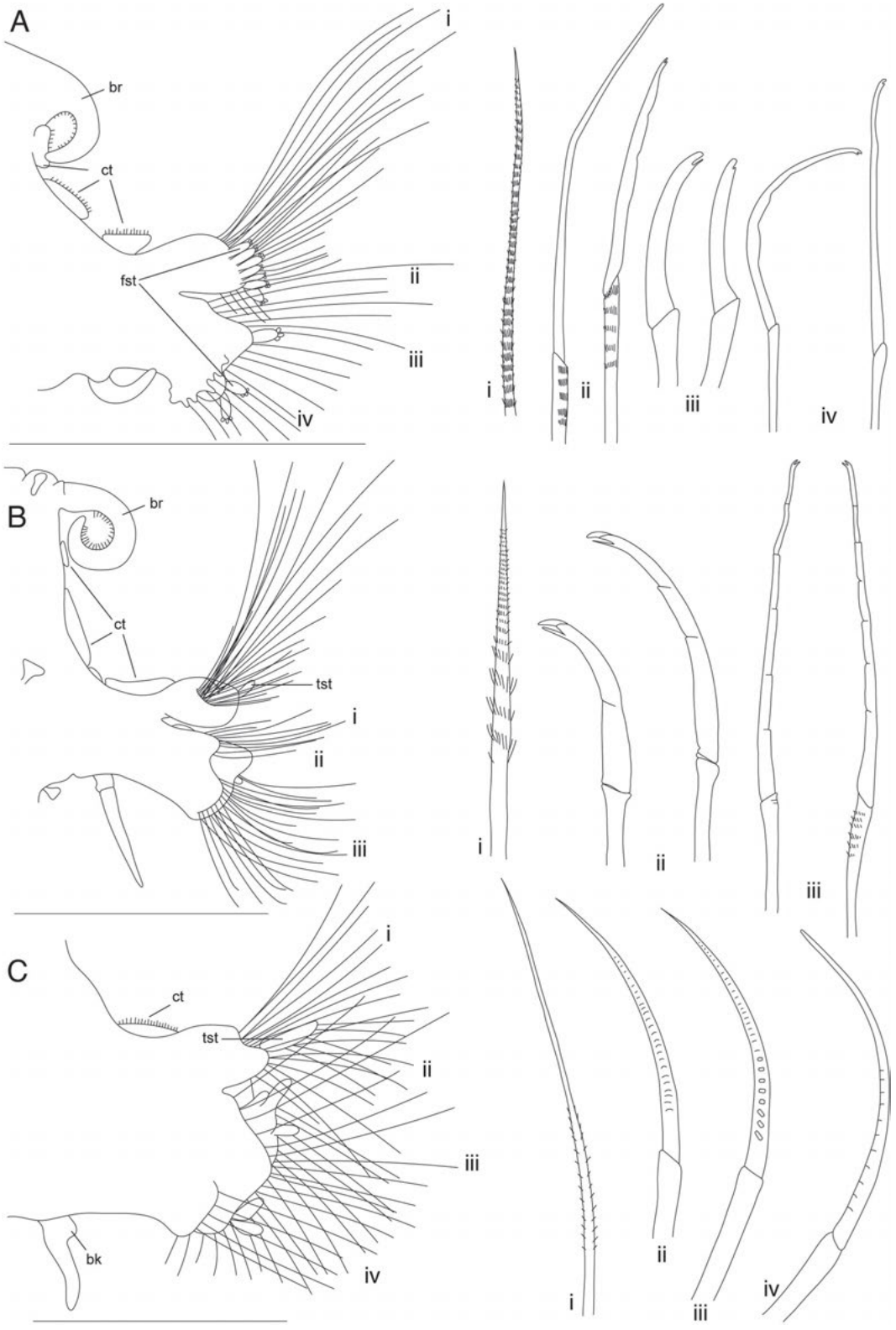


Fig. 7.13.1.5.1.7: Parapodia in anterior view from middle of body (on left), with position of enumerated chaetae (on right) indicated: Sigalioninae. A, *Fimbriosthenelais hirsuta* (Potts, 1910), from Wehe (2007), showing (i) notochaeta, (ii) upper neurochaetae, (iii) neurochaetae of C-shaped group, and (iv) lower neurochaetae. B, *Sigalion shimodaensis* Imajima, 2006, from original description, showing (i) spinose simple neurochaeta, (ii) upper neuropodial falcigers, and (iii) middle neuropodial falcigers. C, *Sthenolepis japonica* (McIntosh, 1885), from Wehe (2007), showing (i) notochaeta, (ii) upper neuropodial spiniger, (iii) middle neuropodial spiniger, and (iv) lower neuropodial spiniger. bk, basal knob at outer lateral base of ventral cirrus; br, branchia; ct, ctenidium; fst; fimbriate stylode; tst, terminal notopodial stylode. Scale bars: A, C, 1 mm; B, 0.5 mm.

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entire (Figs. 7.13.1.5.1.6E and 7.13.1.5.1.8A). In the sigalionin genera *Euthalenessa*, *Fimbriosthenelais*, *Sigalion*, *Sthenelais*, and *Willeysthenelais*, the distal articles of many neurochaetae are multiarticulate (Figs. 7.13.1.5.1.6C and 7.13.1.5.1.7A–B).

Neurochaetae are often arranged in three groups within the neuropodium: an upper anterior group, a C-shaped posterior group that usually contains the most strongly developed neurochaetae, and a lower anterior group.

Ventral cirri are inserted on the ventral edge of the neuropodium and consist of a basal cirrophore and an elongate, distally tapering cirrostyle. In most species of the subfamilies Sthenelanellinae, Sigalioninae, and Pelogeniinae, the outer lateral part of the cirrophore shows a basal knob (Fig. 7.13.1.5.1.7C). This knob is absent in species of *Euthalenessa*, *Neoleanira*, *Pholoides*, and *Sigalion* and is weakly developed in *Ehlersileanira*, *Leanira*, *Neopsammolyce*, and *Sthenelanella*. The basal knob is papilliform in some species of *Willeysthenelais* (Fig. 7.13.1.5.1.5H). In *Mustaquimsthenelais*, *Willeysthenelais* (Fig. 7.13.1.5.1.5H), and all Pelogeniinae (Fig. 7.13.1.5.1.8A), except *Psammolyce* and *Hartmanipsammolyce*, the inner lateral base of the cirrophore bears one to several additional elongate papillae. Further papillae may arise from the ventral surface of the body and extend to near the ventral cirrus. The inner lateral papilla in *Mustaquimsthenelais dendropapillata* Wehe (2007) is exceptional in being almost as strongly developed as the ventral cirrus itself and in having a longitudinal series of side branches (Wehe 2007).

The body ends with the pygidium, which bears the dorsoposteriorly oriented anus and a lateral pair of elongate pygidial cirri.

Internal morphology

Despite the size of the family, surprisingly little information has been published on the anatomy of sigalionids. Members of the subfamily Pholoinae have been more intensely studied than those of other subfamilies.

The original description of *Sthenelais limicola* (Ehlers, 1864) (as *Sigalion*) was unusually detailed and included a thorough treatment of the digestive tract and nephridia. Darboux (1900) provided further information on the gut of other sigalionins and observed that the intestine has segmental diverticula, which is also known from other scale worms. More recently, Heffernan (1988) described the gut structure in the pholoin *Pholoe baltica* (as *P. minuta*). The observations published by Wolf (1986) on the presence of probable venom glands closely associated with the jaws of sigalionids are summarized below.

Pharynx. Sigalionds have a muscular axial pharynx that when everted through the mouth may extend anteriorly far beyond the prostomium. The anterior edge of the fully everted pharynx is crowned by a circle of terminal papillae, 9 dorsal + 9 ventral in Pholoinae (Fig. 7.13.1.5.1.4I) and *Pholoides*, 11 + 11 in Pelogeniinae and most species of Sigalioninae, 13 + 13 in some species of *Fimbriosthenelais*, and 13 or more + 13 or more in *Sthenelanella*.

Jaws. All sigalionids have four jaws, distributed as one dorsal and one ventral pair positioned just inside the lumen of the everted pharynx. According to Wolf (1986), who studied the jaws of *Metaxypsamma uebelackerae* Wolf, 1986, *Sthenelais* sp., *Dayipsammolyce ctenidophora* (Day 1973) (as *Psammolyce*), *Pholoe* sp., *Ehlersileanira incisa* (Grube, 1877), and *Pisione* sp., each jaw has an internal canal associated with an organ that he assumed to be a venom gland. Wolf was unable to find an external opening of the canal near the tip of the jaw, and further research would be useful to verify that a venom delivery system does exist in sigalionids.

Nervous system. The most complete treatment of the nervous system in a sigalionid was given by Åkesson (1963), who demonstrated the presence of corpora pedunculata in the brain of *Pholoe inornata* Johnston, 1839 (as *Pholoe minuta*). Corpora pedunculata have been implicated in the coordination of complex behaviors and have been described in several other scale worms, as well as in Nereididae, Hesionidae, and possibly Serpulidae (Evans 1971, Lindsay 2009, Heuer et al. 2010).

In his detailed paper on the segmental musculature of polychaetes, Storch (1968) included information on two sigalionins, *Sthenelais boa* (Johnston, 1833) and *Neoleanira tetragona* (as *Leanira*). He found the segmental musculature to be very similar in these two species and summarized that it is somewhat simplified in comparison to that found in other scale worm families.

Darboux (1900) characterized the circulatory system of sigalionids as closed and the nephridia as mixonephridia. Goodrich (1945) confirmed the latter observation in a study of annelid nephridia that included a species of *Sthenelais*. He concluded that the mixonephridia function as both excretory and genital ducts. Metanephridia of juvenile *Pholoe inornata* (as *P. minuta*) were studied by Bartolomaeus and Ax (1992) and were found to lack mesodermal elements.

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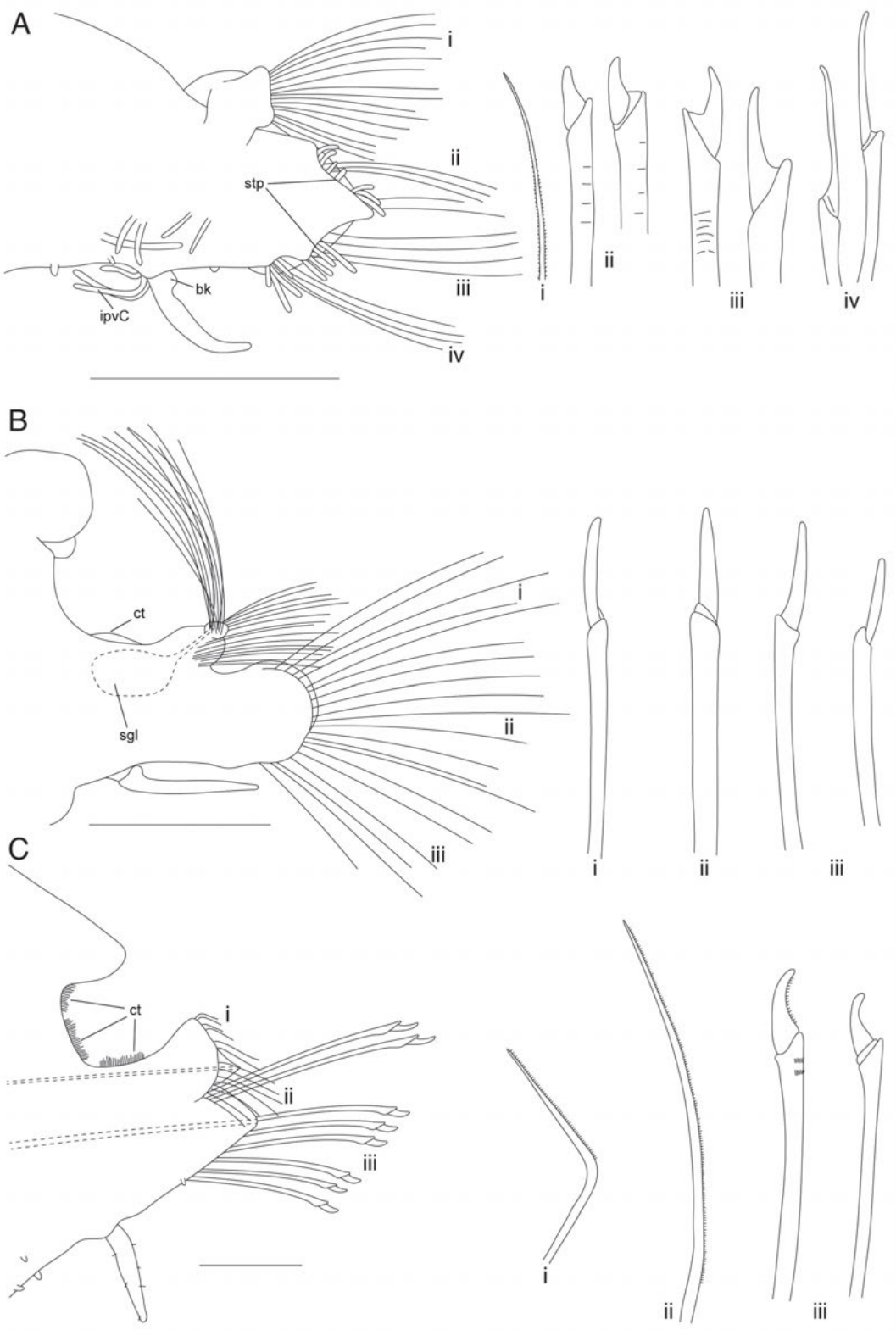


Fig. 7.13.1.5.1.8: Parapodia in anterior view from middle of body (on left), with position of enumerated chaetae (on right) indicated: Pelogeniinae (A), Sthenelanellinae (B), Pholoinae (C). A, *Pelogenia rigida* (Grube, 1868), from Wehe (2007), showing (i) notochaeta, (ii) upper neuropodial falcigers, (iii) middle neuropodial falcigers, and (iv) lower neuropodial falcigers. B, *Sthenelanella ehlersi* (Horst, 1916), from Pettibone (1969), showing (i) upper, (ii) middle, and (iii) lower neuropodial spinigers. C, *Pholoe polymorpha* (Hartmann-Schröder, 1962), from Pettibone (1992b), showing (i) geniculate notochaeta, (ii) notochaeta, and (iii) upper and lower falcigers. bk, basal knob at outer lateral base of ventral cirrus; ct, ctenidium; ipvC, papilla at inner lateral base of ventral cirrus; sgl, spinning gland; stp, stylode-like papillae. Scale bars: A, 1 mm; B, 0.5 mm; C, 100 µm.

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In a paper on the ultrastructure of elytra in a species of *Pholoe*, Heffernan (1990) concluded that elytra play a role in the animal's respiration by participating in the creation of water currents over the dorsum, as well as being capable of sensory perception.

Reproduction and development

Most genera of Sigalionidae are considered gonochoristic with external fertilization by free spawning. Sexual dimorphism is not recorded, and until maturation, distinguishing sexes is impossible if gametes are not present. Within Pisioninae, separate sexes are easily distinguishable, as males have modified parapodia with species-specific penile structures that enable true internal copulation (see Pisioninae in Gonzalez et al. 2017, chapter 7.13.1.5.2. pp. 139). Three genera of Pholoinae, namely, *Laubierpholoe*, *Taylorpholoe,* and *Imajimapholoe*, exhibit brooding, whereby vitellogenic oocytes initiate in middle segments before developing embryos are deposited below (*Imajimapholoe* and *Taylorpholoe*) or within (*Laubierpholoe*) the elytra of those segments (Pettibone 1992b, Westheide 2001). Pettibone (1992b) distinguished this as a form of viviparity; however, Westheide (2001) argues that this is likely overreaching and in fact a situation where expelled embryos utilize this space for maturing. This type of external gestation appears to have evolved independently several times among annelids with interstitial forms, for example, in Nerillidae and Syllidae (Westheide 2001). Consequently, this external gestation is also indicative of internal fertilization, coinciding with a reduced number of oocytes and other reproductive adaptations to an interstitial lifestyle (Westheide 1984). This suggests that internal fertilization may also be common within Pholoinae, with multiple independent evolutions within Sigalionidae.

Little is known surrounding spermatogenesis and oogenesis in Sigalionidae. It is generally considered that sigalionids are polytelic and that reproductive structures lie in segments posterior to segment 16–17 (Heffernan et al. 1983). The only fully known reproductive cycle in sigalionids is that of *Pholoe minuta* (Fabricius, 1780) (Heffernan et al. 1983, Heffernan and Keegan 1988a, b). Sexes within *P. minuta*, as in other elytrigerous annelids, are indeterminable until mature, when large masses of spermatozoa or oocytes are easily discernable within the coelom (Heffernan et al. 1983). The release of gametes in *P. minuta* is through paired mixonephridia (coelomoducts). Again, these are only differentiated when fully mature and are located along the venter on gamete-bearing segments near the base of the parapodia (Heffernan et al. 1983). Gametes vacate the coelom through a ciliated coelomostome and continue out through a narrow ciliated duct (Christie 1982). These reproductive morphological characters are common among errant annelids and are likely to be found in many other sigalionid species. Both sexes of *P. minuta* spawn during late spring, when local phytoplankton blooms will provide nutrients for their planktonic larvae (Heffernan et al. 1983, Heffernan and Keegan 1988a). Sperm of *P. minuta* have a bullet-shaped head with an unmodified acrosome and a long filamentous flagellum (Heffernan and Keegan 1988a). Christie (1982), however, found differing sperm morphologies and egg sizes among other species of *Pholoe*, including both "primitive" and "aberrant" types (see Franzén 1956), illustrating a greater spermatogenetic and oogenetic variability than previously thought (Rouse and Pleijel 2001). It is unknown whether other sigalionid genera also have seasonal spawning or similar sperm morphologies.

Larvae of sigalionids are poorly known. Fertilization and early development in *Pholoe minuta* show an eight-cell stage within 4 h of fertilization and nonswimming gastrulae at 16 h postfertilization (Heffernan and Keegan 1988b). Trochophore larvae are consistent with those of other annelids and can be found swimming in the water column after 1–2 days. Eyespots, early cephalization, anal cirri, and feeding develop between 4 and 8 days in *P. minuta*. Distinct cephalic lobes are present in the metatrochophore, as well as rudimentary appendages, a ciliated mouth and a two-chambered gut (Heffernan and Keegan 1988b). Rates of development are not consistent among the larvae, as parapodial lobes and even dorsal cirri were occasionally observed as well. Nectochaete larvae of *P. minuta* have three to four chaetal segments, two pairs of eyes, and a bilobed prostomium, whereas notopodial lobes and elytra are still absent (Heffernan and Keegan 1988b). *P. minuta* settles at the four-segment stage, whereas in *Pholoe inornata* (Johnston, 1839) (as *P. synopthalmica* (Claparède, 1868)), settlement occurs when larvae have five segments (Cazaux 1968). Based on rearing experiments, *P. minuta* has a planktonic larval stage that lasts more than 3–4 weeks. Postlarval eight-segment stages are nearly fully recognizable, having sculptured elytra with marginal and surface features and distinguishable noto- and neuropodia as well as noto- and neurochaetae (Blake 1975). Active feeding at this stage is questionable, as lipid droplets are still present in the gut region.

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Comparable information for other species is lacking for all sigalionids except *Sthenelais boa* and *Sthenelais fusca* Johnson, 1897 (Cazaux 1968, Blake 1975, 2017). For both species, however, only metatrochophore and nectochaete stages have been described. In *S. fusca*, seven-segment nectochaetes are still planktotrophic and resemble other elytrigerous polychaetes (Blake 2017). Nectochaetes of *S. fusca* have a hemispherical anterior region with eyespots and a small protruding knob analogous to a median antenna. The prototroch contains 4–5 rows of rapidly beating cilia with the addition of multiple ciliary bands along the body (Blake 2017). Rudimentary tentacular cirri and serrated capillary chaetae are visible on segment 1, and both noto- and neuropodia are distinguishable along the rest of the body, with capillary notochaetae and compound neurochaetal spinigers. Elytra are present and can be found on segments 2, 4, 5, and 7. Metatrochophore and nectochaete larvae of *S. boa* differ from those of *S. fusca* in having fewer segments but well-developed antennae and cirri (tentacular and parapodial). Both species show developed elytra, and in *S. boa*, numerous papillae are present, both on the elytra as well as on the body (Blake 2017).

Sthenelais fusca reaches the postlarval stage at eight segments. Ciliary bands have been completely lost, and prostomial characters, including a median antenna, are clearly visible (Blake 2017). Both noto- and neurochaetae can be found on segment 1, tentacular cirri are more elongated, and fully developed elytra can be found throughout the rest of the body. Dorsal cirri at this stage in *S. fusca* are still reduced to small lobes, and parapodial features (i.e., bracts) are still lacking.

Additional reproductive and developmental data are unknown, making our knowledge mostly assumptive from the above-mentioned species and from other elytrigerous groups. Seasonal reproductive cycles and a long maturation time (1–3 years) make sigalionids particularly difficult to rear in artificial aquaria settings.

Biology and ecology

Sigalionids are found worldwide in marine habitats, commonly from the intertidal zone to abyssal depths, both as infauna or epifauna. Sigalionids are also known to inhabit several extreme environments, including interstitial sands (i.e., *Pholoe* and *Laubierpholoe*), marine caves, and whale falls, or being chasmolithic (i.e., *Pholoides*) among carbonates associated with deep-sea chimneys and cold seeps (Jumars et al. 2015, Gonzalez et al. 2018). Soft sands and mud are preferred substrates; however, sigalionids are also known from fine gravel and coarse sands. Large sigalionids are highly active, capable of rapid burrowing in a variety of sediment types to escape predation and/or to mask their presence. This rapid burrowing resembles a sinking motion and is a product of crack propagation, whereby chaetal action pushes away the sediment in the path of least resistance (Dorgan et al. 2006). Alternatively, smaller species (i.e., members of Pholoinae) are capable of crawling along soft bottoms or on holdfasts, rock crevices, shell gravel, or among oyster (or similar molluscan) reefs (Blake 1995). Few sigalionids are known to be truly pelagic; however, Pettibone (1970a) observed large specimens of *Euthalenessa oculata* (Peters, 1854) at the water surface, potentially coinciding with reproductive behaviors.

Similar to other elytrigerous annelids, the presence of two pairs of beak-like jaws suggests a predatory mode of feeding. However, for most genera, it is unknown whether they use active or sit-and-wait predation (Jumars et al. 2015). Stable isotope and fatty acid analyses of a few sigalionids, including *Sthenelais boa* (Johnston, 1833), *Labioleanira yhleni* (Malmgren, 1867), and *Pelogenia arenosa* (Delle Chiaje, 1830), are all indicative of carnivory (van Oevelen et al. 2009, Schaal et al. 2010, Fanelli et al. 2011, Würzberg et al. 2011). Interstitial forms, including Pisioninae (see Gonzalez et al. 2017), most likely actively predate on small protists or metazoans inhabiting the interstitium. Sit-and-wait predation is known in *Sthenelais berkeleyi* Pettibone, 1971, as it lies buried vertically or in an oblique orientation in the sediment, utilizing its palps to determine prey size before attacking (Pernet 2000). Sit-and-wait predation is also suggested for all members of Sthenelanellinae, as they live in self-built tubes in soft sands and mud.

True tube construction in sigalionids is only known in Sthenelanellinae and involves the utilization of specialized notopodial chaetal sacs. These structures were originally overlooked, but subsequent collections recovered specimens encased in fibrous tubes reinforced with sediment (Pettibone 1969). Where tube morphology is known, they are found to be lined with mucus and to be vertically oriented. Tubes constructed by *Sthenelanella corallicola* Thomassin, 1972 in coral sand reach lengths of 8 cm and have a larger diameter than the worm (Thomassin 1972). It is unknown to what extent the animals vacate their tubes, reconstruct them, or even ventilate them.

Unlike species of *Sthenelanella*, burrows constructed by *Sthenelais berkeleyi* are excavated by robust

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neurochaetae at angles approximating 45° and extending only as long as the worm. Pernet (2000) extensively investigated these burrows and their inhabitants, reporting that specimens of *S. berkeleyi* would lie motionless for days unless spooked or enticed by prey. Because no mucus was used to construct these burrows, any retreating motion into the sediment would cause it to collapse or to close, requiring specimens to redesign their burrow openings frequently. Ventilation is enabled by the anterior orientation of the chaetae and parapodia of segment 1, aided by intertwining of the median antenna and tentacular cirri. The two half-cylinders found on the left and right sides create a cylindrical opening that connects the anterior with the lateral spaces between the body wall and elytra. Heavy ciliation on segment 1 directs oxygenated water inward from the sediment surface and channels it into the lateral spaces. Ctenidia continue to direct the inflow posteriorly, and this synchronized coordination of beating cilia and the associated morphological features has been termed the "chaetal snorkel" (Pernet 2000). Dye tracing showed that the incurrent flow is continuous and requires no apparent muscular activity, allowing the animals to remain undetectable to predators and prey passing by.

It is unknown whether other species of *Sthenelais* exhibit similar burrow construction and ventilation by a chaetal snorkel; however, the great majority of species in Sigalioninae, Sthenelanellinae, and Pelogeniinae have anteriorly projecting chaetae and parapodia on segment 1, inner tentacular lobes, and ciliated spaces along the lateral margins of the body. This adaptation in *Sthenelais berkeleyi* may be strictly ecological, as other species inhabit oxygenated or well-ventilated substrates and may not need to use such strategies. It is interesting to note, however, that non-sigalionid scale worms belonging to Polynoidae (*Halosydna brevisetosa* Kinberg, 1856) and Aphroditidae (*Aphrodita aculeata* Linnaeus, 1758) also use various ciliary and muscular ventilation strategies underneath their elytra and along their lateral margins, potentially as a response to ecological and environmental parameters (van Dam 1940, Lwebuga-Mukasa 1970).

Phylogeny and taxonomy

The original family designation for Sigalionidae, "Sigalionina," was erected by Kinberg (1856) with the description of the four genera *Sthenelais*, *Sigalion*, *Leanira,* and *Psammolyce*. Because of its broad range of morphological characters, the taxonomy of the family has been confused since the nineteenth century. Taxonomical uncertainty is still prevalent today, even with the implementation of modern molecular techniques.

In the past, it was generally accepted that *Sigalion mathildae* Audouin & Milne Edwards in Cuvier, 1830 was the first described species of Sigalionidae (see Muir 1989, Rouse and Pleijel 2001). However, several combined phylogenetic analyses have challenged this claim (see Struck et al. 2005, Wiklund et al. 2005, Norlinder et al. 2012), and Gonzalez et al. (2018) finally synonymized "Pholoidae" as being part of Sigalionidae. Based on these recent analyses, we conclude that the first described species was actually *Pholoe longa* (Müller, 1776) (as *Aphrodita longa* — superseded).

The systematics of Sigalionidae had changed very little before the implementation of phylogenetic analyses. Like other scale-bearing families, Sigalionidae was included in Aphroditiformia by Levinsen (1883), and several defining morphological contributions and revisions have been made by Pettibone (e.g., Pettibone 1969, 1970a, b, c, 1971, 1992a, b, 1997) and others. The first morphological phylogenetic analysis to include original members of Sigalionidae was presented by Rouse and Fauchald (1997), recovering them in a deeply nested position and as the sister group to those scale-bearing families that lack compound neurochaetae. In the following years (see Pleijel and Dahlgren 1998, Rouse and Pleijel 2001), additional morphological analyses showed that several revisions were needed within Aphroditiformia. Rouse and Pleijel (2001) recognized the likelihood of Sigalionidae being paraphyletic with regards to "Pholoidae," necessitating thorough cladistic analyses within all of Aphroditiformia.

Sigalionidae continued to be recovered paraphyletic in both molecular and combined molecular and morphological analyses in 2005 (Struck et al. 2005, Wiklund et al. 2005), recovering *Pisione remota* (Southern, 1914) and *Pholoe baltica* Ørsted, 1843 (or *Pholoe pallida* Chambers, 1985 in Wiklund et al. 2005) nested within or in a trichotomy with traditional sigalionid taxa. In contrast to earlier studies based only on morphology, the inclusion of a molecular partition no longer recovered those families with compound neurochaetae as the deepest nodes of Aphroditiformia, but rather nested among families lacking compound neurochaetae. Regardless of these findings, no taxonomical revisions were conducted, leaving Sigalionidae paraphyletic until 2012. Using a combination of molecular and morphological analyses, Norlinder et al. (2012) recovered similar tree topologies to

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those of previous studies (i.e., Struck et al. 2005, Wiklund et al. 2005), albeit with a slightly larger and more inclusive data set. Therein, "Pisionidae" was formally synonymized with Sigalionidae, as they were consistently recovered nested among sigalionid taxa. However, Norlinder et al. (2012) made no further taxonomic decisions because of low sample size, still leaving Sigalionidae paraphyletic with regard to "Pholoidae."

Part of the aim of the most recent systematic reevaluation of Aphroditiformia (Gonzalez et al. 2018) was to address the lingering paraphyly of Sigalionidae using both molecular and combined molecular and morphological analyses, as well as total data set analyses using terminals represented only by morphological characters. In all analyses, Gonzalez et al. (2018) recovered Sigalionidae paraphyletic, leading to the formal synonymization of "Pholoidae" with Sigalionidae and the definition of five subfamilies to highlight consistently recovered clades with unique morphological character combinations (Gonzalez et al. 2018). The subfamilies Pisioninae and Pholoinae were delineated for all taxa that had been assigned to the former families "Pisionidae" and "Pholoidae," respectively, and Sthenelanellinae was erected for the species of *Sthenelanella*. Gonzalez et al. (2018) also reinstated the Sigalioninae, a historical rank for all elytrigerous annelids with compound neurochaetae (Grube 1857). However, this clade is currently a paraphyletic assemblage of genera, likely to be revised as more taxa are made available for combined molecular and morphological comparisons. Because Sigalionidae is continually recovered nested between other scale-bearing families, character reconstructions highlight that compound neurochaete are secondarily derived and have evolved separately among aphroditiforms and can no longer be considered the plesiomorphic state of Aphroditiformia (Rouse and Fauchald 1997, Gonzalez et al. 2018).

Overview of classification

The subfamily structure in the following overview is based on Gonzalez et al. (2018). Information on the number of species in each genus is from Aungtonya and Eibye-Jacobsen (2014), supplemented by Aungtonya and Eibye-Jacobsen (2016) and Read and Fauchald (2018). The genus *Mayella* Hartmann-Schröder, 1959 is excluded, as it most likely represents a juvenile polynoid.

Sigalionidae Kinberg, 1856 (252 species)
- Sigalioninae Kinberg, 1856 (*sensu* Gonzalez et al. 2018) (134 species)
  - *Ehlersileanira* Pettibone, 1970b (2 species)
  - *Euthalenessa* Darboux, 1900 (5 species)
  - *Fimbriosthenelais* Pettibone, 1971 (9 species)
  - *Horstileanira* Pettibone, 1970b (2 species)
  - *Labioleanira* Pettibone, 1992a (2 species)
  - *Labiosthenolepis* Pettibone, 1992a (3 species)
  - *Leanira* Kinberg, 1856 (11 species)
  - *Mustaquimsthenelais* Wehe, 2007 (2 species)
  - *Neoleanira* Pettibone, 1970c (4 species)
  - *Pholoides* Pruvot, 1895 (5 species)
  - *Sigalion* Audouin & Milne Edwards in Cuvier, 1830 (29 species)
  - *Sthenelais* Kinberg, 1856 (41 species)
  - *Sthenolepis* Willey, 1905 (13 species)
  - *Willeysthenelais* Pettibone, 1971 (6 species)
- Pelogeniinae Chamberlin, 1919 (33 species)
  - *Claparedepelogenia* Pettibone, 1997 (1 species)
  - *Dayipsammolyce* Pettibone, 1997 (1 species)
  - *Hartmanipsammolyce* Pettibone, 1997 (1 species)
  - *Heteropelogenia* Pettibone, 1997 (2 species)
  - *Neopsammolyce* Pettibone, 1997 (5 species)
  - *Pelogenia* Schmarda, 1861 (13 species)
  - *Pottsipelogenia* Pettibone, 1997 (5 species)
  - *Psammolyce* Kinberg, 1856 (5 species)
- Sthenelanellinae Gonzalez et al., 2018 (5 species)
  - *Sthenelanella* Moore, 1910 (5 species)
- Pholoinae Kinberg, 1857 (*sensu* Gonzalez et al. 2018) (26 species)
  - *Imajimapholoe* Pettibone, 1992b (1 species)
  - *Laubierpholoe* Pettibone, 1992b (5 species)
  - *Metaxypsamma* Wolf, 1986 (1 species)
  - *Pholoe* Johnston, 1839 (18 species)
  - *Taylorpholoe* Pettibone, 1992b (1 species)
- Pisioninae Ehlers, 1901 (*sensu* Gonzalez et al. 2018) (54 species)
  - *Anoplopisione* Laubier, 1967 (2 species)
  - *Pisione* Grube, 1857 (46 species)
  - *Pisionella* Hartman, 1939 (1 species)
  - *Pisionidens* Aiyar & Alikunhi, 1943 (5 species)

Emended diagnoses of subfamilies and genera (excluding Pisioninae)

Sigalioninae Kinberg, 1856 (sensu Gonzalez et al. 2018)

Type genus: *Sigalion* Audouin & Milne Edwards in Cuvier, 1830

134 species

Diagnosis: Sigalionids usually with auricles on ceratophore of median antenna. Lateral antennae present (exception: *Pholoides*), usually inserted on segment 1 (exception: *Sigalion*). Inner and outer palpal sheaths

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usually present. Segment 1 usually with inner tentacular lobes. Dorsal cirri may be present on segment 3. Neuropodia and notopodia usually with stylodes. Simple neurochaetae may be present. Majority of neurochaetae compound canaliculate spinigers or variously developed falcigers, including multiarticulate falcigers (exceptions: *Mustaquimsthenelais* and *Pholoides*). Ventral cirri usually with outer lateral basal knob. Dorsal and ventral body surface typically smooth (exceptions: some members of *Fimbriosthenelais* and *Willeysthenelais*) (see Kinberg 1856, Gonzalez et al. 2018).

***Ehlersileanira* Pettibone, 1970b**
Type species: *Sthenelais incisa* Grube, 1877
2 species
Diagnosis: Sigalionins with ceratostyles of median and lateral antennae biarticled. Facial tubercle present. Segment 1 without inner tentacular lobes. Simple neurochaetae present. Majority of neurochaetae compound canaliculate spinigers (Pettibone 1970b, Imajima 2003, Aungtonya and Eibye-Jacobsen 2016).

***Euthalenessa* Darboux, 1900**
Type species: *Thalenessa digitata* McIntosh, 1885
5 species
Diagnosis: Sigalionins without auricles on ceratophore of median antenna. Eyes placed on raised ocular areas. Lateral antennae inserted on both prostomium and median surface of segment 1. Facial tubercle present. Ventral tentacular cirri longer than dorsal tentacular cirri. Ctenidia may be present on lateral lips. Dorsal cirri present on segment 3. Marginal papillae of elytra palmate. Neurochaetae compound falcigers, some of which are multiarticulate (Pettibone 1970a, Imajima 2003, Wehe 2007).

***Fimbriosthenelais* Pettibone, 1971**
Type species: *Sthenelais longipinnis* Grube, 1869
9 species
Diagnosis: Sigalionins with or without outer palpal sheaths. Segment 1 with dorsal ctenidia. Ctenidia present on lateral lips. Parapodial stylodes with distal crown of papillae. Simple neurochaetae present. Majority of neurochaetae falcigers, some of which are multiarticulate. Ventral surface of body may be strongly papillated (Pettibone 1971, Wehe 2007).

***Horstileanira* Pettibone, 1970c**
Type species: *Horstileanira vanderspoeli* Pettibone, 1970c
2 species
Diagnosis: Sigalionins with dorsal auricles on segment 1. Simple neurochaetae present. Majority of neurochaetae compound canaliculate spinigers (Pettibone 1970c, Wehe 2007).

***Labioleanira* Pettibone, 1992a**
Type species: *Leanira yhleni* Malmgren, 1867
2 species
Diagnosis: Sigalionins without inner tentacular lobes. Lateral lips with labial lobes. Simple neurochaetae may be present. Majority of neurochaetae compound canaliculate spinigers (Horst 1917, Pettibone 1992a, Wehe 2007).

***Labiosthenolepis* Pettibone, 1992a**
Type species: *Leanira laevis* McIntosh, 1885
3 species
Diagnosis: Sigalionins with dorsal ctenidia on segment 1. Lateral lips with labial lobes. Neurochaetae compound canaliculate spinigers (Pettibone 1992a, Aungtonya 2007).

***Leanira* Kinberg, 1856**
Type species: *Leanira quatrefagesi* Kinberg, 1856
11 species
Diagnosis: Sigalionins with ceratostyles of median and lateral antennae biarticled. Ceratophore of median antenna without auricles. Facial tubercle present. Segment 1 without inner tentacular lobes. Lateral lips with labial lobes. Simple neurochaetae may be present. Majority of neurochaetae compound canaliculate spinigers (Pettibone 1970b, Wehe 2007).

***Mustaquimsthenelais* Wehe, 2007**
Type species: *Mustaquimsthenelais dendropapillata* Wehe, 2007
2 species
Diagnosis: Sigalionins with dorsal ctenidia on segment 1. Ctenidia may be present on lateral lips. Marginal papillae of elytra may be arborescent-branched. Simple neurochaetae may be present. Majority of neurochaetae compound heterocheligers and compound falcigers, some of which are multiarticulate. Ventral cirri with inner lateral papilla, which may be elongated and bear a longitudinal series of side branches (Wehe 2007).

***Neoleanira* Pettibone, 1970c**
Type species: *Sigalion tetragonum* Ørsted, 1845
4 species

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Diagnosis: Sigalionins with elongate lateral antennae. Segment 1 with dorsal ctenidia. Elongate dorsal cirri present on segment 3. Neurochaetae compound canaliculate spinigers (Pettibone 1970c, Imajima 2003).

***Pholoides* Pruvot, 1895**
Type species: *Pholoe dorsipapillata* von Marenzeller, 1893
5 species
Diagnosis: Sigalionins (membership uncertain) without auricles on ceratophore of median antenna. Lateral antennae absent. Inner palpal sheaths rudimentary. Segment 1 without inner tentacular lobes and with only one pair of tentacular cirri. Elytra on posterior part of body on every second segment. Elytra rather stiff, with concentric rings on surface. Branchiae absent. Neurochaetae compound falcigers with short, falcate, unidentate distal article (Pettibone 1992b, Imajima 2003, Padovanni and Amaral 2004).

***Sigalion* Audouin & Milne Edwards in Cuvier, 1830**
Type species: *Sigalion mathildae* Audouin & Milne Edwards in Cuvier, 1830
29 species
Diagnosis: Sigalionins with median antenna (when present) centrally placed on prostomium, with poorly defined ceratophore and without auricles. Lateral antennae inserted on prostomium. Facial tubercle may be present. Segment 1 without inner tentacular lobes. Dorsal cirri present on segment 3. Marginal papillae of elytra pinnate. Notochaetae distally minutely bidentate. Simple neurochaetae present. Majority of neurochaetae compound falcigers, some of which are multiarticulate (Muir 1989, Mackie and Chambers 1990, Imajima 2006, Wehe 2007).

***Sthenelais* Kinberg, 1856**
Type species: *Sthenelais helenae* Kinberg, 1856
41 species
Diagnosis: Sigalionins with dorsal ctenidia on segment 1. Ctenidia present on lateral lips. Simple neurochaetae present. Majority of neurochaetae compound falcigers, some of which are multiarticulate (Pettibone 1971, Imajima 2003, Wehe 2007).

***Sthenolepis* Willey, 1905**
Type species: *Leanira japonica* McIntosh, 1885
13 species
Diagnosis: Sigalionins with dorsal ctenidia on segment 1. Ctenidia present on lateral lips. Simple neurochaetae present. Majority of neurochaetae compound canaliculate spinigers (Aungtonya 2003, Wehe 2007).

***Willeysthenelais* Pettibone, 1971**
Type species: *Sthenelais diplocirrus* Grube, 1875
6 species
Diagnosis: Sigalionins with a ciliated ridge fused to the dorsal surface of the tentacular parapodia, often with an anterior (auricle-like) lobe, on segment 1. Simple neurochaetae present. Majority of neurochaetae compound falcigers, some of which are multiarticulate. Outer lateral basal knob on ventral cirri may be papilliform. Ventral cirri with inner lateral papilla. Ventral surface of body may be strongly papillated (Pettibone 1971, Wehe 2007).

Pelogeniinae Chamberlin, 1919
Type genus: *Pelogenia* Schmarda, 1861
33 species
Diagnosis: Sigalionids without auricles on ceratophore of median antenna; ctenidia may be present. Lateral antennae present, inserted on segment 1. Inner palpal sheaths present, outer palpal sheaths absent. Segment 1 with inner tentacular lobes (sheaths). Segment 2 may have a middorsal, papillary hump. Dorsal cirri may be present on segment 3. Elongate papillae (similar to stylodes in other subfamilies) may be present on neuropodia and notopodia. Simple neurochaetae absent. Neurochaetae elongate, distally bifid or entire falcigers (exception: *Psammolyce*). Ventral cirri with outer lateral basal knob and usually also with inner lateral papilla(e). Middorsal and ventral body surfaces, as well as elytra, with numerous adhesive papillae, usually with attached foreign material (Pettibone 1997).

***Claparedepelogenia* Pettibone, 1997**
Type species: *Lepidopleurus inclusus* Claparède, 1868
Monotypic
Diagnosis: Pelogeniins with elongate neuropodial acicular lobes on segment 2. Segment 2 with middorsal, papillary hump. Dorsal cirri present on segment 3 (Claparède 1868, Pettibone 1997).

***Dayipsammolyce* Pettibone, 1997**
Type species: *Psammolyce ctenidophora* Day, 1973
Monotypic
Diagnosis: Pelogeniins with ctenidia and lateral ridges on ceratophore of median antenna. Facial tubercle present. Dorsal cirri absent on segment 3 (Day 1973, Pettibone 1997).

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***Hartmanipsammolyce* Pettibone, 1997**
Type species: *Psammolyce pendula* Hartman, 1942
Monotypic
Diagnosis: Pelogeniins with ctenidia on ceratophore of median antenna. Segment 2 with middorsal, papillary hump. Elongate neuropodial acicular lobes present on segment 3. Dorsal cirri absent on segment 3 (Hartman 1942, Pettibone 1997).

***Heteropelogenia* Pettibone, 1997**
Type species: *Psammolyce articulata* Day, 1960
2 species
Diagnosis: Pelogeniins with ctenidia on ceratophore of median antenna. Facial tubercle present. Elongate neuropodial acicular lobes present on segment 3. Dorsal cirri present on segment 3. Marginal papillae on elytra and neuropodial papillae multiarticulate (Day 1960, Pettibone 1997).

***Neopsammolyce* Pettibone, 1997**
Type species: *Psammolyce petersi* Kinberg, 1856
5 species
Diagnosis: Pelogeniins with or without facial tubercle. Segment 2 with middorsal, papillary hump. Dorsal cirri absent on segment 3. Marginal papillae of elytra and neuropodial papillae may be multiarticulate (Kinberg 1856, Pettibone 1997).

***Pelogenia* Schmarda, 1861**
Type species: *Pelogenia antipoda* Schmarda, 1861
13 species
Diagnosis: Pelogeniins with dorsal cirri on segment 3. Posterior notochaetae in each notopodium elongate, thread-like (Schmarda 1861, Pettibone 1997, Wehe 2007).

***Pottsipelogenia* Pettibone, 1997**
Type species: *Psammolyce gracilis* Potts, 1910
5 species
Diagnosis: Pelogeniins with ctenidia and lateral ridges on ceratophore of median antenna. Facial tubercle present. Dorsal cirri present on segment 3 (Potts 1910, Horst 1913, Pettibone 1997).

***Psammolyce* Kinberg, 1856**
Type species: *Psammolyce flava* Kinberg, 1856
5 species
Diagnosis: Pelogeniins with elongate neuropodial acicular lobes on segment 2. Segment 2 with middorsal, papillary hump. Dorsal cirri absent on segment 3. Neurochaetae aberrant spinigers, distal articles short and distally entire, elongate and distally bifid, or elongate and deeply furcate (Kinberg 1856, Horst 1913, Pettibone 1997).

Sthenelanellinae Gonzalez et al., 2018
Type genus: *Sthenelanella* Moore, 1910
5 species
Diagnosis: Sigalionids with semispherical, nodular auricles on ceratophore of median antenna. Eyes placed on raised ocular areas. Lateral antennae present, inserted on segment 1. Palpal sheaths absent. Segment 1 with inner tentacular lobes (lamellae). Dorsal cirri absent on segment 3. Neuropodia and notopodia without stylodes. Notopodia on median and posterior segments with large specialized sacs ("spinning glands") that produces elongate, fiber-like chaetae used to reinforce tube. Simple neurochaetae absent. Neurochaetae compound spinigers with short, sickle- or rod-shaped distal article. Ventral cirri with outer lateral basal knob. Dorsal and ventral body surfaces typically smooth. Animals live in tough, fibrous tubes (Horst 1916, Pettibone 1969, Thomassin 1972, Imajima 2003, Wehe 2007).

***Sthenelanella* Moore, 1910**
Type species: *Sthenelanella uniformis* Moore, 1910
5 species
Diagnosis: As for subfamily.

Pholoinae Kinberg, 1857 (*sensu* Gonzalez et al. 2018)
Type genus: *Pholoe* Johnston, 1839
26 species
Diagnosis: Sigalionids without auricles or ctenidia on ceratophore of median antenna. Lateral antennae present or absent, when present inserted on segment 1. Inner palpal sheaths rudimentary, outer palpal sheaths absent. Segment 1 without inner tentacular lobes and without chaetae. Dorsal cirri absent on segment 3. Branchiae absent. Notopodia may have a terminal stylode, neuropodial stylodes may be present. Some notochaetae geniculate. Simple neurochaetae absent. Neurochaetae compound falcigers with short, falcate, unidentate distal article. Ventral cirri without outer lateral basal knob. Dorsal and ventral body surfaces typically smooth (Pettibone 1992b, Gonzalez et al. 2018).

***Imajimapholoe* Pettibone, 1992b**
Type species: *Pholoe parva* Imajima & Hartman, 1964
Monotypic
Diagnosis: Pholoins with median antenna inserted occipitally on prostomium. Lateral antennae absent. Embryos

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brooded beneath elytra. Interstitial animals (Imajima and Hartman 1964, Pettibone 1992b).

***Laubierpholoe* Pettibone, 1992b**
Type species: *Pholoe antipoda* Hartman, 1967
5 species
Diagnosis: Pholoins with median antenna inserted anteriorly on prostomium. Lateral antennae absent. Embryos brooded within elytra. Interstitial animals (Laubier 1975, Pettibone 1992b, Westheide 2001).

***Metaxypsamma* Wolf, 1986**
Type species: *Metaxypsamma uebelackerae* Wolf, 1986
Monotypic
Diagnosis: Pholoins with median antenna inserted anteriorly on prostomium. Lateral antennae absent. Elytra replaced by nodular lobes with 2–4 filiform papillae. Notopodia absent. Interstitial animals (Wolf 1986, Pettibone 1992b).

***Pholoe* Johnston, 1839**
Type species: *Pholoe inornata* Johnston, 1839
18 species
Diagnosis: Pholoins with median antenna inserted anteriorly on prostomium. Lateral antennae present or absent. Facial tubercle may be present. Some species are interstitial (Pettibone 1992b, Wu et al. 1994).

***Taylorpholoe* Pettibone, 1992b**
Type species: *Pholoe minuta hirsuta* Rullier & Amoureux, 1979
Monotypic
Diagnosis: Pholoins with median antenna inserted occipitally on prostomium. Lateral antennae present. Facial tubercle present. Embryos brooded beneath elytra. Interstitial animals (Rullier and Amoureux 1979, Pettibone 1992b).

Acknowledgments

The authors thank Günter Purschke, Markus Böggemann, and Wilfried Westheide (University of Osnabrück, Germany) for their patience and assistance during the preparation of this paper. They further thank Katrine Worsaae (Marine Biological Section, University of Copenhagen, Denmark) for her helpful discussions and access to recently collected material. Finally, the insightful remarks provided by the reviewers were extremely helpful in allowing the authors to improve this paper.

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Brett C. Gonzalez, Katrine Worsaae, and Danny Eibye-Jacobsen

7.13.1.5.2 Sigalionidae, Pisioninae Ehlers, 1901

Introduction

Pisionins are comprised of a relatively small group of infaunal benthic annelids that have only been reported from sediments dominated by sand or, more rarely, mud or gravel. With the exception of *Pisione longipalpa* Uschakov, 1956, which was described from material taken off the Kuril Islands at a depth of over 900 m, all species have been found in intertidal or shallow subtidal habitats. One species, *Pisione garciavaldecasasi* San Martín, López & Comacho, 1998, occurs in the rivers of Coiba Island, off the Pacific coast of Panamá. All other species are either strictly marine or occur in both marine and brackish waters. Pisionins are found throughout the world, although there are no reports from polar regions, and the number of species known from tropical, subtropical, and warm boreal waters is significantly higher than in cold boreal regions (Gonzalez et al. 2017).

Four genera (Fig. 7.13.1.5.2.1A) are considered valid: *Anoplopisione* Laubier, 1967 (2 species); *Pisione* Grube, 1857 (46 species and 4 subspecies); *Pisionella* Hartman, 1939 (1 species); and *Pisionidens* Aiyar & Alikunhi, 1943 (5 species).

Morphology

External Morphology

Detailed information on size, number of segments, and coloration is provided in the biology and ecology section. The external morphology of members of the genus *Pisionidens* differs considerably from that of other pisionins and will be treated separately below.

Prostomium. In *Pisione*, *Pisionella*, and *Anoplopisione*, the prostomium is strongly reduced, often visible as a small, elevated diamond-shaped or rounded area surrounded laterally and anteriorly by the first segment (Figs. 7.13.1.5.2.1B and 7.13.1.5.2.2H). It is devoid of appendages except in *Pisionella hancocki* Hartman, 1939, which has a well-developed median antenna. Nuchal organs appear to be absent in *Pisione* and *Pisionidens* (Purschke et al. 1997), which is probably related to the reduction of the prostomium. The brain is usually visible as two medially fused lobes that extend posteriorly into segment 3 or 4 (chaetiger 2 or 3). Numerous corpora pedunculata or "mushroom bodies" are present on the surface of the posterior half of the brain (Åkesson 1961, for *Pisione remota* (Southern, 1914)). One or two pairs of small, black, subepidermal eyes (Figs. 7.13.1.5.2.1A, B, 7.13.1.5.2.2A, H, and 7.13.1.5.2.3) lie above this region of the brain (absent in *Anoplopisione maxillata* Hartmann-Schröder, 1974). The peristomium has been thought to be limited to the lips (Rouse and Pleijel 2001). A pair of ventral, nonarticulated sensory palps with well-developed basal sheaths arise anterolateral to the mouth and are directed forward (Figs. 7.13.1.5.2.1C and 7.13.1.5.2.2D–E). The length of the palps usually equals that of 5–10 segments.

Tentacular segment. The first segment, often called the tentacular or "buccal" segment, is directed anteriorly, with its two sides meeting medially in front of the prostomium (Fig. 7.13.1.5.2.1B). In scanning electron micrographs (SEM), a furrow is usually visible running from the anterior end of the animal to the apical tip of the prostomium (Fig. 7.13.1.5.2.2F). The first segment bears a pair of elongate, cirriform, dorsal tentacular cirri at the anterior end, and beneath them, a pair of small, short, ampullaceous ventral tentacular cirri (i.e., semi-spherical with a terminal papilla) (Fig. 7.13.1.5.2.2E). In *Pisionella hancocki*, these ventral tentacular cirri are cirriform, but only half as long as the dorsal tentacular cirri. A highly characteristic feature of most species of *Pisione* and *Anoplopisione* in segment 1 is the presence of a pair of strongly developed, distally broadened, truncate aciculae, often with varying dentition. Termed buccal aciculae, they are distally emergent and directed anteromedially (Figs. 7.13.1.5.2.1B and 7.13.1.5.2.2F). Thus, they are visible at the anterior end of the animal, medial to the dorsal tentacular cirri, pointing obliquely toward one another. Based on larval histology, Åkesson (1961) concluded that these aciculae are notopodial, originating from segment 2 (chaetiger 1) (Fig. 7.13.1.5.2.3). However, buccal aciculae may be absent, or vary within populations, as seen in *Pisione koepkei* Siewing, 1955, *Pisione oerstedii pulla* Westheide, 1974, and *Pisionella hancocki*.

Parapodia and chaetae. In general, all subsequent segments of the body are usually provided with dorsal and ventral cirri, two internal aciculae per parapodium and chaetae, with segment 2 being the first chaetiger (Figs. 7.13.1.5.2.1 and 7.13.1.5.2.2). However, in *Anoplopisione*, chaetae do not begin until segment 3 (Fig. 7.13.1.5.2.1A) and are also absent in the reduced parapodia of the posterior half of the body. Dorsal and ventral cirri are typically short and ampullaceous along the entire body with the exception of the ventral cirri of segment 2 and the dorsal cirri of segment 3. The ventral cirri of segment 2,

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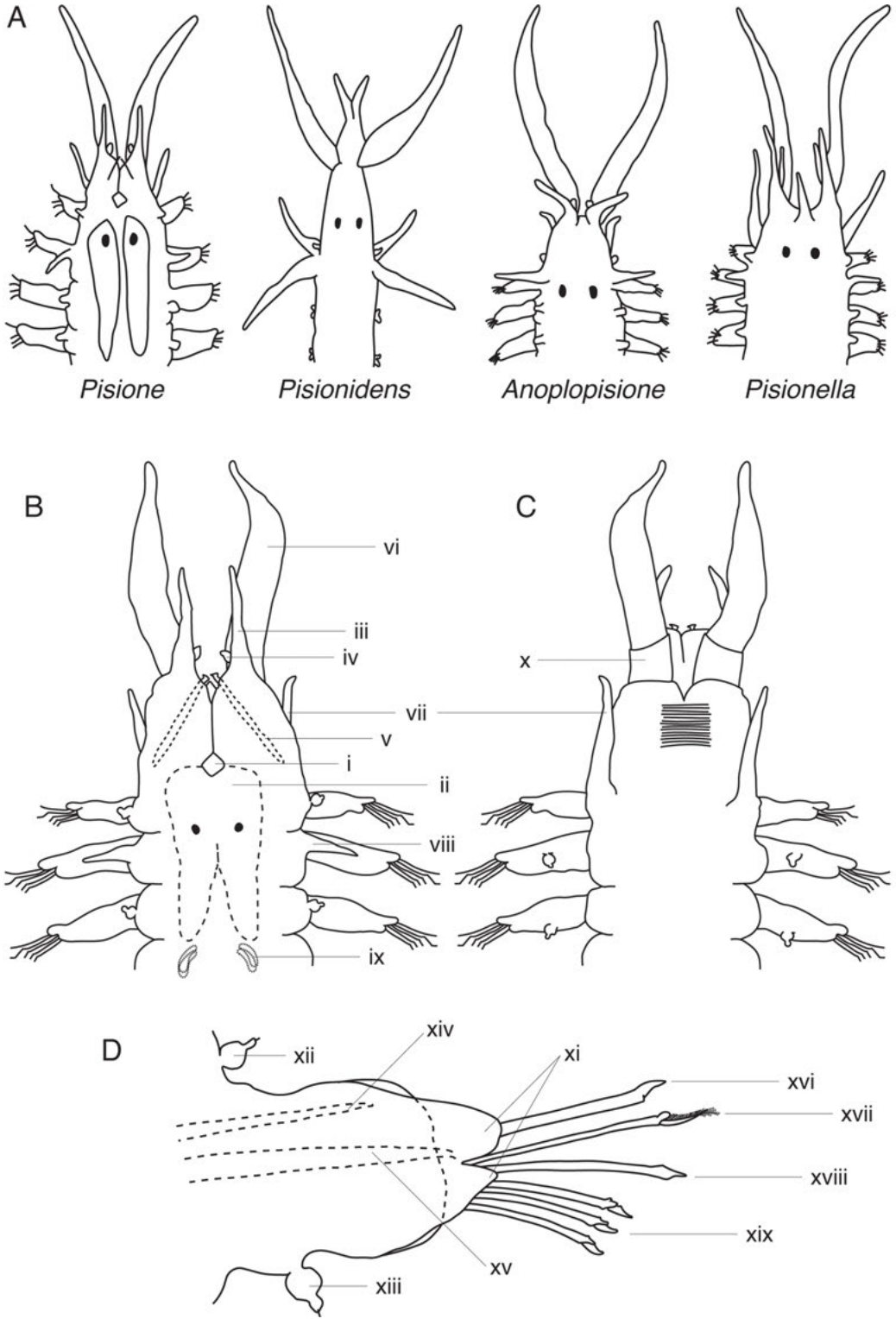


Fig. 7.13.1.5.2.1: External morphology of Pisioninae. A, Dorsal view of anterior end of all four valid genera. B, Schematic representation of anterior end of *Pisione*, dorsal view. C, Schematic representation of anterior end of *Pisione*, ventral view. D, Anterior view of parapodium. Morphological traits labeled are homologous (if present) across all four genera. i, prostomium; ii, brain; iii, dorsal tentacular cirrus; iv, ventral tentacular cirrus; v, buccal acicula; vi, palp; vii, buccal cirri of segment 2; viii, dorsal cirrus (elongated) of segment 3; ix, paired jaws; x, inner/outer palpal sheaths; xi, prechaetal lobes; xii, ampullaceous dorsal cirrus; xiii, ampullaceous ventral cirrus; xiv, notoacicula; xv, neuroacicula; xvi, supraacicular simple chaeta; xvii, long-bladed falcigerous or spinigerous compound chaeta; xviii, infraacicular simple chaeta; xix, falcigerous compound chaetae. All figures redrawn with permission from Ryohei Yamanishi (from Yamanishi 1998).

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being referred to as the buccal cirri, are considerably elongated compared to the rest of the ventral cirri, cirriform in shape and directed forward in the majority of species (Figs. 7.13.1.5.2.1C and 7.13.1.5.2.2B, D). Typically, the dorsal cirri of segment 3 are also cirriform, and in about one third of the species, they are elongated and at least twice the length of the surrounding dorsal cirri (i.e., *Pisione guanche* San Martín, López & Núñez, 1999) (Figs. 7.13.1.5.2.1B and 7.13.1.5.2.2D). Dorsal cirri are attached to the body wall above the parapodium, whereas ventral cirri are attached at variable positions along the ventral edge of the parapodium (Figs. 7.13.1.5.2.1D, 7.13.1.5.2.2D, and 7.13.1.5.2.4). The neuroaciculae of body segments are longer and more strongly developed than the notoaciculae, often distally curved downward, and may have an emergent tip. Notopodia are represented only by the notoaciculae, all chaetae being neuropodial (Figs. 7.13.1.5.2.1D and 7.13.1.5.2.4). In a few species, the notoaciculae are emergent, with the exposed tip protruding from a slight notopodial swelling or lobe (e.g., *Pisione primitiva* de Wilde & Govaere, 1995). Neuropodia have a uni- or bilobed prechaetal lobe.

The number of chaetae per neuropodium is modest, and they are always arranged in a single vertical row, minimally with one simple supraacicular chaeta and three (rarely only two) compound subacicular chaetae with short, falcigerous distal blades. In addition to these, some species have one or two simple chaetae and/or one or two compound chaetae, one of which may have a long falcigerous or spinigerous distal blade, always subacicular in position, but dorsal to the falcigers with short blades (Figs. 7.13.1.5.2.1D and 7.13.1.5.2.4). Supraacicular simple chaetae usually have a subdistal process that causes them to strongly resemble compound chaetae in which the distal blade is fused to the shaft (Fig. 7.13.1.5.2.4). The compound chaetae all have one ligament (Hutchings 2000). In segments specialized for copulation, the parapodia are modified to at least some degree, most strongly in males (see detailed description below). The pygidium is provided with a single pair of elongate cirri.

Morphology of *Pisionidens*. Species of *Pisionidens* differ from other pisionins primarily in the development of the prostomium, as it does not appear that segment 1 is specialized in the same manner as in other genera (for a different interpretation, see Siewing 1954 and Hartmann-Schröder 1970). The prostomium is large and conical, bearing a pair of cirriform lateral antennae at its tip (Figs. 7.13.1.5.2.1A and 7.13.1.5.2.2C). A pair of palps emerge subdistally from the prostomium but they lack basal sheaths. The first segment is elongated, and occurs at a level similar to that of segment 2 in other pisionins. Dorsal and ventral cirri are short and ampullaceous, except the ventral or buccal cirri of segment 2 and the dorsal cirri of segment 3, which are both elongate in comparison to those of other segments (see Petersen et al. 2016). True parapodia are strongly reduced in adults, initiating either from segment 7 or 8, containing aciculae but no chaetae. In juveniles, compound chaetae occur in the anteriormost five to six segments (Aiyar and Alikunhi 1940, Siewing 1954, Hartmann-Schröder 1970).

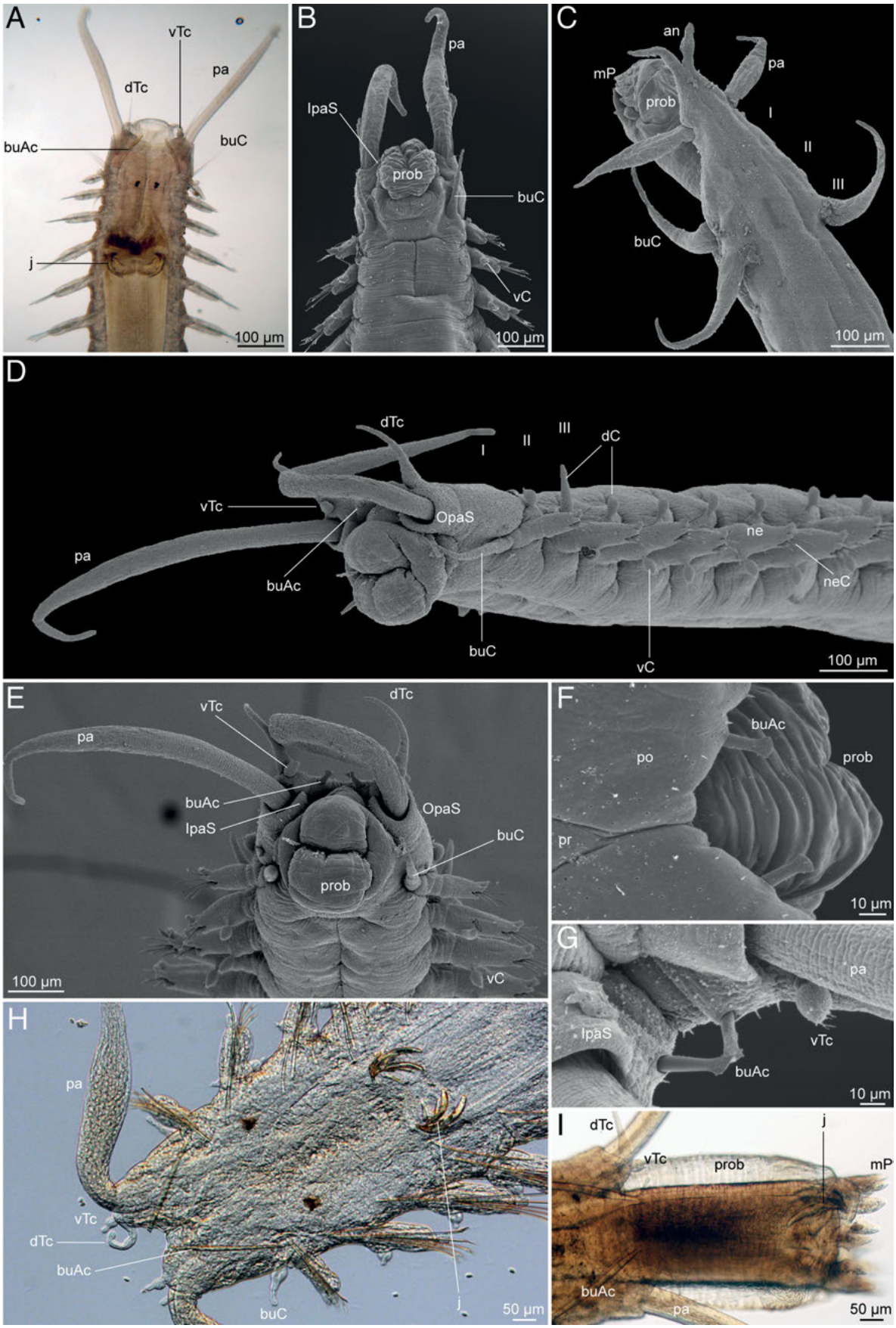
Body structure. The body surface of pisionins is smooth but may contain numerous cilia, as well as several pore openings for various glands and sensory organs (Govaere and de Wilde 1993). The glands on the dorsal surface of the neuropodia and the medial side of the ventral cirri are adhesive (Åkesson 1961), whereas many others are presumed to produce mucus that aids in movement through the sandy sediment. In *Pisione* and *Pisionidens,* a papillated stylode with adhesive discs or glandular pores is present on the prechaetal lobes of the neuropodia (e.g., *Pisione garciavaldecasasi*) (San Martín et al. 1998, Petersen et al. 2016) (Fig. 7.13.1.5.2.5A–D). In *Pisionidens ixazaluohae* Petersen, Gonzalez, Martínez & Worsaae, 2016, lateral pore fields are present along the dorsal surface of the body wall between the true parapodia (Fig. 7.13.1.5.2.5E).

Anatomy

General characteristics. The anterior part of the digestive tract can be everted as an axial, muscular pharynx. When everted, a ring of 14 or more papillae surrounds the distal opening of the pharynx (Fig. 7.13.1.5.2.2I). Within its lumen, and proximal to the opening, are four jaws, two dorsal and two ventral (absent in *Anoplopisione minuta* Laubier, 1967), which are associated with venom glands (Fig. 7.13.1.5.2.2H). As in many small-sized annelids, a circulatory system is absent (Smith and Ruppert 1988) and the nephridia are basically protonephridia (Stecher 1968). According to Åkesson (1961), sterile segments contain protonephridia with solenocytes, which are supplemented by gonoducts in fertile segments. The nephridia are modified in segments with copulatory organs (males) or receptacula semines (females) (Fig. 7.13.1.5.2.6A, B). Hutchings (2000) and Rouse and Pleijel (2001) both characterized the nephridia of *Pisionidens* as protonephromixia.

Morphology of reproductive organs. In female pisionins, ovigerous segments usually alternate with sterile segments specialized for copulation in a median and/or posterior section of the body (Alikunhi 1941, 1951). For example, in *Pisionidens indica* (Aiyar &

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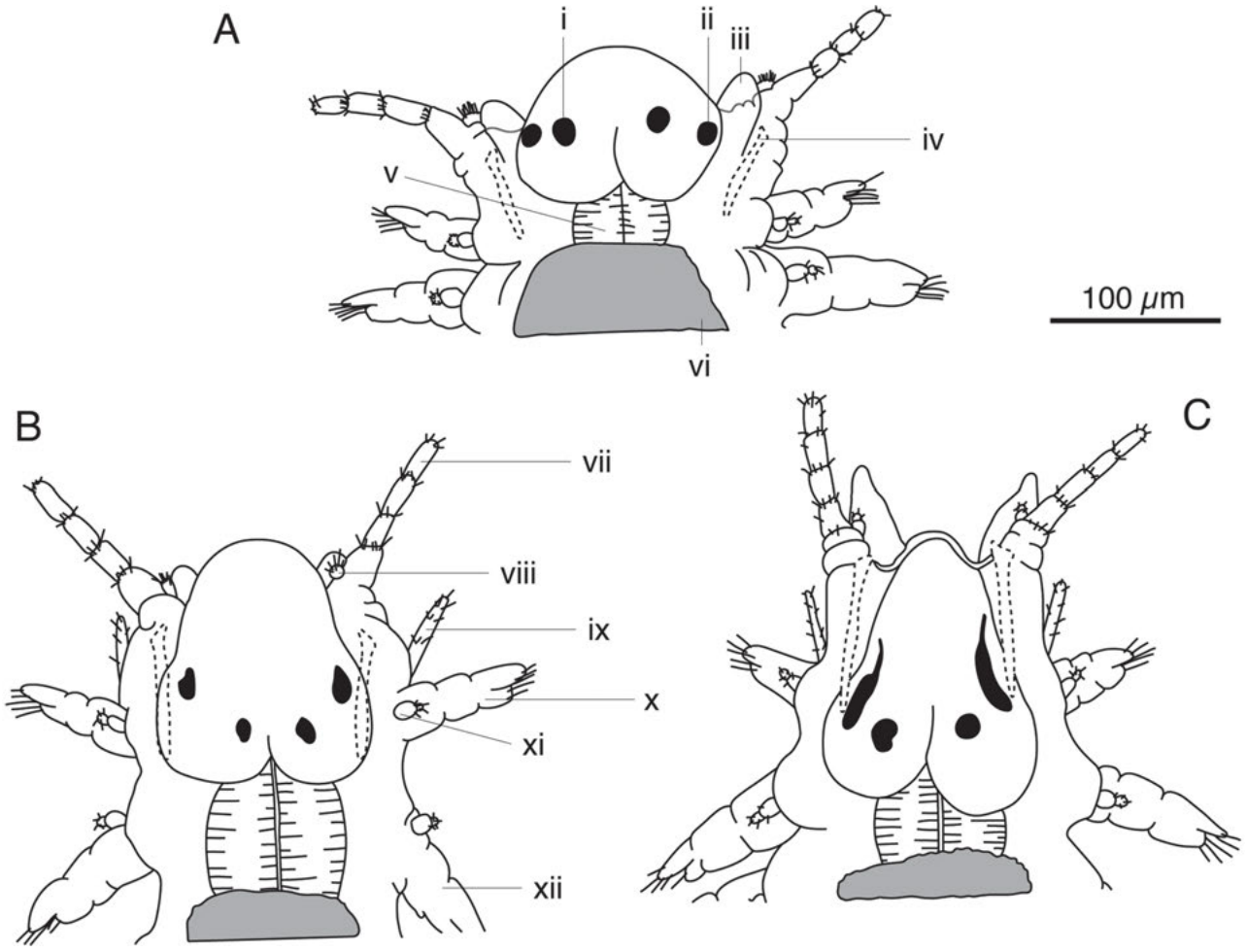


Fig. 7.13.1.5.2.3: Three successive stages in the process of **"**torsion**"** in a metatrochophora larva of *Pisione remota* (Southern, 1914) during metamorphosis. A, Larva with three chaetigerous segments. B, Larva with three to four chaetigerous segments. Tentacular and buccal cirri visible. C, Larva with six to seven chaetigerous segments. Dorsal tentacular cirri longer than parapodia and buccal acicula approaching final position. i, median eye; ii, lateral eye; iii, palp; iv, buccal acicula; v, pharynx; vi, intestine; vii, dorsal tentacular cirrus; viii, ventral tentacular cirrus; ix, buccal cirrus of segment 2; x, parapodium of segment 2; xi, dorsal cirrus of segment 2; xii, parapodium of segment 3. Redrawn from Åkesson (1961).

Alikunhi, 1940), there are 7–11 ovigerous segments alternating with sterile segments beginning around segment 35 (Hartmann-Schröder 1970). In mature female pisionins, the mass of eggs in fertile segments (Fig. 7.13.1.5.2.5N) is so great that they may bulge into neighboring segments. Oviducts penetrate the posterior septum of each fertile segment and open to the exterior at the ventral base of the parapodia of the following segment (Fig. 7.13.1.5.2.6B). This opening also leads to the receptaculum seminis, in which spermatozoa are

◂**Fig. 7.13.1.5.2.2:** Overview of characters associated with the prostomium and anterior segments. A, Dorsal view of *Pisione* cf. *alikunhi* Tenerelli, 1965, showing protruding buccal aciculae and jaws. Photograph courtesy of Alejandro Martínez. B, Ventral view with position of buccal cirri (segment 2) in *Pisione* sp. from México. C, Prostomium of *Pisionidens ixazaluohae* Petersen, Gonzalez, Martínez & Worsaae, 2016, with first three segments indicated. D and E, Lateral and terminal views of *Pisione guanche* San Martín, López & Núñez, 1999, illustrating the defining characters of *Pisione*. F, Prostomium and buccal aciculae of *Pisione* sp. from México. G, Ventral view of buccal aciculae of *Pisione remota* (Southern, 1914). H, Light micrograph of anterior segments of *Pisione bulbifera* Yamanishi, 1998, illustrating the position of jaws and buccal aciculae. I, Protruding proboscis and mouth papillae of *P.* cf. *alikunhi*. Photograph courtesy of Alejandro Martínez. I–III, segment numbers; an, antenna; buAc, buccal acicula; buC, buccal cirrus; dC, dorsal cirri; dTc, dorsal tentacular cirrus; IpaS, inner palpal sheath; j, jaws; mP, mouth papillae; ne, neuropodium; neC, neurochaetae; OpaS, outer palpal sheath; pa, palp; po, pores; pr, prostomium; prob, proboscis; vC, ventral cirrus; vTc, ventral tentacular cirrus. Images C–H from Gonzalez et al. (2017).

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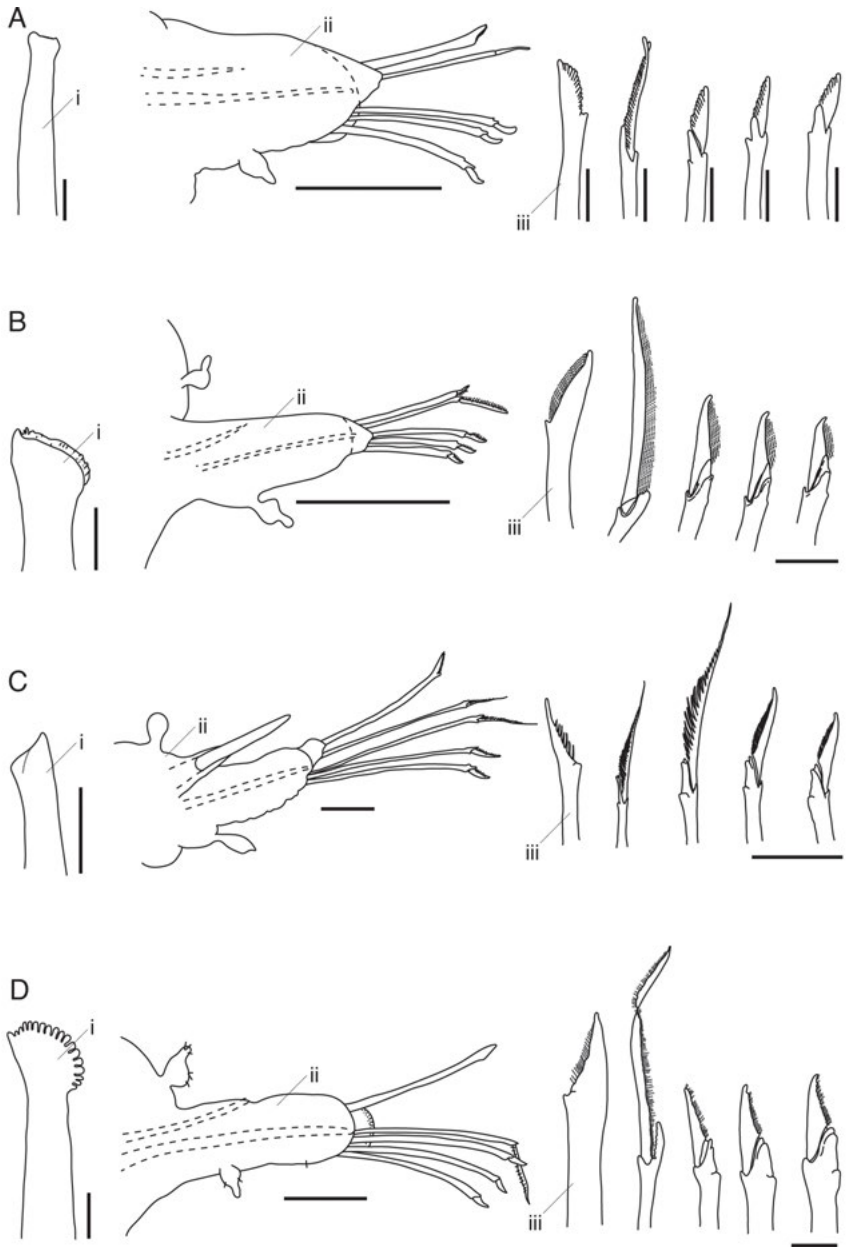
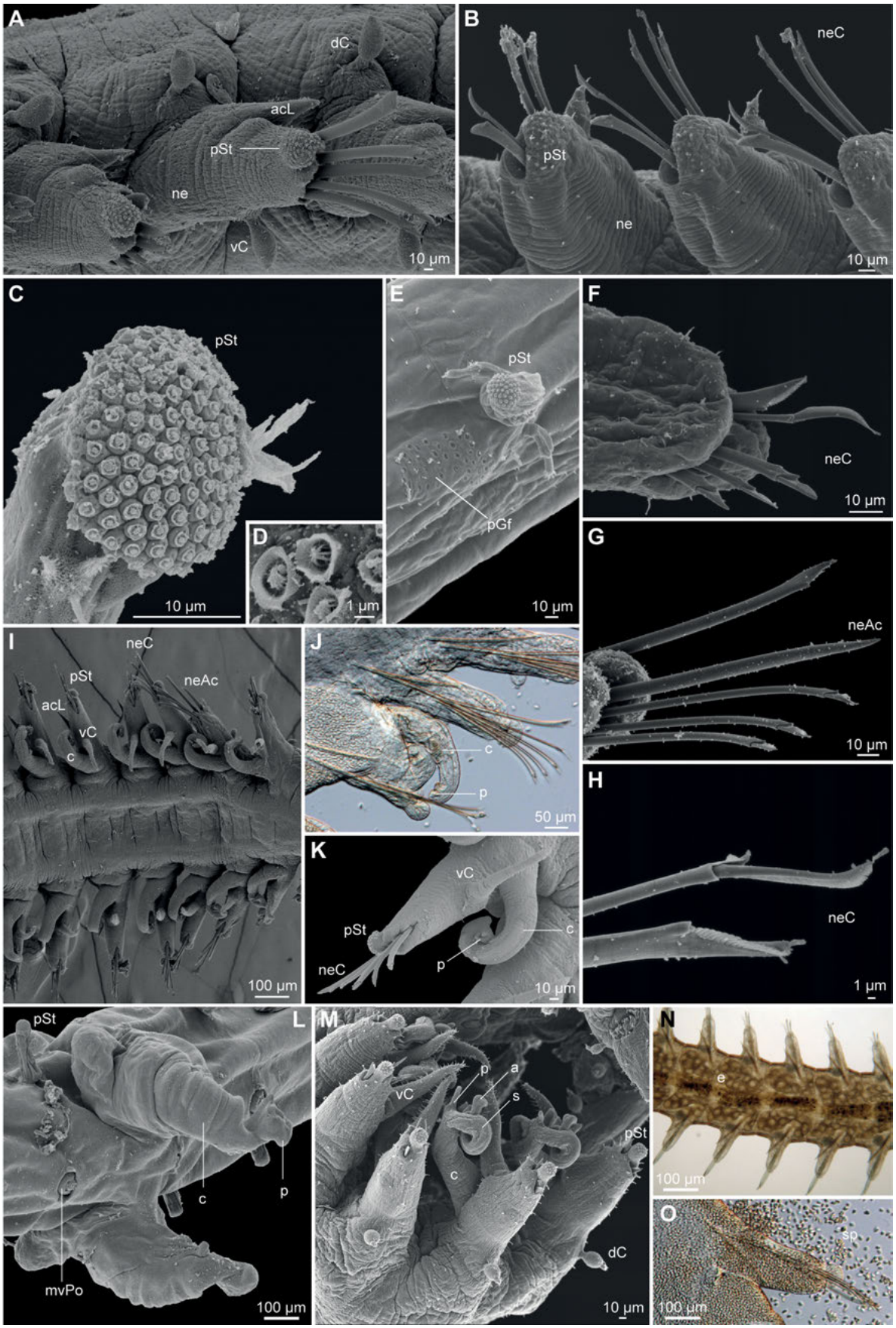


Fig. 7.13.1.5.2.4: Examples of variations in buccal aciculae (i), parapodia (ii), and neurochaetae (iii, line specifically indicating supraacicular simple chaeta) seen throughout *Pisione*. A, *Pisione umbraculifera* Yamanishi, 1998, segment 30; scales 0.01 mm (i, iii) and 0.1 mm (ii). B, *Pisione garciavaldecasasi* San Martín, López & Camacho, 1998, anterior parapodium; scales 14 µm (i, iii) and 0.35 mm (ii). C, *Pisione inkoi* Martínez, Aguirrezabalaga & Adarraga, 2008, middle parapodium; scales 20 µm (i), 50 µm (ii), and 25 µm (iii). D, *Pisione hainanensis* Wu, Ding & Huang, 1998, segment 13 (long-bladed falciger from segment 18); scales 10 µm (i, iii) and 100 µm (ii). All images redrawn from original descriptions.

▸**Fig. 7.13.1.5.2.5:** Variations of parapodia, neurochaetae, and male copulatory organs seen in Pisioninae. A, Middle parapodial segments of *Pisione guanche* San Martín, López & Núñez, 1999, with acicular lobes and papillated stylode. B, Middle parapodial segments of *Pisione* sp. from México. Note the variation in the positioning of the papillated stylode. C, Detailed view of the papillated stylode with adhesive discs from *Pisionidens ixazaluohae* Petersen, Gonzalez, Martínez & Worsaae, 2016. D, Close detail of several adhesive disks from the papillated stylode of *Pisione guanche*. E, Detail of parapodial gland field in *Pisionidens ixazaluohae*. F, Neurochaetae of *Pisione hartmannschroederae* Westheide, 1995. G, Neurochaetae of *Pisione remota* (Southern, 1914), with protruding neuroacicula. H, Detail of supraacicular simple and long-bladed compound neurochaetae of *Pisione hartmannschroederae*. I, Male copulatory structures present on middle segments of *Pisione guanche*. J, Light micrograph of male copulatory organ and penis of *Pisione bulbifera* Yamanishi, 1998. K, Copulatory organ, including penis, of *Pisione remota*, with detail of ventral cirrus, neurochaetae, and modified stylode with papillated/adhesive discs. L, Midventral pores, penis, and copulatory organ of *Pisionidens ixazaluohae* Petersen, Gonzalez, Martínez & Worsaae, 2016. M, Male copulatory structures of *Pisione* cf. *vestigialis* Yamanishi, 1998, including penis, sheath-like arc, and superior stem. N, Middle segments of female *Pisione* cf. *alikunhi* Tenerelli, 1965 with eggs. Photograph courtesy of Alejandro Martínez. O. Light micrograph of *Pisione bulbifera* showing sperm both internally and externally. a, sheath-like arc; acL, acicular lobe; c, copulatory organ; dC, dorsal cirrus; e, egg; mvPo, midventral pore; ne, neuropodium; neAc, neuroacicula; neC, neurochaetae; p, penis; pGf, parapodial glandular field; pSt, papillated stylode; s, superior stem; sp, sperm; vC, ventral cirrus. Images A–M and O from Petersen (2015), Petersen et al. (2016), and Gonzalez et al. (2017).

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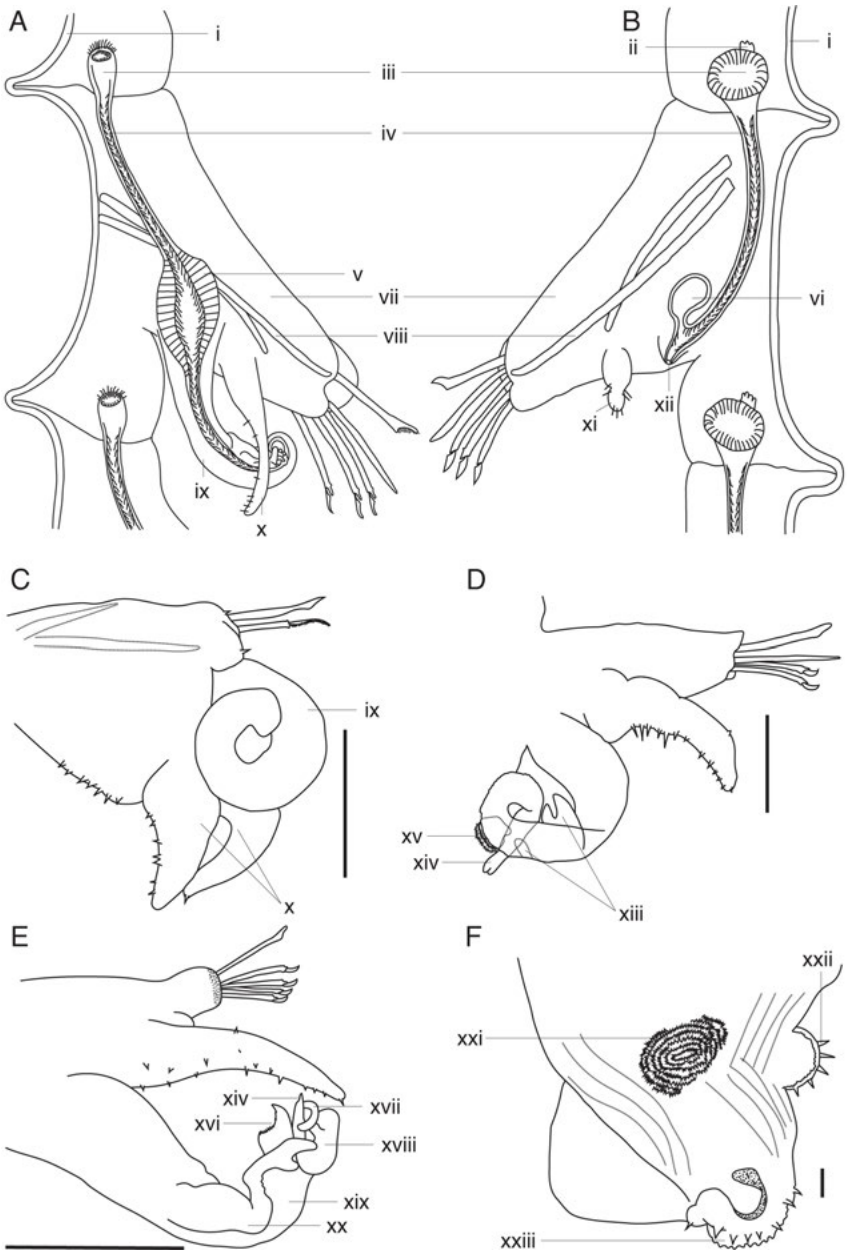


Fig. 7.13.1.5.2.6: Male and female genital tracts of *Pisione* with examples of male copulatory organ variation. A, *Pisione remota* (Southern, 1914), male copulatory organ and genital tract. B, *Pisione remota*, female genital tract. C, Male copulatory organ of *Pisione papuensis brevis* Yamanishi, 1998; scale 0.1 mm. D, Male copulatory organ of *Pisione brevicirris platycauda* Yamanishi, 1998; scale 0.1 mm. E, Male copulatory organ of *Pisione vestigalis* Yamanishi, 1998; scale 0.1 mm. F, Male copulatory organ of *Pisione gopalai vannifera* Yamanishi, 1998; scale 0.1 mm. i, intestine; ii, nephridial section; iii, genital funnel; iv, gonoduct; v, vesicula seminalis; vi, receptaculum seminis; vii, parapodium; viii, neuroacicula; ix, copulatory organ; x, modified ventral cirrus; xi, ventral cirrus; xii, gonopore; xiii, bidigitate process; xiv, penis; xv, spinous pad; xvi, cuticular plate; xvii, sheath-like arc; xviii, spiral part; xix, superior stem; xx, inferior stem; xxi, spinous papillae; xxii, fan-like appendage; xxiii, hood. A and B redrawn from Stecher 1968, C–F redrawn with permission from Ryohei Yamanishi (Yamanishi 1998).

deposited during copulation and continue to mature until oviposition and fertilization take place. The area around the common opening of the oviduct and receptaculum is swollen as a genital papilla, which in some species (e.g., *Pisione papuensis* Govaere & de Wilde, 1993) is protected by a genital flap. According to Aiyar and Alikunhi (1940), in *Pisionidens indica*, every other segment of this region has a midventral pore that may play a role during copulation. Hartmann-Schröder (1970) was unable to verify this on material from South Africa, although the presence of similar pores in males has been reported in all described species of *Pisionidens* (Petersen et al. 2016) (Fig. 7.13.1.5.2.5L).

In male pisionins, a large number of median and posterior segments produce sperm. However, usually only some of these segments show specializations related to copulation (Figs. 7.13.1.5.2.5I–M and 7.13.1.5.2.6C–F). There is a great amount of variation between and within species with regard to the number and distribution of segments that bear copulatory organs. In a majority of small species (less than 10 mm long), male copulatory organs are present only on a single segment. In larger species, the number is higher, e.g., 1–7 in *Pisionidens indica* (according to Hartmann-Schröder 1970); 3–4 in *Pisione umbraculifera* Yamanishi, 1998; 3–5 in *Pisione garciavaldecasasi*; 10 or more in *Pisione ungulata* de

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Wilde & Govaere, 1995; 7 to about 25 in *Pisione vestigialis* Yamanishi, 1998; 20–45 in *Pisione africana* Day, 1963 (according to Yamanishi 1998); and 40–76 in *Pisione remota*. In many of these species, including all but one of those just mentioned, copulatory organs are found on consecutive segments. In *P. garciavaldecasasi*, copulatory organs are placed eight to nine segments apart from one another. Alternatively, male copulatory organs may also occur on nonsequential segments, as in *Pisione laubieri* Hartmann-Schröder, 1970 and in *Pisione parva* de Wilde & Govaere, 1995, which, despite being only up to 2.5 mm long has two to three copulatory segments.

Each male copulatory apparatus is composed of up to three elements: the copulatory organ itself, the ventral cirrus, and the neuropodium (e.g., *Pisione galapagensis* Westheide, 1974 and *Pisione hartmannschroederae* Westheide, 1995). Accessory structures along the copulatory organ may be present (Fig. 7.13.1.5.2.6C–F). In some species, the copulatory organ can be interpreted as a strongly developed genital papilla, which is usually about as long as the accompanying neuropodium. In other species, the parapodial stem fuses to the copulatory organ, loosely resembling the parapodia (e.g., *Pisione papuensis brevis* Yamanishi, 1998). The copulatory organ houses a large seminal vesicle in which the spermatozoa are stored (Fig. 7.13.1.5.2.6A). The spermioduct typically opens near the tip of the cuticular penis. Different species display diagnostic specializations or accessory structures of the copulatory organ. For example, in *Pisione brevicirra platycauda* Yamanishi, 1998, the copulatory organ is spiraled and has a bidigitate process halfway along its length, a subdistal spinous pad, and a cuticular penis (Fig. 7.13.1.5.2.6D). In *Pisione gopalai vannifera* Yamanishi, 1998, a fan-like appendage is present, as well as a spinous pad and a spinous hood that covers the penis (Fig. 7.13.1.5.2.6F). *Pisione paucisetosa* Yamanishi, 1998 is similar but has three spinous pads. The strangest copulatory organ is probably that of *Pisione vestigialis*, in which the organ is divided into superior and inferior limbs that are connected to one another by a thin membrane (Figs. 7.13.1.5.2.5M and 7.13.1.5.2.6E). A similar condition is also present in *Pisione hermansi* Gradek, 1991, bearing various accessory structures including a cuticular plate and a sheath-like arc. The ventral cirri of copulatory segments in male pisionins may enlarge and become greatly elongated (cirriform) (Fig. 7.13.1.5.2.5K), may contract, or may exhibit other modifications, including various processes or even a row of cuticular spines along the ventral edge (Fig. 7.13.1.5.2.6C). In *P. papuensis,* the ventral cirri of the copulatory segments become paired and twice as large as the other ventral cirri (Fig. 7.13.1.5.2.6C). In other species, they may be fused to the copulatory organ (e.g., *Pisione laubieri*), or in some cases, both the copulatory organ and the ventral cirrus may be fused to the neuropodium to form one massive lobe (e.g., *P. parva*, *P. paucisetosa* and *Pisione gopalai* Alikunhi, 1941) (Fig. 7.13.1.5.2.6F). In many species, the neuropodia of copulatory segments are unmodified (e.g., *P. brevicirra platycauda*) (Fig. 7.13.1.5.2.6D), but in some cases, the chaetae are reduced in number (e.g., *Pisione martinsi* Hartmann-Schröder, 1974) or completely absent (Fig. 7.13.1.5.2.6F), particularly in species in which the neuropodium, ventral cirrus, and copulatory organ are completely fused as a single organ. The neuropodium itself is often elongated and bent downward, but the dorsal cirri and aciculae are usually unmodified. Within the genus *Pisione*, Yamanishi (1998) defined five groups based solely on specializations of the male copulatory apparatus. The actual process of copulation is described below.

Biology and ecology

By far, the largest species of *Pisione* is *P. oerstedii* Grube, 1857, with a length of up to 118 mm and up to 140 segments. Typically, most pisionins are small, with only about 10 species attaining a length greater than 20 mm. For example, *Pisione mista* Yamanishi, 1998 reaches a length of 25 mm, is up to 1.4 mm wide without parapodia and 2.2 mm broad with parapodia, and has upward of 120 segments. The smallest species is *Anoplopisione minuta*, being just over 1 mm long, 0.15 mm wide without parapodia, and having 17 segments. All pisionins are infaunal and most species are small enough to be classed as meiofauna but too large to be regarded as truly interstitial. Regardless, pisionins have continued to be considered as interstitial rather than infaunal due to their similarities to other interstitial taxa (e.g., Polygordiidae), which possess a similarly elongated and slender body. Within Aphroditiformia, the lack of elytra (= scales) is hypothesized to be a leading adaptation to interstitial environments (Struck et al. 2005). The most likely scenario, based on size and the lack of motile ciliary bands, is that rather than moving between grains of sand, pisionins are active burrowers that force their way through the sediment using muscular movements of their body and parapodia, with their palps potentially playing a further role in pulling the animal forward (Laubier 1967). Practically nothing is known about their feeding habits; however, some authors consider them to be subsurface deposit feeders or grazers while others state that they

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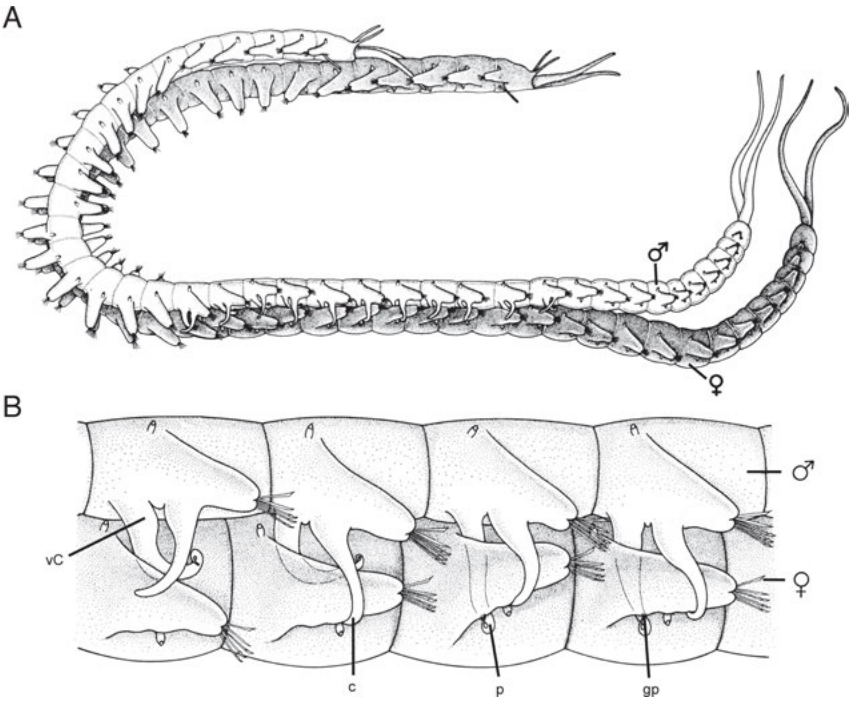


Fig. 7.13.1.5.2.7: Copulation as observed in *Pisione remota* (Southern, 1914). A, Display of male (♂) pressing its venter to the dorsal surface of the female (♀). B, Phases of copulation, from clasping of female parapodia by the enlarged ventral cirri of male copulatory segments, to insertion of penis into female gonopore. ♂, male; ♀, female; c, copulatory organ; gp, gonopore; p, penis; vC, ventral cirrus. Drawings modified from Stecher (1968).

are predatory. The latter view is supported not only by the fact that almost all pisionins have jaws (apparently absent in *Anoplopisione minuta*), but that their jaws are connected to venom glands (Wolf 1986).

Pisionins are unusual among annelids in being one of the few groups where true copulation is known to take place. Certain parapodia are modified into specialized copulatory organs (see detailed description above), displaying strong sexual dimorphism. Copulation (see Fig. 7.13.1.5.2.7) has been observed in *Pisione remota* and involves the male pressing its venter to the dorsal surface of the female, clasping its parapodia with the enlarged ventral cirri of the copulatory segments and using the copulatory organs themselves to insert sperm into the receptacula semines of the female (Stecher 1968). In this particular species, the female has a greater number of segments with receptacula than the male has copulatory organs, so the male moves along the body of the female in order to fill all of them. Westheide (1988) studied the spermatozoa of this species and found that they are unusual in being rod-shaped and aflagellate (see Fig. 7.13.1.5.2.5O for a different species). Furthermore, he observed that the spermatozoa undergo a complicated maturation process within the receptacula semines of the female. Sperm may be stored for several months, and fertilization takes place during oviposition, as the receptaculum opens into the oviduct very close to its external opening (Fig. 7.13.1.5.2.6B).

A large number of eggs are produced during spawning (up to 800 in *Pisione remota* according to Stecher 1968) (Fig. 7.13.1.5.2.5N), hatching as trochophora larvae. This relatively high number of eggs and the larval type are not typical of the reproductive specializations often seen in meiofaunal organisms (Yamanishi 1998), suggesting that pisionins are relative newcomers to the infaunal habitat. Banse (1957) and Åkesson (1961) provided detailed descriptions of the various metatrochophoral stages of *P. remota*. These larvae are free swimming and planktotrophic, using a unique ventral gland to produce mucus nets that are used to capture phytoplankton. *Pisione* larvae can spend up to 10 days in the water column before settling. Metamorphosis begins at the eight-segment stage, which precedes the animal beginning its life in the sediment. An important component of this metamorphosis is the phenomenon of "torsion," involving the migration of the first segment to an anterior position where it completely surrounds the prostomium (Fig. 7.13.1.5.2.3).

Phylogeny and taxonomy

The first pisionid to be described was *Pisione oerstedii* from Chile, and in the original description, Grube (1857) speculated that this new form could be related to Phyllodocidae or Glyceridae. This appears to be based on a

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misinterpretation of the prostomium and jaws, yet similar conclusions were reached by Aiyar and Alikunhi (1940) based on other characters. However, it was Levinsen (1887) who was first to recognize that pisionids are probably closely related to scale worms (Aphroditiformia). This opinion was shared by Southern (1914) and Hartman (1939), although the latter also mentioned Hesionidae as a possibility. Ehlers (1901) was less precise, naming scale worms in addition to Nephtyidae, Hesionidae, and Syllidae as possible relatives.

Since Åkesson (1961) published his detailed study of the larval development of *Pisione remota*, all authors, with the exception of Rouse and Fauchald (1997), have placed Pisionidae as the sister group of, or within, Aphroditiformia. Åkesson (1961) pointed out five characters that support this view: the general larval type being very similar to that of *Pholoe*; the development of segment 1 with its parapodia pointing forward (this would not apply to *Pisionidens*); the transverse fold that separates the stomach from the intestine in larvae; the configuration of the jaws as a dorsal and a ventral pair accompanied by a terminal ring of proboscideal papillae; and the presence of corpora pedunculata on the surface of the brain. In Åkesson's opinion, there were only two elements that were not in agreement with the conclusion that pisionids are at least the closest living relatives of the scale worms, the complete absence of any trace of elytra during ontogeny and the absence of metanephridia. Both circumstances could, however, be related to the small size of pisionids and their infaunal pseudo-interstitial lifestyle (Yamanishi 1998). A detailed comparison of pisionids to a *Pholoe*-like ancestor is discussed in Yamanishi (1998), which further corroborates the recent morphological and molecular placement of the group.

In their cladistic analyses of annelid families based solely on morphological characters, Rouse and Fauchald (1997) placed Pisionidae as the sister group of a clade consisting of Glyceridae, Goniadidae, and Paralacydoniidae. This was followed by Pleijel and Dahlgren (1998), who carried out morphological analyses of the families belonging to Phyllodocida, concluding that pisionids were the sister group of Aphroditiformia, albeit they were only represented by a single terminal (*Pisione remota*). Based on a combination of both morphological characters and molecular (18S rDNA and COI) sequences, Wiklund et al. (2005) carried out an analysis of Aphroditiformia, recovering Sigalionidae paraphyletic with both "Pisionidae" and "Pholoidae" nested within. This exact same result was simultaneously obtained by Struck et al. (2005), although the latter study did not include morphological characters, but was based on a similar dataset to that of Wiklund et al. (2005). Zrzavý et al. (2009) carried out several analyses that included almost all families of annelids based on 93 non-group-specific morphological characters and sequences from six genes. In their results, *Pisione* was consistently recovered nested within scale worms, sister to Sigalionidae and "Pholoidae"; however, again only one or two terminals represented each family. Norlinder et al. (2012) conducted a combined morphological and molecular phylogenetic study of scale worms, increasing the number of terminals and including a representative from both *Pisione* and *Pisionidens*. Findings from this study corroborated that of the previous three, recovering "Pisionidae" nested within Sigalionidae, as well as recovering a sister relationship between *Pisione* and *Pisionidens*. Results from this study led to the formal synonymization of "Pisionidae" with Sigalionidae; however, their conclusions still left the Sigalionidae paraphyletic with regard to "Pholoidae." The recent systematic investigation of Aphroditiformia by Gonzalez et al. (2018) corroborated that of Norlinder et al. (2012) and formally erected the subfamily Pisioninae that included an emended diagnosis for the group, while formally replacing the former family designation that continues to linger in the literature.

Up until Rouse and Pleijel (2001), no phylogenetic studies had been carried out within pisionids. Yamanishi (1998) discussed a potential grouping of *Pisione* species based on similar male copulatory structures; however, this was purely interpretive and lacked any morphological character analysis. Gonzalez et al. (2017) investigated reproductive and nonreproductive morphological characters in *Pisione* based on Yamanishi's (1998) copulatory organization. This study concluded that earlier attempts to associate copulatory organization with a biogeographical grouping of species were not valid, illustrating that both reproductive and nonreproductive characters are essential in identifying and describing species of *Pisione*. Members of the genera *Pisionella* and *Pisionidens* exhibit fundamental differences from other pisionids, and future studies of their ontogeny and phylogenetic positions are needed to fully understand their relationships within Aphroditiformia and the processes by which Pisioninae have become adapted to their interstitial habitat.

Up until 1939, only two species of pisionids had been described (*Pisione oerstedii* and *Pisione remota*), and the genus was considered rare (Hartman 1959). The steady rise in the number of species found since then primarily reflects an increase in studies targeting meiofaunal organisms. Regardless, the fact that detailed regional investigations, including of Japan (Yamanishi 1976, 1992, 1998)

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and Papua New Guinea (Govaere and de Wilde 1993, de Wilde and Govaere 1995), have led to the description of many new species suggests that the diversity of Pisioninae is greater than previously thought.

Diagnoses of genera

Anoplopisione Laubier, 1967

Type species: *Anoplopisione minuta* Laubier, 1967
2 species
Diagnosis: Prostomium reduced, surrounded laterally and anteriorly by segment 1. Antennae absent. Emergent buccal aciculae present. Parapodia and chaetae present from segment 3, posterior half of body with reduced parapodia lacking chaetae. Jaws present or absent.

Pisione Grube, 1857

Type species: *Pisione oerstedii* Grube, 1857
46 species, 4 subspecies
Diagnosis: Prostomium reduced, surrounded laterally and anteriorly by segment 1. Antennae absent. Emergent buccal aciculae present (exceptions: *Pisione koepkei* and *Pisione oerstedii pulla*). Parapodia and chaetae present from segment 2. Jaws present.

Pisionella Hartman, 1939

Type species: *Pisionella hancocki* Hartman, 1939
Monotypic
Diagnosis: Prostomium reduced, surrounded laterally and anteriorly by segment 1. Well-developed median antenna present. Emergent buccal aciculae absent. Parapodia and chaetae present from segment 2. Jaws present.

Pisionidens Aiyar & Alikunhi, 1943

Type species: *Pisionella indica* Aiyar & Alikunhi, 1940
5 species
Diagnosis: Prostomium well developed, conical. Lateral antennae present. Segment 1 unmodified. Emergent buccal aciculae absent. Parapodia initiating from segments 4–7, strongly reduced. Chaetae absent in adults, juveniles with parapodia and chaetae on five to six anterior segments. Jaws present.

Acknowledgments

The authors thank Wilfried Westheide, Günter Purschke, (University of Osnabrück) and Markus Böggemann (University of Vechta) for their patience and assistance during the preparation of this paper.

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Guillermo San Martín and María Teresa Aguado

7.13.2 Syllidae Grube, 1850

Introduction

Syllidae is one of the most complex and difficult families of polychaetes, with a large number of described genera and species. Pamungkas et al. (2019) estimated that there are 103 genera and 993 species. The World Polychaete Database (Read and Fauchald 2020) accepts more than 1100 species. In this paper, we recognize 77 genera and around 964 valid species.

They may be very abundant and diverse in coastal samples, but identification is sometimes difficult and time consuming. Usually, they are small to very small (few millimeters long), and examination of characters must be done carefully under good compound microscopes, preferably using polarized transmitted light, the Nomarsky system, or, if possible, a scanning electron microscope (San Martín and Aguado 2012). Despite the family's taxonomic difficulty, it is relatively easy to recognize a syllid by its distinctive autapomorphic character in the anterior gut, the proventricle (or proventriculus), which is very conspicuous and generally easy to observe by transparency (Figs. 7.13.2.1, 7.13.2.3, 7.13.2.12, 7.13.2.13, and 7.13.2.32).

The first reference to syllids was in 1771, when O.F. Müller described and drew a species that he named *Nereis armillaris*; the species was later transferred to the genus *Syllis* Savigny in Lamarck (1818). The same author (O.F. Müller 1776, 1788a, b, 1789, 1806) described and figured several polychaetes, which were later recognized as syllids, currently considered as belonging to the genera *Syllis* and *Myrianida* Milne Edwards, 1845. When O.F. Müller (1788a) examined for the first time a male stolon of *Myrianida*, he considered it to be a new species and named it *Nereis corniculata*. Müller was the first author to describe the distinctive reproduction of these worms, although he considered it was asexual fission, analogous to that of naidid oligochaetes. Several years later, a reproductive female stolon, named as *Sacconereis helgolandica*, was described by M. Müller (1855) (see Biology and Ecology, below, and also Fig. 7.13.2.21).

O.F. Müller and contemporary authors included the syllid species that they described within the genus *Nereis* Linnaeus, 1758. Savigny in Lamarck (1818) erected the genus *Syllis*, which was later to give name of the family for a species he described and named as *Syllis monilaris*. Lamarck separated *Syllis* and *Nereis* but considered both genera to be very close to each other and separated the former as the "nereidids syllines." This was the time at which Syllidae appeared for the first time in the zoological classification.

The name (although its etymology is not reported in any published study) probably comes from Greek mythology: *Syllis* (Συλλις) was a Naiad nymph, from Sicyon (a city in southern Greece), daughter of Asopos (a river) and Métopé' (another nymph); she was one of Apollo's lovers and mother of Zeukippos, who became king of the city (http://www.theoi.com/Nymphe/NympheSyllis.html; http://gw5.geneanet.org/index.php3?b=thor2007&lang=es;p=syllis;n=mythologie+grecque). References to *Syllis* are present in books 2, 6, and 7 of Pausanias, a traveler, geographer, and chronicler of the II Century (Pausanias 1994, in the Spanish version, for an original in Greek with French translation).

In 1841, Delle Chiaje described the species *Syllis gracilis* and recognized it as belonging to same genus as other species that he had already described. Previously, Audouin and Milne Edwards (1832, 1833a, b, c, d, 1834) had described several syllid species that were included within *Syllis*, in the tribe of the "tentaculated nereidids." Grube (1840) described two new more species, *S. gracilis* (*non* Delle Chiaje) and *Syllis vittata*. In the same year, Johnston (1840a, b, c, d, e) described many species of syllids, as well as a new genus that he named *Ioida*, for the species *Ioida macrophthalma*, which he considered close to *Syllis*, but having two fascicles of chaetae per parapodium rather than only one (they were, in fact, sexual stolons). Rathke (1843) described two new species of *Syllis*: *Syllis cornuta* and *Syllis tigrinoides*; Örsted (1843a) erected *Polybostrichus* as a genus, but it was later found to be a male stolon of *Myrianida* (see Malaquin 1893, Potts 1911). A year later, Örsted (1844) proposed a new classification of the Annelida and erected two new valid genera (Örsted 1845a, b), *Syllides* and *Exogone*, and examined and drew several phases of development for the species *Exogone naidina*. During the 1840s, other authors, such as Quatrefages (1843), Milne Edwards (1845), and Leuckart (1849), described several modes of reproduction in species of the genera *Syllis* and *Myrianida* from northern European waters.

Grube (1850) started a new phase, not only in the history of syllids but also in that of the whole annelid group. In his work *Die Familien der Anneliden*, Grube revised all of the annelid families and proposed a new classification, which became the basis of all later studies of the group. Most of the families erected by Grube still persist.

Syllids lacked a distinct and defined position within the polychaetes, and the authors who erected new genera simply described them, without any further attempt at

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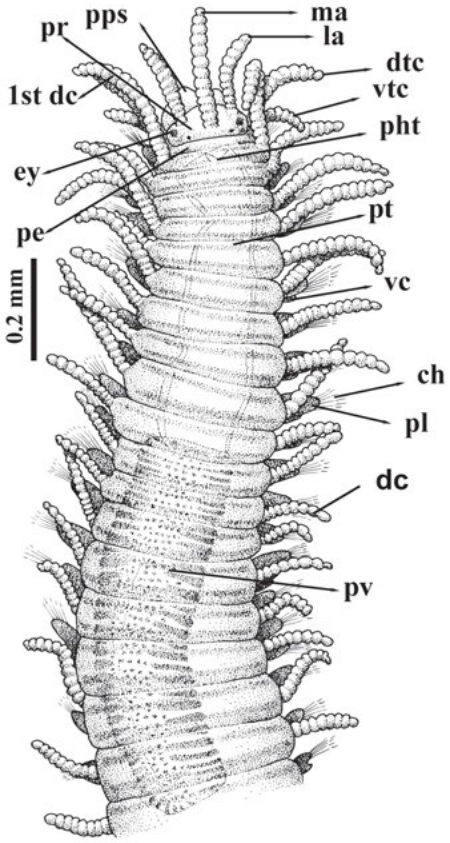


Fig. 7.13.2.1: Habitus of *Syllis gracilis* Grube, 1840; ma, median antenna; la, lateral antenna; dtc, dorsal tentacular cirrus; vtc, ventral tentacular cirrus; pht, pharyngeal tooth; phx, pharynx; vc, ventral cirrus; ch, chaetae; pl, parapodial lobe; dc, dorsal cirrus; prv, proventricle; pe, peristomium; ey, eye; 1st dc, first dorsal cirrus; pr, prostomium; pps, palps. Modified from San Martín (2003); San Martín's original drawing modified by Jordi Corbera.

classification. Grube grouped the genera and erected two families, currently referable to the Syllidae:

Family Syllidea, composed of well-characterized genera: *Syllis* (which then included *Syllides* Örsted, 1845); *Exogone* Oersted, 1845; *Myrianida* Milne Edwards, 1845; *Autolytus* Grube, 1850; as well as *Cystonereis* and *Ioida*.

Family Amytidea, which included reproductive stolons of different syllids such as *Polybostrichus* and others.

A few years later, Krohn (1852a) demonstrated that *Syllis prolifera* Krohn (*non* Müller) reproduces by the detachment of sexual fragments, male or female, to produce an alternation of generations. M. Müller (1855) made observations on *Sacconereis* and revealed its identity as a sexual form of *Myrianida* (as *Autolytus*).

Agassiz (1862) observed and described all the reproductive phases of *Autolytus cornutus* (Agassiz, 1862) (currently *Proceraea cornuta*) and verified and expanded on observations previously made by other authors, demonstrating the reproduction of syllids by means of sexual stolons. From that moment, syllids received special attention from a number of naturalists, who published many observations on reproduction with descriptions of new genera and species. A number of excellent papers that described most of the known common species and genera was published by, among others, Johnston (1828, 1829, 1833, 1865), Örsted (1843a, b), Quatrefages (1843, 1865), Grube (1855, 1857, 1860, 1863, 1870, 1878), Krohn (1852a, b), Gosse (1855), Schmarda (1861), Costa (1862, 1864, 1867), Pagenstecher (1862), Claparède (1863, 1864, 1868, 1870, 1875), Ehlers (1864, 1887, 1897), Malmgren



Fig. 7.13.2.2: *Myrianida pinnigera* (Montagu, 1808). A, Original color drawing, after Montagu (1808). B, Living specimen, with chain of stolons (Original Jacinto Pérez Dieste) (from NW Spain). Scales not available.

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(1867), Bobretzky (1870), Marenzeller (1874, 1875, 1879, 1888, 1890), Marion and Bobretzky (1875), Langerhans (1879, 1881, 1884), Webster (1879), Czerniavsky (1881a, b, 1882), Webster and Benedict (1884, 1887), McIntosh (1885), Saint-Joseph (1886, 1895, 1902), Viguier (1886), Fauvel (1896), Verrill (1874, 1882, 1885, 1900), Johnson (1901), and Haswell (1885). Most of these papers dealt with the European fauna, but there were some on polychaetes from the east coast of the United States and Australia and from the results of worldwide collections. Malaquin's (1893) studies are worth of a special mention as he published, in 1893, the first monograph of the family, in which all current knowledge on the family was collated, new classifications added, several genera revised, new species described, and new and interesting observations and studies on the morphology, histology, reproduction, and development were made. Before him, two other authors had worked on the nature of the proventricle, a special structure of the digestive tract present only in this family; Eisig (1881) demonstrated that it is formed of muscular columns, and Haswell (1886, 1921) showed that they are formed by striated muscle fibers.

Studies from the subsequent years, of first half of the twentieth century, were similar to those from the later nineteenth century. The contributions of Ehlers (1900, 1901a, b, 1907, 1908, 1913), Gravier (1900a, b, 1905, 1906), Pierantoni (1903), Augener (1913, 1918, 1922, 1924, 1927), Benham (1915, 1921a, b), Chamberlin (1919), Fauvel (1919, 1921, 1923a, b, 1930, 1932, 1933, 1934a, b, 1939, 1953, among others), Treadwell (1914, 1917, 1924, 1925, 1931, 1945), Haswell (1920a, b), Berkeley (1923), Berkeley and Berkeley (1938), Prenant (1925), McIntosh (1908), Monro (1930, 1933, 1936a, b, 1937, 1939a, b), Moore (1906, 1907, 1908, 1909), Zachs (1933), Hartman (1945, 1948), Wesenberg-Lund (1950), and others are notable, as well as several authors of late nineteenth century who continued their work in the early twentieth century. Numerous syllid taxa were described from worldwide seas during these years. During the second half of the twentieth century, there were important contributions from Banse (1959, 1968, 1971, 1972), Bellan (1959, 1964), Ben-Eliahu (1977a, b), Campoy (1982), Cognetti (1953a, b, 1955, 1957, 1961, 1965), Day (1951, 1953, 1954, 1957, 1960, 1963, 1967, 1973), Hartman (1953, 1954, 1959, 1961, 1967), Garwood (1991), Gidholm (1962, 1965, 1966, 1967), Hartmann-Schröder (1956, 1958, 1959, 1960, 1962a, b, 1965a, b, 1971a, b, 1973, 1974a, b, 1977, 1979, 1980, 1981a, b, 1982, 1983, 1984, 1986, 1987, 1989, 1990, 1991, 1992, 1993a, b, 1996), which described many species and genera of Syllidae from all around the world, Hartmann-Schröder and Rosenfeldt (1988, 1990, 1992), Imajima (1966a, b, c, d, 2003), Imajima and Hartman (1964), Knox (1957, 1960), Knox and Cameron (1970), Laubier (1960, 1966, 1968), Licher (1996, 1999), Licher and Kuper (1998), Rioja (1941, 1943, 1946, 1947a, b, 1958, 1959, 1960, 1962), Riser (1991, 1997), Westheide (1974a, b, 1990a, b), Perkins (1981), Uebelacker (1982, 1984), Russell (1989a, b, c, 1990), Nygren (2004), San Martín (1982, 1984a, b, c, 1990, 1991a, b, c, 1992, 1994, 2002, 2003, 2004, 2005, San Martín & Aguado (2012)), San Martín & Aguirrezabalaga (1988), San Martín & Alós (1989), San Martín & Bone (1999), San Martín & Hutchings (2006), San Martín & López (2003), San Martín & Nishi (2003), San Martín & Sardá (1986), San Martín & Worsfold (2015), San Martín, Aguado & Álvarez-Campos (2014), San Martín, Aguado & Murray, (2007), San Martín, Álvarez-Campos & Aguado, (2013), San Martín, Rozbaczylo, & Díaz-Díaz (2017a), San Martín, Álvarez-Campos & Hutchings (2017b), San Martín, Ceberio & Aguirrezabalaga (1996), San Martín, Hutchings & Aguado (2008a), San Martín, Hutchings & Aguado (2008b), San Martín, Hutchings & Aguado (2010), San Martín, Ibazábal, Jiménez & López (1997), San Martín, López & Aguado (2009)), and Kudenov and Harris (1995). Contemporary researchers who specialize mainly in taxonomy and systematics of syllids are as follows: M. T. Aguado, whose main contributions focus not only on the phylogeny of syllids (Aguado and San Martín 2009, Aguado et al. 2007, 2012, 2015a, 2016, Aguado and Bleidorn 2010) but also on taxonomy (Aguado and San Martín 2006, 2007, 2008, Aguado et al. 2005, 2006, 2008a, b, 2015b, c), and more recently in species delimitation (Aguado et al. 2019); M. Böggemann (Böggemann 2009, Böggemann et al. 2003, Böggemann and Westheide 2004, Böggemann and Purschke 2005); M. E. Çinar (Çinar 2003, 2005, 2007, Çinar and Gambi 2005); Z. Ding (Ding and Westheide 1997, 2008, Ding et al. 1998); C. J. Glasby (Glasby 1994, 2000, Glasby and Watson 2001, Glasby and Aguado 2009), D. Martin (Martin et al. 1990, 2002, 2003, 2008, 2009); L. Musco (Musco and Giangrande 2005a, b, Musco et al. 2005); J. M. Nogueira (Nogueira and San Martín 2002, Noguiera and Yuanda-guarin 2008, Nogueira et al. 2001, 2004); J. Núñez (Núñez and San Martín 1991, Núñez et al. 1992a, b, 1995, 2009); A. Nygren (Nygren 1999, 2004, Nygren and Gidholm 2001, Nygren and Pleijel 2007, 2010); J. Parapar (Parapar and San Martín 1992, Parapar et al. 1994, 1996a, b, 2000); J. Ruíz-Ramírez (Ruiz-Ramírez and Salazar-Vallejo 2001, Ruiz-Ramírez and Harris 2008); R. Sardá (Sardá 1984, Sardá and San Martín 1992, Sardá et al. 2002); and others. During recent decades, researchers have been inclined to focus their efforts on a single or small number of polychaete families rather than all families as before, and our knowledge of syllids from all around the world has greatly increased.

Moreover, during the most recent years, numerous papers dealing with Syllidae have been published,

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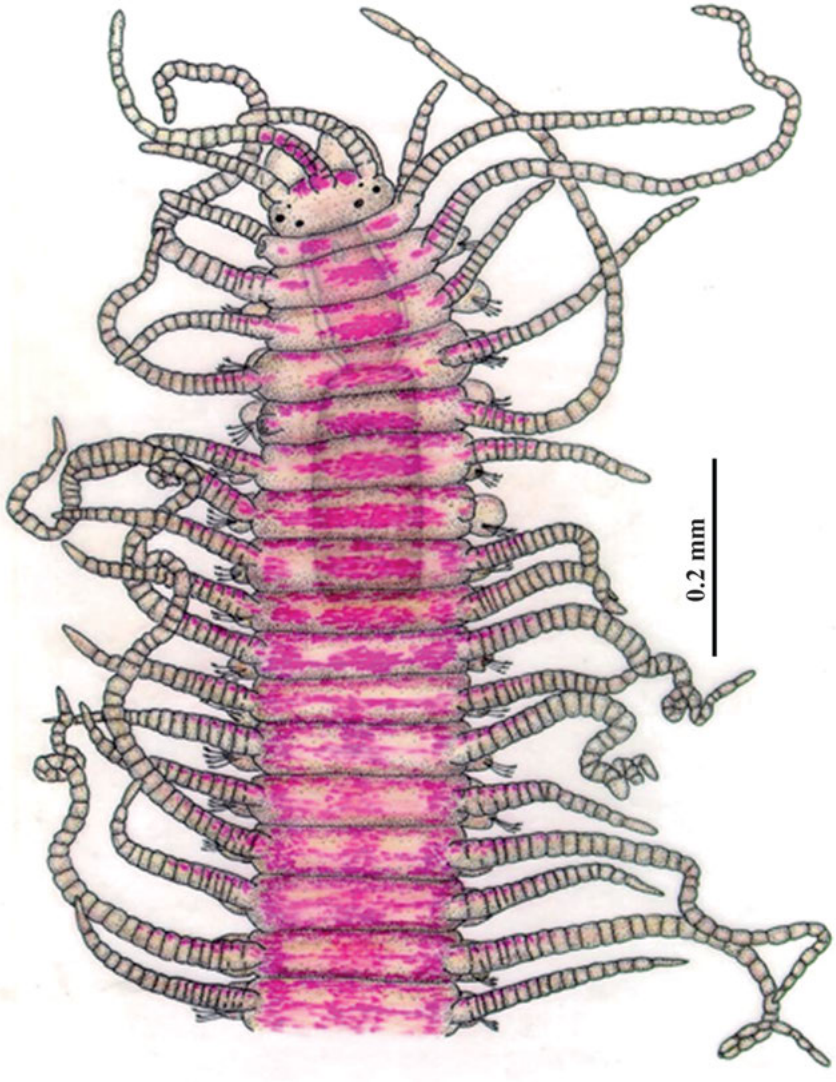


Fig. 7.13.2.3: *Haplosyllis chamaeleon* Laubier, 1960. Colored drawing, anterior end, dorsal view. San Martín's original drawing.

focusing the topics in others matters than pure taxonomy or systematics, such as bioluminescence (Deheyn and Latz 2009, Zörner and Fischer 2007, Gaston and Hall 2000, Verdes and Gruber 2017, Verdes et al. 2018, Mitani et al. 2018, 2019, Brugler et al. 2018, Schultz et al. 2018, Kotlobay et al. 2019), ecology (Bone and San Martín 2003, Cacabelos et al. 2010, López and Gallego 2006, Musco 2012, Quintas et al. 2013, del Pilar Russo et al. 2014, Serrano et al. 2006), biogeography (Musco and Giangrande 2005a, Mikac and Musco 2010, Aguado and Glasby 2015), sperm ultrastructure (Lepore et al. 2006, Musco et al. 2008, 2010), reproduction (Ponz-Segrelles et al. 2018, 2020), regeneration (Aguado et al. 2015c, Weidhase et al. 2016, 2017, Ribeiro et al. 2018, 2019, 2020, 2021), musculature (Filippova et al. 2010), phylogenetics (Álvarez-Campos et al. 2018, Verdes et al. 2018, and others already cited), and associations with protozoans (Álvarez-Campos et al. 2014a). Schmidbaur et al. (2020) recently published a detailed study on the nervous system of the Syllidae.

However, numerous papers on the taxonomy of this family have been also published during the most recent years, some dealing on specific genera, cited below, or geographical areas (e.g., Egypt: Abd-Elnaby and San Martín 2011, Abd-Elnaby 2010, 2011, 2014, 2017, 2019; Chile: Álvarez-Campos and Verdes 2017, Rozbaczylo et al. 2017, San Martín et al. 2017a, Soto and San Martín 2017a, b, 2020; México: Granados-Barba et al. 2003, Ruiz-Ramírez 2011, Salcedo-Oropeza et al. 2011, 2016; Brazil: Fukuda et al. 2015, Paresque et al. 2015, 2016a, Nogueira et al. 2001, 2004; North Sea and neighboring areas: Lucas et al. 2012, 2017b, San Martín and Worsfold 2015, Dietrich et al. 2015; Portugal: Martins et al. 2013; Red Sea and close areas: Ba-Akdah et al. 2018, Lucas et al. 2019; Venezuela: San Martín and Bone 1999, Liñero and Díaz 2011; Deep sea: Barroso et al. 2017, Langeneck et al. 2018; and Eastern Mediterranean: Faulwetter et al. 2011a, among others).

Identification books totally or partially devoted to syllids, with keys, drawings, and descriptions include

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those of Fauvel (1923a), covering the French coasts in particular; Day (1967) for South Africa; and Campoy (1982) and San Martín (2003) for the Iberian Peninsula. There are excellent general summaries on the family Syllidae in Glasby (2000) and Pleijel (2001).

Morphology

Size. Members of the family Syllidae are polychaetes of very small to medium size, usually a few millimeters long, although some species of the genus *Trypanosyllis* Claparède, 1864, *Syllis*, and *Megasyllis* San Martín, Hutchings & Aguado, 2008 can reach large sizes; *Trypanosyllis sanchezi* Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018, from deep areas in Northern Spain, living inside a sponge, is one of the longest syllids known, reaching 200 mm length, 7 mm width, with more than 500 chaetigers; *Trypanedenta gigantea* (McIntosh, 1885) from Antarctica may reach 90 mm in length and 7 mm in width; and *Megasyllis corruscans* (Haswell, 1885), an Australian species, reaches up to 140 mm in length and 5 mm in width, for 150–200 segments.

Body pattern. *Syllis ramosa* McIntosh, 1879 and *Ramisyllis multicaudata* Glasby, Schroeder and Aguado, 2012 show an interesting body pattern, with one head and multiple branches in a "tree-like" structure (Glasby et al. 2012; Ponz-Segrelles et al. 2021). In *Ramisyllis*, some specimens have been found with more than 500 ramifications, and each terminal branch may have as many as 120 segments, whereas interbranch sections may range from 3 to 30 segments (Glasby et al. 2012). If the branches would be joined end to end, the final length could exceed those of the longest known worms. Usually, the body is subcylindrical, ventrally flattened, and dorsally convex (Figs. 7.13.2.1, 7.13.2.4, and 7.13.2.5), although in some genera (*Trypanosyllis*; *Trypanedenta* Imajima & Hartman, 1964; *Trypanobia* Imajima & Hartman, 1964; *Trypanospina* Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018; *Xenosyllis* Marion & Bobretzky, 1875; *Eurysyllis* Ehlers, 1864; *Plakosyllis* Hartmann-Schröder, 1956), and some species of *Branchiosyllis* Ehlers, 1887, it is dorsoventrally flattened and ribbon-like (see Figs. 7.13.2.28B, D, 7.13.2.29D, F, 7.13.2.30E; 7.13.2.31A, E, F, 7.13.2.32C, and 7.13.2.33A–C). Two species (*Branchiosyllis orbiniiformis* San Martín, Hutchings & Aguado, 2008 and *Branchiosyllis bonei* San Martín, Álvarez-Campos & Aguado, 2013) are laterally compressed, with parapodia and chaetae dorsally directed. In most taxa, the number of segments is related to body size, so members of the subfamily Exogoninae,

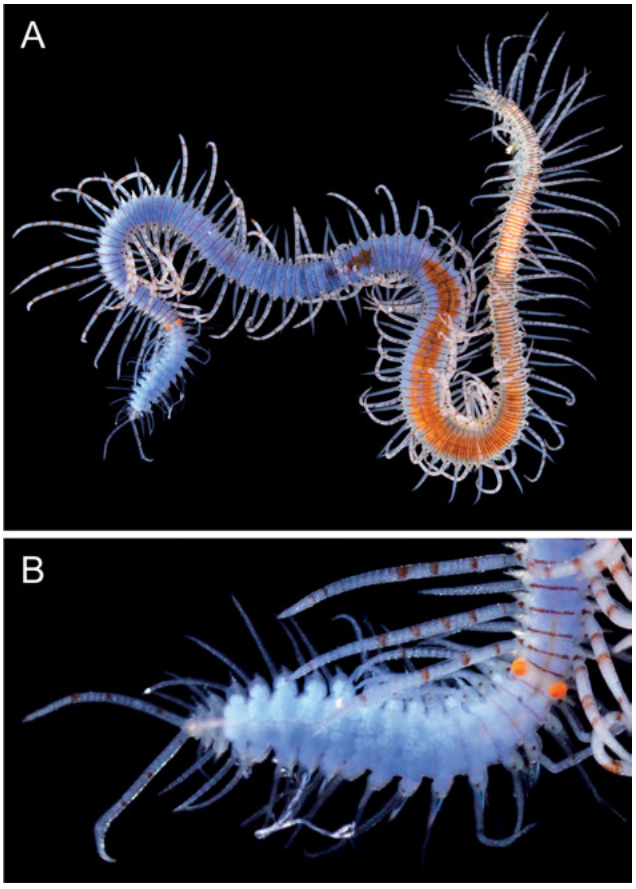


Fig. 7.13.2.4: *Syllis maganda* Martínez & San Martín, 2020. A, Complete specimen, developing a stolon. B, detail of stolon. Original photo of Alexander Semenov.

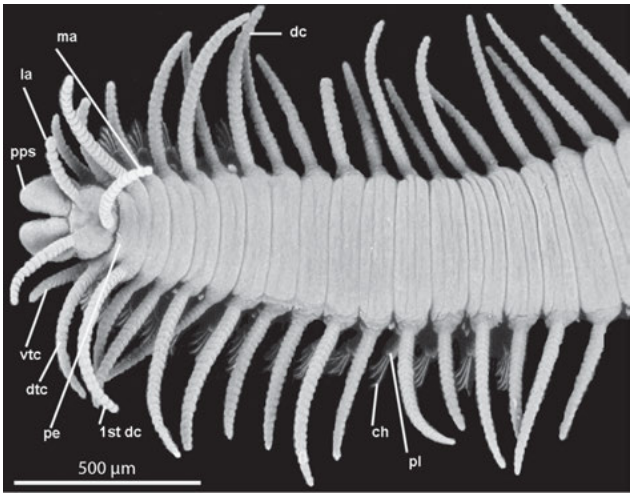


Fig. 7.13.2.5: SEM picture of *Syllis amica* Quatrefages, 1865, morphology; ma, median antenna; la, lateral antenna; dtc, dorsal tentacular cirrus; vtc, ventral tentacular cirrus; vc, ventral cirrus; ch, chaetae; pl, parapodial lobe; dc, dorsal cirrus; pe, peristomium; ey, eye; 1st dc, first dorsal cirrus; pr, prostomium; pps, palps. Modified from San Martín (2003).

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which are usually very small, have few segments (about 30), whereas the larger species of the Syllinae may have 200–300 segments or more. In some genera, such as *Amblyosyllis* Grube, 1857, and *Brachysyllis* Imajima & Hartman, 1964, the number of segments is small (14–17) and fixed for each species, but the body is of medium size, as the segments are long and wide (Figs. 7.13.2.37A, B and 7.13.2.38A). In other genera, there is a degree of fusion of segments (e.g., *Murrindisyllis* San Martín, Aguado & Murray, 2007, *Synmerosyllis* San Martín, López & Aguado, 2009) (see Figs. 7.13.2.34F and 7.13.2.39E).

For general morphology, see Figs. 7.13.2.1, 7.13.2.5, and 7.13.2.6, as well as the figures corresponding to each genus. The body varies little in width; usually, it is progressively wider from the prostomium to the midbody segments, with the widest part in the proventricular segments, then becoming progressively more slender, tapering suddenly in posterior segments; in members of the genus *Haplosyllis* Langerhans, 1879, this posterior tapering is very marked. As mentioned above, the single species of the genus *Ramisyllis*, as well as *Syllis ramosa*, has a ramified body (Glasby et al. 2012).

Color. Many species of syllids lack colors and are semitransparent (Figs. 7.13.2.12, 7.13.2.13, 7.13.2.18A, C, and 7.13.2.27A, B, D, 7.13.2.32, 7.13.2.37, 7.13.2.41) so that it is

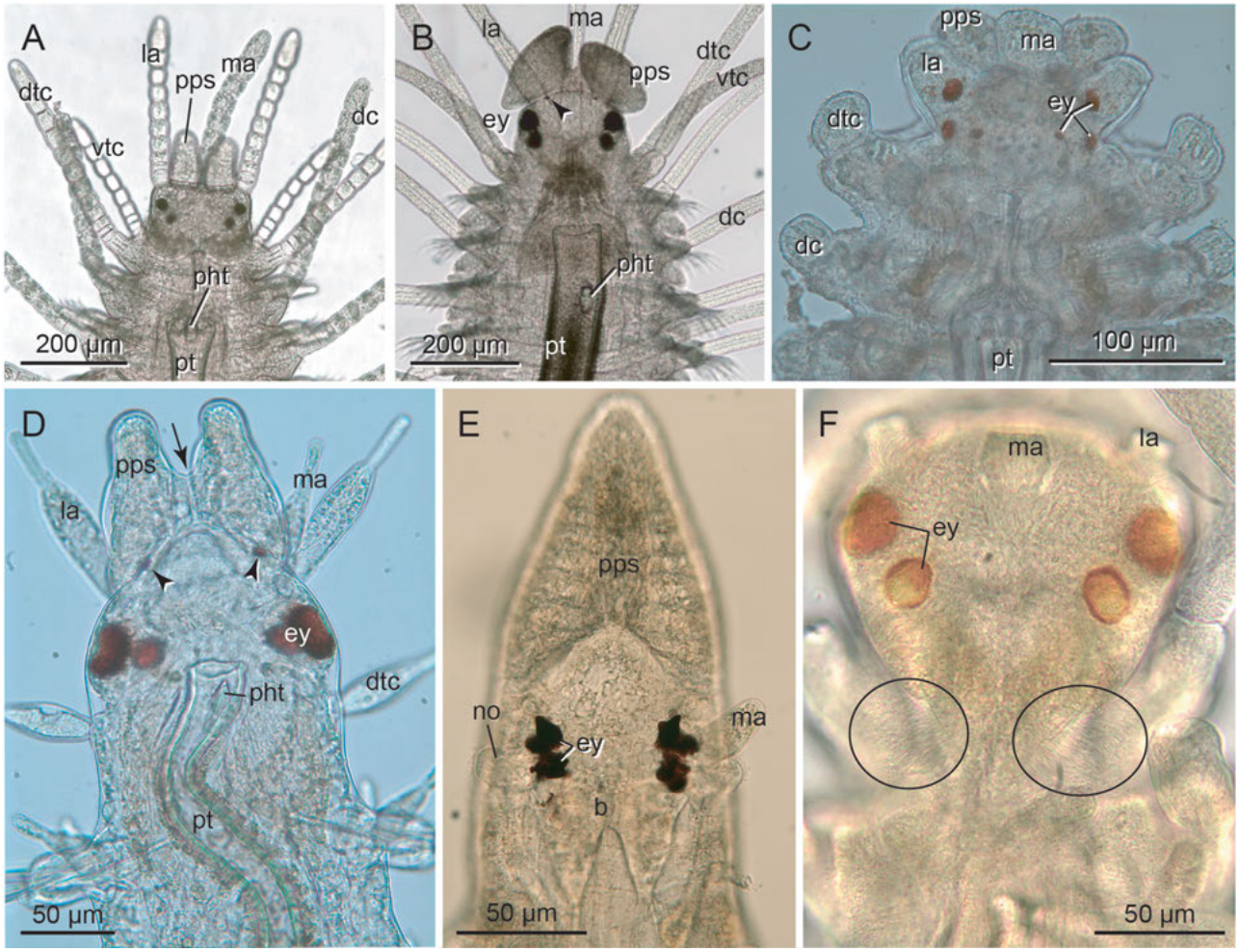


Fig. 7.13.2.6: Anterior ends and sensory structures; **A**, *Pseudosyllis brevipennis* Grube, 1863. Anterior end with articulated antennae (la, ma) tentacular cirri (dtc, vtc); palps (pps) free. **B**, *Opisthodonta* sp. Anterior end with basally fused, foliaceus and broadly extended palps (pps), pharyngeal tooth (pht) situated in anterior third of pharyngeal tube, arrowhead points to anterior eye spots. **C**, *Eurysyllis tuberculata* Ehlers, 1864. Anterior end with spherical dorsal tubercles and similarly shaped antennae (la, ma) and dorsal cirri (dc); note the three pairs of eyes, anteriormost being the largest eyes. **D**, *Parapionosyllis* sp. Anterior end with long, basally fused palps (pps, arrow), antennae (la, ma), and tentacular cirri (dtc) bowling-pin shaped, arrowheads point to anterior eye spots. **E**, *Parexogone hebes* (Webster & Benedict, 1884), anterior end with completely fused palps (pps), nuchal organs (no) visible as small papillae, eyes with irregular outline. **F**, *Eusyllis* sp. Anterior end with large eyes (ey) and nuchal organs (encircled), appendages partly broken off. Originals G. Purschke, Osnabrück.

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easy to observe the gut through the body wall; however, others are distinctly opaque, as in members of the genus *Megasyllis* (see Fig. 7.13.2.30B), and there are several brightly colored species with red, yellow, orange, violet, brown, etc., longitudinal or transversal bands, spots, etc. (see Figs. 7.13.2.2, 7.13.2.3, 7.13.2.4, 7.13.2.29A–E, 7.13.2.31C, E, 7.13.2.33A, B, and 7.13.2.37B).

Prostomium. The prostomium is well developed and semicircular to pentagonal to rectangular, to square, with rounded margins (see Figs. 7.13.2.1, 7.13.2.3, 7.13.2.5, and 7.13.2.6). The prostomium has four lensed eyes and, usually, a pair of anterior eyespots without lenses; sometimes, it may be difficult to see the eyes after fixation. There are exceptions, and some species that lack eyes. Syllid eyes were studied by Verger-Bocquet (1983), who summarized all knowledge on this subject, and Bartolomaeus (1992), who studied the eyes of the larvae of *Myrianida prolifera* (O.F. Müller, 1788).

Most syllid species have three antennae: one median and two lateral (see Fig. 7.13.2.1), but occasionally, some (e.g., *Acritagasyllis longichaetosus* Lucas, San Martín & Sikorski, 2010, which has only lateral antennae) or all of them may be absent (e.g., *Exogone acerata* San Martín & Parapar, 1990; *Guillermogonita abyssicola* Böggemann, 2009; species of the genus *Levidorum* Hartman, 1967). Number, position, and shape of antennae are important diagnostic features. Attached to the prostomium, there are two sensory palps, which are more or less triangular, usually frontally directed and sometimes ventrally folded; palps may be totally separated (Figs. 7.13.2.6A, B), fused basally (Fig. 7.13.2.5), with a fusion scar and separated and divergent from midlength, or totally or almost totally fused, in a single piece, sometimes with a distal notch or a thin, indistinct fusion scar (Figs. 7.13.2.6E, 7.13.2.12A, and 7.13.2.26A–I), or the palps may be fused by a membrane that extends along almost their entire length (*Salvatoria* McIntosh, 1885) (Figs. 7.13.2.6D, 7.13.2.12B, and 7.13.2.13A). In some cases, palps are very reduced, entirely covered by the prostomium and difficult to observe, as in several species of *Amblyosyllis*, *Myrianida*, *Proceraea* Ehlers, 1864, and other Autolytinae genera, or even apparently completely absent (*Acritagasyllis* and *Procerastea* Langerhans, 1884). In *Tetrapalpia* San Martín, Hutchings & Aguado, 2008, there is a longitudinal furrow along each palp, which gives the appearance of four palps rather than two (Fig. 7.13.2.31D). The posterior margin of the prostomium may be entire or notched, and sometimes, the sides of prostomium are strongly convex and form two lateral cheeks or lobes, in which eyes are positioned (Figs. 7.13.2.31E and 7.13.2.34F; e.g., *Pionosyllis* Malmgren, 1867, *Trypanosyllis*).

Peristomium. The peristomium, also known as the buccal or tentacular segment, bears the mouth ventrally and is achaetous; usually, it bears two pairs of tentacular (peristomial) cirri, but in some genera, there is a single pair (*Erinaceusyllis* San Martín, 2005; *Exogone*; *Parapionosyllis* Fauvel, 1923; *Parexogone* Mesnil & Caullery, 1918; *Prosphaerosyllis* San Martín, 1984; *Sphaerosyllis* Claparède, 1863; *Karroonsyllis* San Martín & López, 2003) or, exceptionally, none (*Levidorum*). Usually, the peristomium is visible in dorsal view, but it may be reduced and dorsally covered by the prostomium or the first chaetiger, and only the ventral part, with the mouth, and two lateral margins, with the tentacular cirri, are visible. Occasionally, the persitomium contracts and reduces its size after fixation. In *Erinaceusyllis* and *Cicese* Díaz-Castañeda & San Martín, 2001, the peristomium develops dorsolaterally into two wing-like extensions. Between the prostomium and the peristomium, in dorsolateral position, there may be two nuchal organs generally forming small ciliated pits that are only visible in life, in very well-fixed specimens or in particular species (Figs. 7.13.2.6F and 7.13.2.7A). Nuchal organs

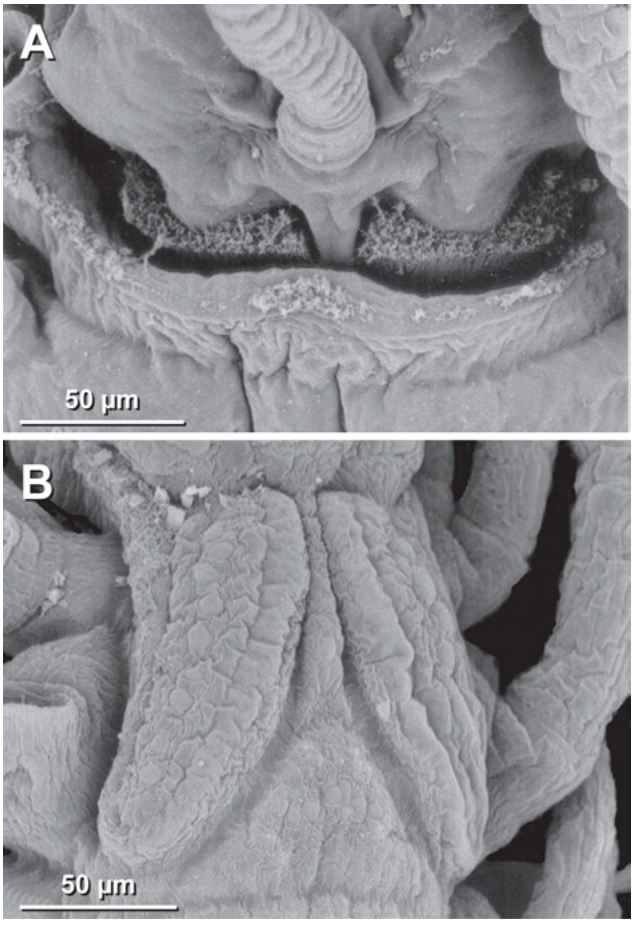


Fig. 7.13.2.7: SEM pictures of the two main types of nuchal organs in Syllidae. A, Ciliated pits (*Syllis corallicola* Verrill, 1900). B, Nuchal lappets (*Proceraea* sp.). After San Martín (2003).

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have been studied in detail in the species *Parapionosyllis manca* Treadwell, 1931, by Lewbart and Riser (1996) and *Neopetitia amphophthalma* (Siewing, 1956) by Purschke (1997). In some genera (*Amblyosyllis*, *Myrianida*, *Proceraea*, and other Autolytinae, *Nuchalosyllis* Rullier & Amoureux, 1979, *Lamellisyllis* Day, 1960, *Clavisyllis* Knox, 1957), the nuchal organs form two lappets, more or less ovate and often ciliated, that can extend over some of the anterior chaetigers (Fig. 7.13.2.7B). San Martín (2003) observed and described some spherical, hirsute structures in the nuchal lappets in *Proceraea aurantiaca* Claparède, 1868, whose function is still unknown. These structures bear a minute papilla ending in a pore, only visible under higher magnifications. These organs are innervated directly from the brain by a pair of nuchal nerves, located in the prostomium; these sensorial elements are protected by a thin, modified cuticle, formed of three coats (Purschke 1997). The brain structure and the innervation of some Syllidae were studied by Orrhage (1996).

In some species of the genera *Odontosyllis* Claparède, 1863; *Opisthosyllis* Langerhans, 1879; and *Xenosyllis* Marion & Bobretzky, 1875, the peristomium forms an occipital flap which covers the posterior end of prostomium; in some species of the subfamily Exogoninae, the peristomium is large and partially or almost completely covers the prostomium (Figs. 7.13.2.26A–C, E, G, I).

Parapodia and chaetae. Segmentation is homonomous, as all segments are very similar. However, details of the chaetae and the number of aciculae per parapodium may indicate ill-defined body regions; the number of segments in these regions varies with the size of the worm. Usually, there is an anterior region after the prostomium and peristomium, in which the parapodia have compound chaetae with relatively long blades, several aciculae per parapodium, and lack simple capillary chaetae. Then, there is a midbody region, with fewer aciculae per parapodium and compound chaetae with shorter and wider blades. Finally, the posterior region has parapodia with usually a single acicula that is distinctly thicker than those in the anterior region, capillary dorsal and ventral chaetae, and fewer compound chaetae per parapodium, with thicker shafts and shorter, wider blades. Dorsal simple chaetae usually appear a few segments further forward than the ventral ones (see Fig. 7.13.2.8 for a typical bundle of chaetae of posterior parapodia). The proventricle is usually at the end of the first, or between the first and the second regions. These regions vary considerably between genera, and there are many exceptions and considerable variability within genera, but the reduction in numbers of chaetae per parapodium and the sizes of the blades of compound chaetae, as well as the numbers of aciculae per

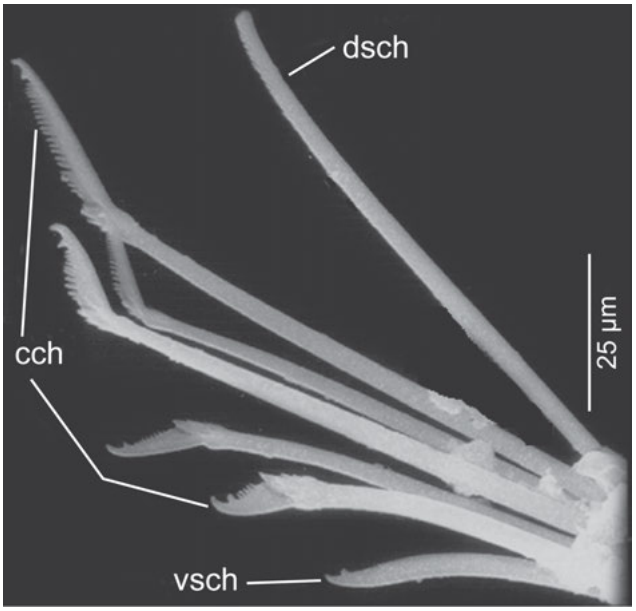


Fig. 7.13.2.8: SEM picture of a chaetal bundle, posterior parapodium, of *Syllis rosea* (Langerhans, 1879). dsch, dorsal simple chaeta; cch, compound chaetae; vsch, ventral simple chaeta. Modified from San Martín (2003).

parapodium and presence of capillary chaetae in the later chaetigers, are the general rule in the Syllidae.

The body ends in a pygidium, which is smaller than the final chaetiger, and has two anal cirri and, sometimes, a short digitiform appendage between the anal cirri (e.g., Figs. 7.13.2.4, 7.13.2.24A, D, 7.13.2.27D, 7.13.2.32A, C, 7.13.2.35A, 7.13.2.36B, 7.13.2.37A, B, 7.13.2.39D, F, 7.13.2.40D, and 7.13.2.41A).

Each body segment, except the peristomium, has a pair of parapodia. Typically, the parapodia of Nereidiformia (Phyllodocida) are biramous, with noto- and neuropodium, bearing dorsal and ventral cirri, noto- and neuroaciculae, and noto- and neurochaetae. In syllids, the notopodium is reduced lacking chaetae and aciculae, and bearing only dorsal cirri, which are usually well developed and sometimes very long (see Figs. 7.13.2.3, 7.13.2.4, 7.13.2.5, 7.13.2.23D, 7.13.2.28E, 7.13.2.29A, 7.13.2.33A, B, 7.13.2.34A–C, F, 7.13.2.35A, 7.13.2.36B, 7.13.2.37A, B, 7.13.2.40C, and 7.13.2.41A, B). During the reproductive period, the parapodia of sexual segments (in epigamy) or of stolons (schizogamy) acquire thin, slightly curved notoaciculae and fascicles of long, slender, slightly flattened notochaetae for swimming (see Figs. 7.13.2.15, 7.13.2.16, and 7.13.2.17A).

Neurochaetae typically include compound forms, but these may be modified into pseudosimple chaetae, which are usually thick and may be formed by either fusion of shafts and blades or by loss of blades and enlargement of shafts. Some genera, like *Haplosyllis* and *Paraprocerastea* San Martín & Alós, 1989, and others, have only pseudosimple

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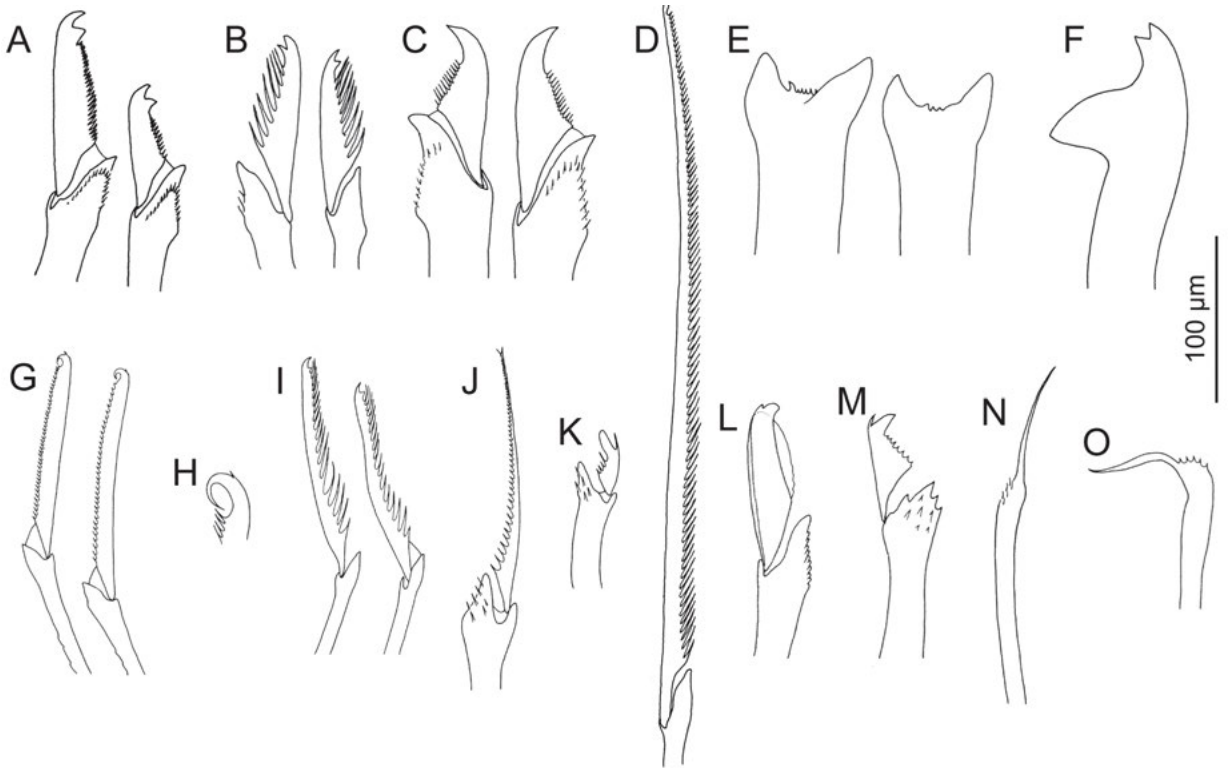


Fig. 7.13.2.9: Some examples of chaetae of the Syllidae. A, Compound bidentate falcigers, with short spines on margin (*Syllis columbretensis* (Campoy, 1982)). B, Compound bidentate falcigers, with long spines on margin (*Syllis garciai* (Campoy, 1982)). C, Compound unidentate falcigers, short spines on margin (*Syllis vittata* Grube, 1840). D, Spiniger-like (*S. garciai*). E, Pseudosimple chaetae, formed by shaft and blade fusion (*Syllis gracilis* Grube, 1840). F, Simple chaeta (*Haplosyllis spongicola* (Grube, 1855)). G, Compound bidentate falcigers, with proximal tooth larger than distal, and curved, contacting with blade margin (*Opisthodonta longocirrata* (Saint-Joseph, 1886)). H, Detail of the distal end of the same. I, Compound elongated falcigers, with double curvature, long spines on margin (*Perkinsyllis anophthalma* (Capaccioni & San Martín, 1989)). J, Compound spiniger-like chaeta. K, Compound bidentate falciger with proximal tooth larger than distal (*Exogone rostrata* Naville, 1933). L, Compound bidentate falciger with traslucent hood (*Streptodonta pterochaeta* (Southern, 1914)). M, Compound bidentate falciger, with proximal tooth larger than distal, short spines on margin (*Myrianida quindecimdentata* (Langerhans, 1884)). N, Dorsal simple chaeta, bayonet shaped (*M. quindecimdentata*). O, same (*Proceraea aurantiaca* Claparède, 1868). San Martín's original drawings modified by Jordi Corbera. After San Martín (2003).

chaetae (Figs. 7.13.2.9F and 7.13.2.10F), whereas *Procerastea* has some compound chaetae together with pseudosimple chaetae (Martin and Britayev 1998) as well as some species of *Syllis* (Figs. 7.13.2.9E and 7.13.2.10E). The articulation of shafts and blades is usually heterogomph but sometimes hemigomph (almost homogomph). Chaetal blades are typically bidentate, with the subdistal tooth smaller than the distal, but a whole range of combinations is possible (see Figs. 7.13.2.9 and 7.13.2.10): the subdistal tooth may be reduced or even absent, in which case the chaetae appear to be unidentate, or the distal tooth may be reduced or absent, with the presence of a long subdistal tooth; in some cases, the subdistal tooth may be bent down to join the inner margin of the blade (Figs. 7.13.2.9G, H). Species of the genera *Brania* Quatrefages, 1865 and *Parapionosyllis* Fauvel, 1923 have chaetal blades with very thin, spine-like subdistal teeth and coarse, rounded distal teeth. The inner margin of each blade has a longitudinal series of spines. In most cases, the chaetal blades have moderate, more or less straight spines, which are slightly curved at the end; the longest spines are toward the base of the blade, with a gradation to shorter spines distally. There may be several rows of short spines, only visible under SEM, which appear as a hood under a light microscope (Fig. 7.13.2.9L). The spines may be very long and directed upward to extend beyond the tips of the blades (Fig. 7.13.2.10D). By contrast, some spines may be extremely short so that the blades appear to be smooth or almost smooth. The blades that characterize the genus *Branchiosyllis* represent a special case, in which some or all blades are turned to 180° of their original position, to appear as claws, called ungulae (Góngora-Garza et al. 2011).

Usually, each posterior parapodium has a solitary dorsal and a ventral simple, capillary chaeta; exceptionally, there may be two dorsal simple chaetae per parapodium, and in the subfamily Autolytinae, as well as in

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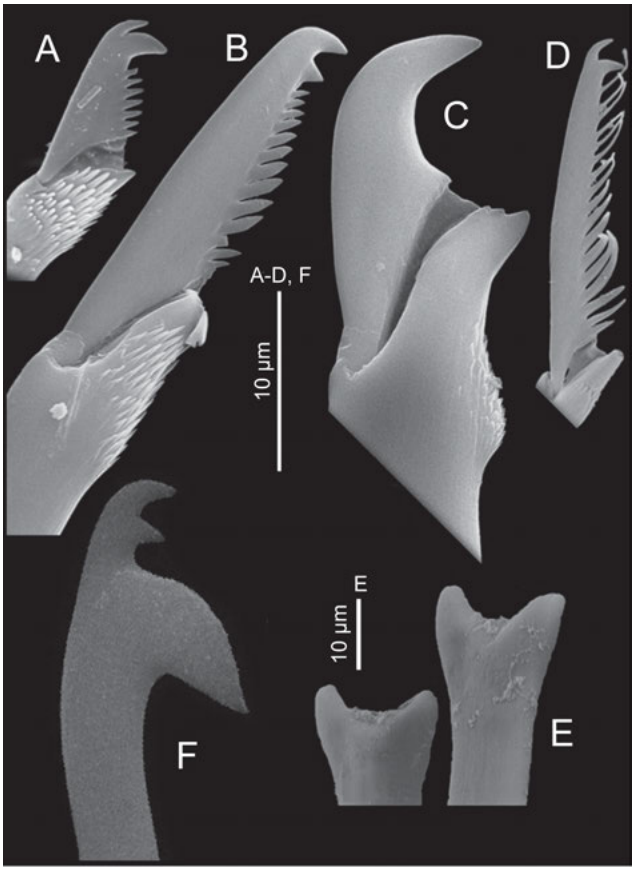


Fig. 7.13.2.10: SEM pictures of different kinds of chaetae in the Syllidae. A, Compound bidentate falciger, with proximal tooth larger than distal, short spines on margin (*Paraehlersia ehlersiaeformis* (Augener, 1913)). B, Compound bidentate falciger, with short spines on margin. C, Compound unidentate falcigers, smooth on margin (*Branchiosyllis maculata* (Imajima, 1966)). D, Compound elongated falcigers, with double curvature, long spines on margin (*Perkinsyllis heterochaetosa* (San Martín & Hutchings, 2006)). E, Pseudosimple chaetae, formed by fusion of shaft and blade (*Syllis gracilis*). F, Simple chaeta (*Parahaplosyllis brevicirra* Hartmann-Schröder, 1990). A, D, After San Martín & Hutchings (2006); B, C, after San Martín *et al.* (2008b); F, after San Martín *et al.* (2010); E, after San Martín (2003).

several genera of other subfamilies, the ventral simple chaetae are never present. The chaetae of *Acritagasyllis* are unique in the Syllidae; they are all compound with long, filiform, smooth, unidentate blades, more like those of members of the family Phyllodocidae (Lucas et al. 2010). A typical chaetal bundle from a posterior parapodium is shown in Figure 7.13.2.8 and some examples of chaetae in Figures 7.13.2.9 and 7.13.2.10. Inside the parapodial lobe, there is one or more aciculae, whose tips can vary in shape depending on the species (see Fig. 7.13.2.11A–G).

Dorsal cirri may be smooth or articulated. The smooth ones are cylindrical to filiform, more or less elongated (see Figs. 7.13.2.6B, 7.13.2.34B–E, 7.13.2.35A–D, 7.13.2.36B, 7.13.2.39B, 7.13.2.40A, C, D, E, F, and 7.13.2.41A, B). Articulated (or moniliform) dorsal cirri are divided into articles, which may be numerous (see Figs. 7.13.2.1, 7.13.2.3, 7.13.2.4, 7.13.2.5, 7.13.2.6A, 7.13.2.28B–F, 7.13.2.30C, D, G, and 7.13.2.31). There are several examples of pseudoarticulated dorsal cirri, in which articles are not perfectly defined, but the cirri are not totally smooth; there are species with anterior dorsal cirri more or less articulated or pseudoarticulated, with a gradation to less distinct articulation in the midbody and to smooth cirri on posterior segments (Figs. 7.13.2.34A, F, 7.13.2.36A, and 7.13.2.40B). There are also genera with globose (Figs. 7.13.2.28D, 7.13.2.29F, 7.13.2.31A, and 7.13.2.38C), flattened, scale-like (Fig. 7.13.2.39C), pin shaped (Fig.7.13.2.26A, E), or papilliform (Fig. 7.13.2.26D, F) dorsal cirri.

Dorsal cirri are usually present on all parapodia, but in some species, in several different genera, they are absent on the second segment. This is probably a neotenous character (San Martín 1991a, 2003, 2005), as some species have them as adults but lack them as juveniles; consequently, some species acquire dorsal cirri on the second segment, toward the end of their development, and others do not. In *Procerastea*, dorsal cirri are present only on the first chaetiger (Fig. 7.13.2.25I), although the stolons have dorsal cirri on all chaetigers. Ventral cirri are small and absent in the subfamily Autolytinae (probably fused with the parapodial lobe). Ventral cirri vary little within the family; they may be wide and foliaceous or partially fused with the parapodial lobes (e.g., some species of *Opisthodonta* and *Acritagasyllis*), but usually they are short and digitiform. In *Synmerosyllis* and one species of *Eusyllis* Malmgren, 1867, the ventral cirri of first chaetiger are flattened, foliaceous. In *Levidorum*, all appendages (antennae, tentacular and dorsal and ventral cirri) are absent (Fig. 7.13.2.23D). In *Amblyosyllis* and *Brachysyllis*, the last segment lacks chaetae and parapodia and bears two pairs of long cirri.

Epidermis. Species of the genera *Sphaerosyllis*, *Prosphaerosyllis*, *Cicese*, and *Erinaceusyllis* have numerous papillae on the dorsum, of different sizes and arrangement (Figs. 7.13.2.26C, I); papillae are sometimes also present on the palps, parapodia, and dorsal cirri. These papillae accumulate detritus, which can cover the whole dorsum and mask the specimen (Haswell 1920b, Riser 1991). The papillae may be long and digitiform, with a minute distal pore; in some species of *Prosphaerosyllis* (*Prosphaerosyllis multipapillata* Hartmann-Schröder, 1979, *Prosphaerosyllis papillosissima* Hartmann-Schröder, 1979), the dorsal papillae are more or less spherical. In other genera, the dorsum may bear other structures: four longitudinal rows of large tubercles with distal pores in *Eurysyllis* (Figs. 7.13.2.28D and 7.13.2.29F), rugose, longitudinal crests in *Xenosyllis* (Fig. 7.13.2.31F), or one to two

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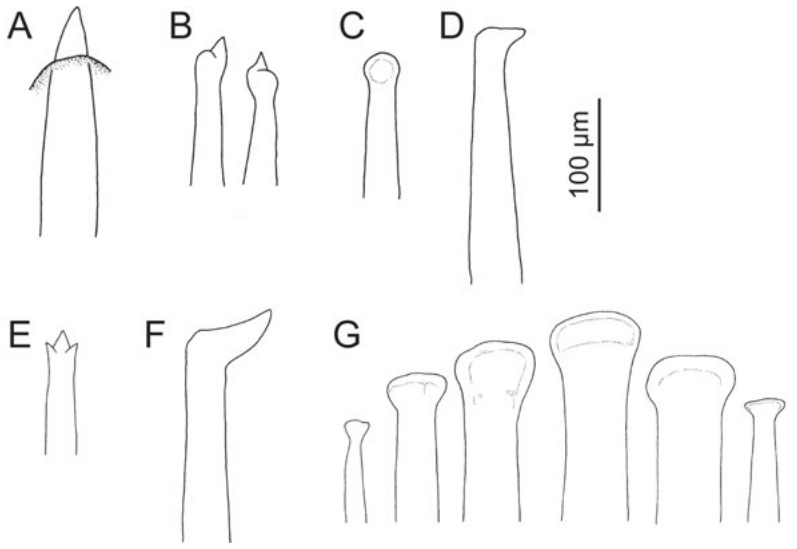


Fig. 7.13.2.11: Different kinds of aciculae. A, Straight, distally pointed, emerging from parapodial lobe (*Syllis variegata* Grube, 1860). B, Acuminate (*Syllis westheidei* San Martín, 1982). C, Distally rounded (*Syllis prolifera* Krohn, 1852). D, Distally bent at right angle (*Syllis cryptica* Ben-Eliahu, 1977). E, Tricuspid (*Eusyllis lamelligera* Marion & Bobretzky, 1875). F, Bent at right angle and distally pointed (*Sphaerosyllis austriaca* Banse, 1959). G, Aciculae of six most anterior chaetigers showing the enlargement of those two to five parapodia (*Streptosyllis websteri* Southern, 1914). San Martín's original drawing modified by Jordi Corbera. After San Martín (2003).

transverse rows of minute tubercles, sometimes spine-like, on the dorsum of each anterior segment. The genus *Trypanospina* Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018, has a densely verrucose body and also bears some triangular spines (Fig. 7.13.2.33F).

The cuticle and the epidermis in the Syllidae are more or less transparent and, consequently, make the internal anatomy relatively easy to study; however, there are some species with a thick, opaque body wall. The gut is the most important structure of internal anatomy for identification and usually easy to observe under a light microscope. In order to study the characteristics of the digestive tract in opaque specimens, it is necessary to dissect or clear them with lactic acid. Detailed studies of the structure of the digestive tract of syllids were made by Haswell (1886, 1921) and more recently by Delgado et al. (1992), Purschke (1988), and Tzetlin and Purschke (2005).

Digestive system. Anteriorly, the gut forms a proboscis or pharynx (Figs. 7.13.2.1, 7.13.2.3, 7.13.2.12A, B, 7.13.2.13A, B, 7.13.2.24A–C, 7.13.2.27A–E, 7.13.2.32A–C, 7.13.2.35A–D, and 7.13.2.41A, B). It is a cylindrical tube followed by a bulbous part, the proventricle. The pharyngeal tube is of variable length depending on the species, ending anteriorly in a crown of soft papillae, usually 10; there may be another subdistal crown of smaller papillae, or papillae may be absent (Figs. 7.13.2.14A–D). Internally, the pharyngeal tube is cuticularized. The pharyngeal tube has some glands as well as a single layer of longitudinal and circular muscles; in some species, tufts of long cilia have been observed on the papillae, which protect ovate pores. The pharyngeal opening is slightly thickened and covered by a dense coat of cilia, distinct under SEM (Fig. 7.13.2.14A, B). The pharyngeal

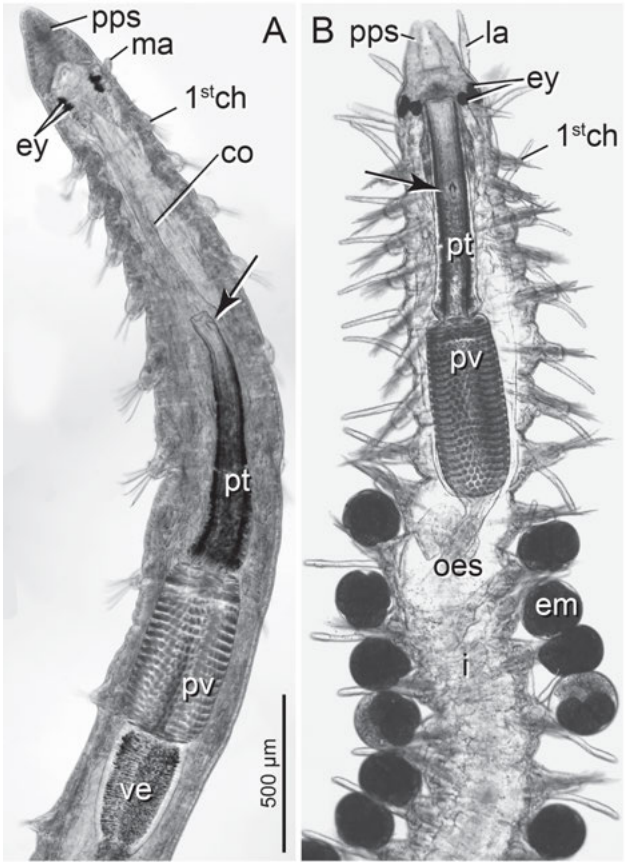


Fig. 7.13.2.12: General outline of the syllid foregut. Arrow points to different positions of the tooth within the pharyngeal tube (pt). Note different positions of resting pharynx. A, *Parexogone hebes* (Webster & Benedict, 1884). B, *Salvatoria opisthodentata* (Hartmann-Schröder, 1979). 1st ch, first chaetiger; co, collar (pharyngeal sheath); em, embryo; ey, pigmented eye; I, intestine; la, lateral antenna; ma, median antenna; oes, esophagus; pps, palps; pt, pharyngeal tube; pv, proventricle; ve, ventricle. Original A G. Purschke, Osnabrück, B W. Westheide, Osnabrück

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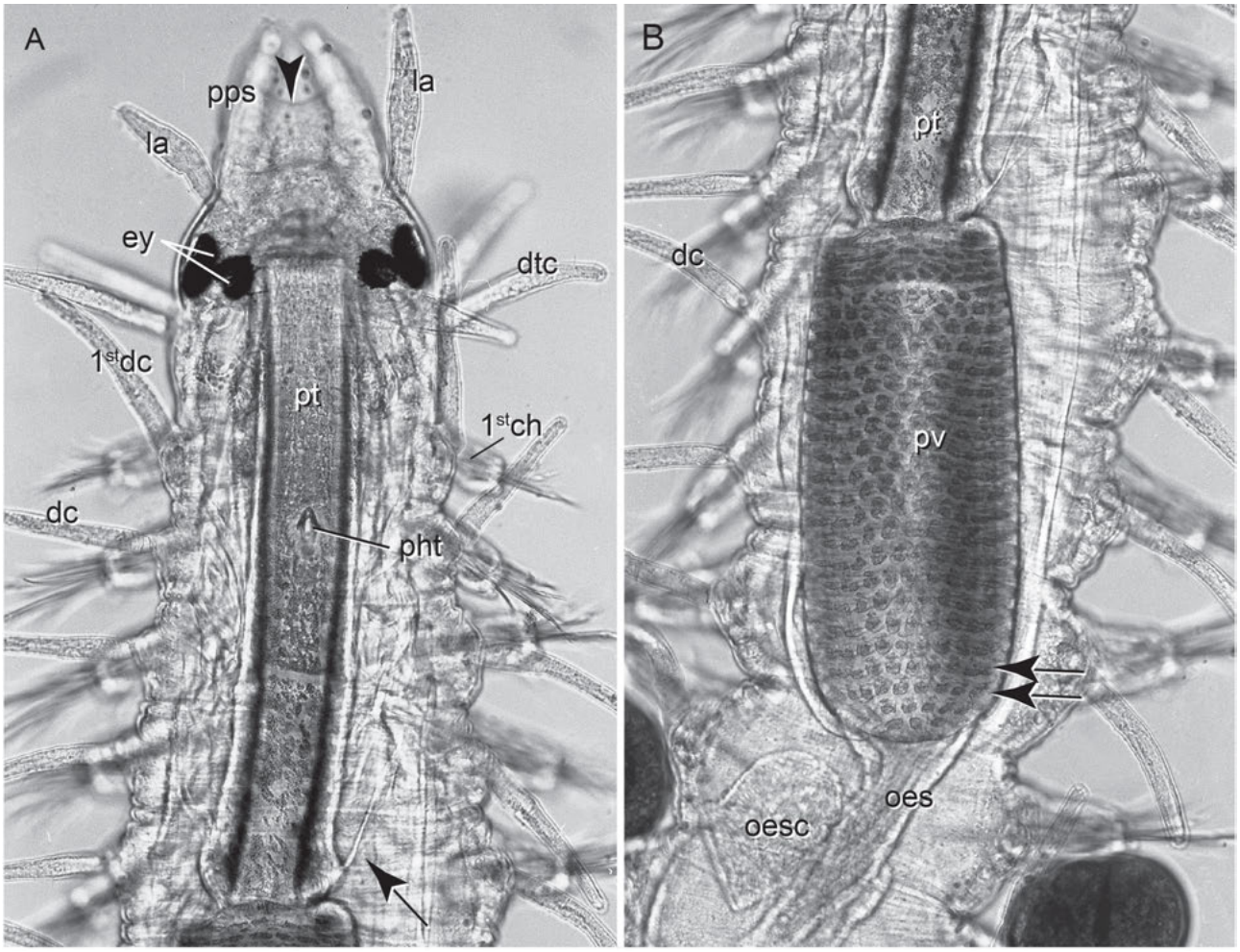


Fig. 7.13.2.13: Structure of the syllid foregut. *Salvatoria opisthodentata* (Hartmann-Schröder, 1979). A, Pharyngeal tube, tooth (pht) situated in the middle of the tube. Arrowhead points to dorsally fused palps (pps); note protractor muscle of pharyngeal tube (arrow). B, Proventricle (pv). Arrows point to adjacent rows of radial muscle fibers. 1st ch, first chaetiger; 1st dc, first dorsal cirrus; dc, dorsal cirrus; dtc, dorsal tentacular cirrus; ey, pigmented eye; la, lateral antenna; oes, esophagus; oesc, esophageal cecum; pht, pharyngeal tooth; pps, palps; pt, pharyngeal tube. Originals W. Westheide, Osnabrück.

tube is usually straight, but sometimes, as in *Amblyosyllis* and members of Autolytinae, it is long, slender, sinuous, sometimes coiled, with many circumvolutions.

The pharyngeal armature is very important in the taxonomy of the genera. Syllid teeth are composed of cuticle, usually sclerotized (Purschke 1988). Some genera lack pharyngeal armature (all the Anoplosyllinae; *Xenosyllis*; *Inermosyllis* San Martín, 2003; *Anguillosyllis* Day, 1963; and *Murrindisyllis*), but most have some kind of dentition; the most typical is a single, middorsal pharyngeal tooth (Fig. 7.13.2.14A, B), usually positioned anteriorly but sometimes in the middle or even the posterior part of the pharynx (*Opisthosyllis*, *Opisthodonta*). In the genus *Trypanosyllis* and other related genera, there is a crown of teeth, the trepan, around the pharyngeal opening, and a middorsal pharyngeal tooth may be present or absent in this genus. In *Trypanosyllis zebra* (Claparède, 1864), it is present in small specimens but not in larger ones (San Martín 2003). In the subfamily Autolytinae, as well as in *Amblyosyllis*, there is a trepan without a middorsal pharyngeal tooth (Fig. 7.13.2.14D). In *Eusyllis*, *Dioplosyllis* Gidholm, 1962, and *Miscellania* Martín, Alós & Sardá, 1990, there is a middorsal tooth and an incomplete ventral denticulate arc (Fig. 7.13.2.14C); in specimens of some species of *Eusyllis*, the denticulate arc may be complete (Brusa et al. 2013). In *Odontosyllis*, there is no middorsal tooth, but there is a ventral denticulate arc, with teeth posteriorly directed; this is in contrast to other genera, in which the denticles or teeth are directed forward. In *Brachysyllis* there is a large dorsal pharyngeal tooth and a ventral crown of five small teeth located on the verge of the inner pharynx surface (Pleijel et al. 2012).

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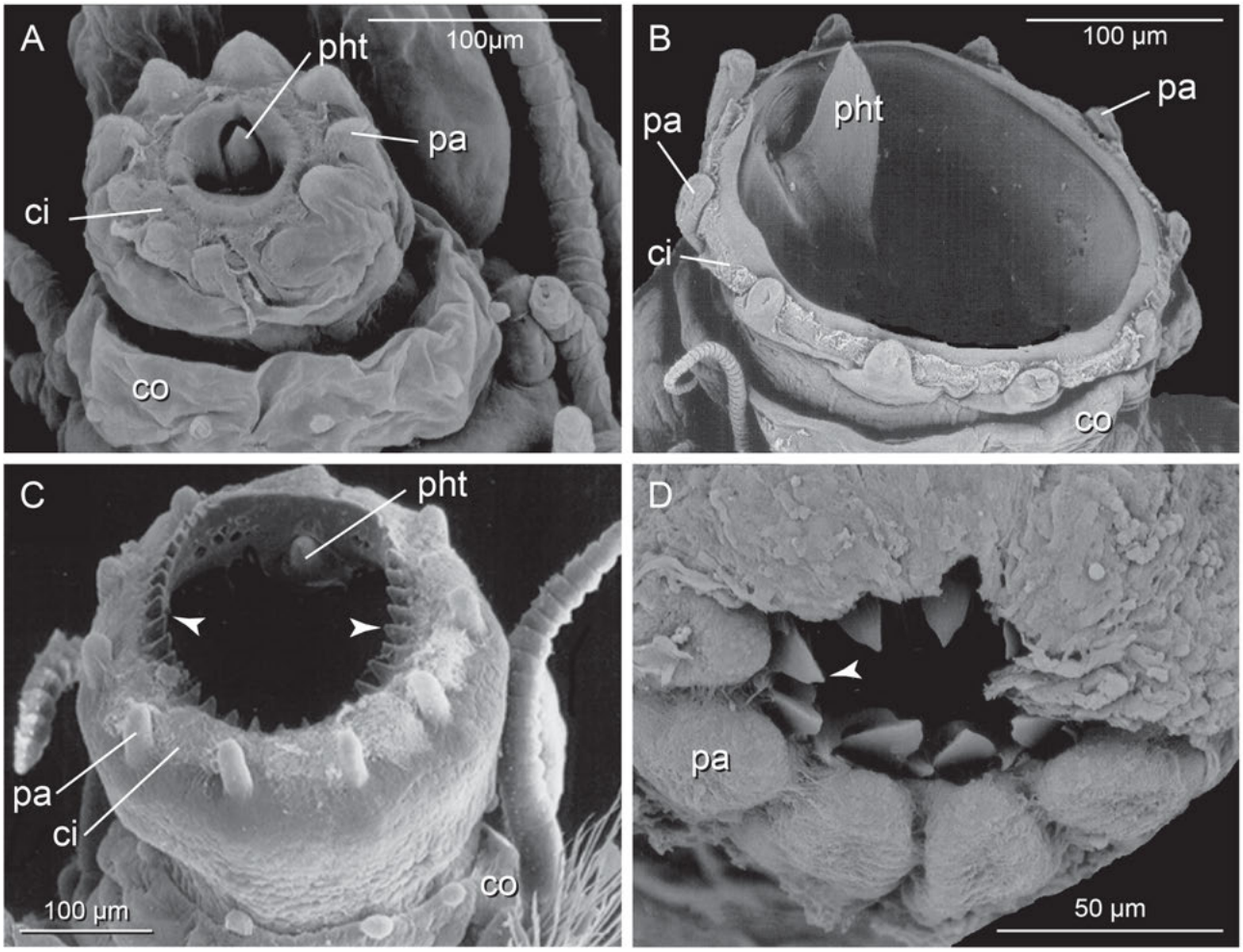


Fig. 7.13.2.14: SEM pictures of everted armed pharynx. A, *Syllis gerundensis* (Alós & Campoy, 1981). B, *Haplosyllis spongicola* (Grube, 1855). C, *Eusyllis assimilis* Marenzeller, 1875; arrowheads point to trepan. D, *Proceraea picta* Ehlers, 1864; arrowhead points to trepan. ci, cilia; co, cover (pharyngeal sheath); pa, papillae; pht, pharyngeal tooth. Modified from San Martín (2003).

Behind the pharyngeal tube, there is a very distinct structure, named the proventricle (Figs. 7.13.2.1, 7.13.2.3, 7.6.12A, B, 7.13.2.13B, 7.13.2.22,7.13.2.24A–C, 7.13.2.27A–E, 7.13.2.32A–C, 7.13.2.35A–D, and 7.13.2.41A, D), with a glandular internal epithelium and thick walls, provided with a series of strong radial muscular fibers; these appear externally as a series of transverse rows, each composed of a number of dots (dark through transmitted light, white under direct light). In the axis of each of these muscle fibers, there are numerous microcrystalline inclusions, which contain calcium and phosphorus and might be connected with calcium metabolism (according to Glasby 2000). The syllid proventricle muscle fibers have the longest recorded sarcomeres in the animal kingdom (Wissocq 1974, del Castillo et al. 1972). The size of the proventricle and the shape and number of muscle cell rows are important taxonomic characters for species identification. Some internal anatomical studies provided evidence of two plates on the internal gut epithelium at the anterior portion of the proventricle (e.g., Malaquin 1893, Schmidbaur et al. 2020, Ribeiro et al. 2020). The proventricle acts as a suction pump (Fauchald and Jumars 1979). Behind the proventricle is the ventricle, a small structure, generally shorter than the proventricle and usually difficult to identify. It is sometimes folded frontally, with glandular walls and weak muscular development (Figs. 7.13.2.12A and 7.13.2.30G). Behind the ventricle, there are usually two lateral gastric caeca, occasionally one or none. Finally, the gut is a long, slender tube that passes through the subsequent segments, narrowing between segments and ending at the anus, located on the pygidium. The intestinal epithelium through the posterior end gradually changes from a more anterior portion with a thicker epithelium and abundant secretory cells into a posterior portion with a thinner epithelium and less secretory cells (Malaquin 1893).

Many species bear glandular pores on various parts of the body (on the dorsum, nuchal lappets, dorsal cirri, antennae, ventral cirri, dorsally on bases of parapodia, etc.),

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arranged according to the genus; sometimes, there is a minute digitiform structure of unknown importance. Usually, the pores are only visible using SEM, but the glands are distinct (San Martín and Aguado 2012). There are several kinds of glands: spiral, within the articles of moniliform dorsal cirri; parapodial glands with rods, with fibrillar, granular, or hyaline material; different types of glands in ventral cirri; epidermal glands; etc. The function of the glands is unknown in most cases; their physiology is an interesting unexplored field of research. Haswell (1920b) suggested that the parapodial glands could secrete an adhesive material to hold the eggs in females. Certainly, these glands (present in females as well as males) are common in species that brood eggs ventrally and develop juveniles attached to the nephridial pores. However, their function in males has not been hypothesized before. Members of the subfamily Autolytinae have three kinds of glandular cells on the body surface: bacillary glands, which produce a secretion rich in polysaccharides, and two kinds of spherical glands, one of which produces a secretion rich in proteins. Furthermore, there are parapodial glands, which extend to the coelomic cavity and open on the bases or on the surfaces of their parapodia (Gidholm 1967, Glasby 2000).

Several species have single or double ciliary bands on some segments, across part or all of the dorsum. In *Myrianida*, there are also cilia on the dorsal cirri, and the palps are usually densely ciliated.

Excretory system. Syllids generally are believed to possess metanephridia in every segment except for the most anterior and posterior ones. However, Kuper (2001) could demonstrate that syllids develop rather diverse structured nephridia ranging from typical protonephridia (e.g., *Salvatoria clavata* (Claparède, 1863) and *Sphaerosyllis hermaphrodita* Westheide, 1990) to typical metanephridia (e.g., *Myrianida brachycephala* (Marenzeller, 1874)) and various intermediate stages. They act as both excretory organs and genital ducts (Goodrich 1945, Glasby 2000).

Bührmann et al. (1996a) and Kuper and Westheide (1997a) have studied the genital organs of the unusual interstitial species *Neopetitia amphophthalma* (Siewing, 1956) and *Sphaerosyllis hermaphrodita*, respectively. The former is dioecious with internal fertilisation, whereas the later is hermaphrodite.

Little is known about the spermatozoa of syllids, but it has been confirmed that the three kinds of spermatozoa recognized by Jamieson and Rouse (1989) are represented (Rouse 1999). The process of spermatogenesis and the ultrastructure of spermatozoa have been studied in some species of the family (Franzén 1982, Bührmann et al. 1996b, Kuper and Westheide 1997b, Kuper 2001, Giangrande et al. 2002, Lepore et al. 2006, Musco et al. 2008).

The karyotypes of syllids have only been studied in 14 species, almost all of them from the Mediterranean Sea (Curini-Galletti et al. 1991). In general, species in the same genus show similar karyotypes, and numbers of chromosomes in the subfamilies Exogoninae and Autolytinae are low (8–16).

Nervous system. The nervous system of Syllidae has been recently studied by Schmidbaur et al. (2020), showing that the position of the brain, the circumesophageal connectives, the stomatogastric nervous system, the longitudinal nerves that traverse each segment, and the innervation of the appendages are relatively uniform across the group. However, other details differ and might be related to the taxon-specific ecological requirements. In some small species, it is possible to observe the bilobed brain by transparence (Fig. 7.13.2.6E).

New techniques, as the microcomputed tomography (MCT), provided new insights and interesting future for the knowledge of the morphology of polychaetes in general (Faulwetter et al. 2013, 2014, Parapar et al. 2017) and also for the syllids, although only three species have been studied up to date, *Syllis garciai*, *Syllis gracilis* and *Ramisyllis multicaudata* (see Faulwetter et al. 2014, Parapar et al. 2017, 2019, Ponz-Segrelles et al. 2021).

Biology and ecology

Most syllids are generally considered omnivores, whereas some groups are identified as carnivorous or detritivorous (Fauchald and Jumars 1979); however, the concrete feeding habits in syllids is still a matter that requires further studies (Jumars et al. 2015). Most members of the subfamily Autolytinae feed on colonial hydrozoans (Malaquin 1893, Allen 1921, Hamond 1969); other syllids predate on corals and bryozoans. Interstitial syllids take minute pieces of detritus, diatoms, and small crustaceans; members of the subfamily Exogoninae are considered to be selective deposit feeders. One Caribbean species of *Odontosyllis* feeds on spionids (Fischer and Fischer 1995), and several species of *Haplosyllis*, as well as *Branchiosyllis oculata* Ehlers, 1887, feed on sponges, taking small pieces of tissue; species of *Haplosyllis* acquire the same color as the prey species (Lattig et al. 2007, Dauer 1973, Pawlik 1983, San Martín 1984a, 2003, Glasby 2000). Lattig et al. (2010a) described a possible case of cannibalism in *Haplosyllis ingensicola* Lattig, Martín & Aguado, 2010. Martínez and San Martín (2020) described a possible case of depredation of a syllid on other; they found a small, unidentified *Haplosyllis* apparently feeding on a dorsal cirrus of *Syllis maganda*. Feeding in many cases involves piercing prey with the pharyngeal tooth/teeth and

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sucking out the contents by means of the pumping action of the proventricle (Fauchald and Jumars 1979). Giangrande et al. (2000) confirmed that some herbivorous species feed on microalgae and fragments of macroalgae, some are deposit feeders, and others are omnivores. These authors conclude that there is a correlation between the pharyngeal armature and the feeding strategies; thus, deposit feeders have a poorly developed pharyngeal tooth and pump detritus directly. Species with well-developed teeth or a trepan may be herbivores, grazing on substrata before pumping plant fragments. However, this generalization is based on very few examples. More evidence from different species and different methods (e.g., stable isotope and fatty acid analyses) are still necessary to provide more information about feeding habits in syllids.

Syllids are parasitized by other polychaetes of the genus *Labrorostratus* Saint-Joseph, 1888 (Family Oenonidae, formerly Arabellidae) (Caullery and Mesnil 1915, Uebelacker 1978, San Martín and Sardá 1986). Uebelacker (1978) found that only 0.2% of the specimens was parasitized. These parasites live in the coelomic cavity of the syllid and are able to fill it completely. Caullery and Mesnil (1915) recorded monstrilloid copepods from coelomic cavity of *Syllis gracilis*, and Siddall and Aguado (2006) reported a haplosporidian parasitizing *Megasyllis nipponica* (Imajima, 1966). Álvarez-Campos et al. (2014a) described three species of Ciliophora living as epibionts on the body surface of several species of syllids. Other epibionts have been also found on the dorsal surface of some species of *Amblyosyllis* (Aguado et al. 2019).

Syllids may be extremely abundant and widespread in coastal samples, although scarcer in deep waters (Desbruyères and Segonzac 1997). However, syllids from deep waters are very interesting, and recent studies have discovered numerous new taxa (e.g., Macioleck 2020). In shallow waters, they are numerous among algae and seagrass rhizomes; they are also very important in the cryptofauna of hard substrata bored by other invertebrates, such as calcareous rocks, bioconcretions of either algae or animals (vermetids, corals), in all kinds of sediment and many species are interstitial (Westheide 1974a, b, 1984, 1988, San Martín 1984b). Samples from any kind of littoral subtrata may contain syllids. Because of their high diversity and numbers, as well as their small size, syllids are one of the most challenging groups to identify in any study of the littoral benthos.

Many species are associated as commensals or parasites of other marine organisms. As most of these syllid species are also present on other substrata, they are facultative commensals. *Branchiosyllis exilis* (Gravier, 1900) has been recorded on ophiuroids; *Haplosyllis chamaeleon* Laubier, 1960 on gorgonians, especially *Paramuricea clavata*; *Syllis armillaris* (O.F. Müller, 1771) on large decapods; *Syllis gracilis* Grube, 1840 on bryozoans, gorgonians, sponges, and hydrozoans; *Haplosyllis spongicola* (Grube, 1855) (and many other species of the genus) in many sponges; *Myrianida pinnigera* (Montagu, 1808) on some tunicates; *Procerastea halleziana* Malaquin, 1893; and *Procerastea nematodes* Langerhans, 1884 associated with colonies of several hydrozoan species. For information on commensalism and parasitism in syllids, see Martin and Britayev (1998, 2018) and Britayev and Antokhina (2012); the former authors reported 19 species of symbiotic syllids, most of them also found in other habitats. Martin et al. (2008) reported an association between an undescribed species of *Haplosyllides* and a shrimp symbiotic with a scleractinian, and Simon et al. (2014) described a new species of *Syllis* associated with holthurians. Members of *Alcyonosyllis* Glasby & Watson, 2001, *Haplosyllis*, and *Imajimaea* Nygren, 2004 are specifically symbionts on several species of octocorals (alcyonaceans and gorgonians) and hexacorals (Glasby and Watson 2001, Glasby and Aguado 2009, Aguado and Glasby 2015). *Syllis ramosa* and *Ramisyllis multicaudata* live within the canals of sponges *Petrosia* (see Glasby et al. 2012, Aguado et al. 2015a, Ponz-Segrelles et al. 2021).

Ecological and biogeographical analyses specifically of syllids have been made by Somaschini and Gravina (1994), Musco and Giangrande (2005a), Çinar (2003), Granados-Barba et al. (2003), López and Gallego (2006), San Martín (1984a, b), Bone and San Martín (2003), Serrano et al. (2006), Musco (2012), and del Pilar-Ruso et al. 2014.

Reproduction and development

The striking methods of reproduction in syllids have long attracted the attention of researchers. Malaquin (1893) and Potts (1911) established the nomenclature for each different phase and state, adopted later by other authors, and currently in use. The family is a large group with around 1000 species that shows a large variety of reproductive modes (e.g., asexual, sexual, hermaphroditism, viviparity, etc.). Several authors have subsequently summarized all knowledge on the reproduction of syllids, as well as its relationship with the systematics of the family (e.g., Okada 1937, Durchon 1959, Durchon and Wissocq 1964, Gidholm 1965, Schroeder and Hermans 1975, San Martín 1984a, 2003, Garwood 1991, Nygren 1999, Fischer 1999, Franke 1999, Glasby 2000, Aguado and San Martín 2009, Aguado et al. 2007, 2012, 2015a).

The sexual reproductive modes involve epitoky, a process of morphological and behavioral modifications in the benthic atokous forms to become planktonic

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epitokous. Epitoky is also present in other families, such as Nereididae. However, in syllids, the variety of epitokous processes is astonishing. There are two main reproductive modes: epigamy and schizogamy or stolonization. Schizogamy can be further subdivided into scissiparity and gemmiparity. Some authors have recently pointed out that this traditional classification for the reproductive processes in Syllidae might not cover the real complexity of reproductive modes (Ponz-Segrelles et al. 2020).

The plesiomorphic reproductive mode is considered to be epigamy (Fig. 7.13.2.15) (Aguado et al. 2007, 2012). This occurs in most members of the subfamilies Anoplosyllinae, Eusyllinae, and Exogoninae, as well as in one genus of Autolytinae (*Epigamia* Nygren, 2004). When individuals reach sexual maturity, they go through some important changes in anatomy and physiology and acquire secondary sexual characteristics: (1) eyes increase in size and the antennae somewhat elongate; (2) from the

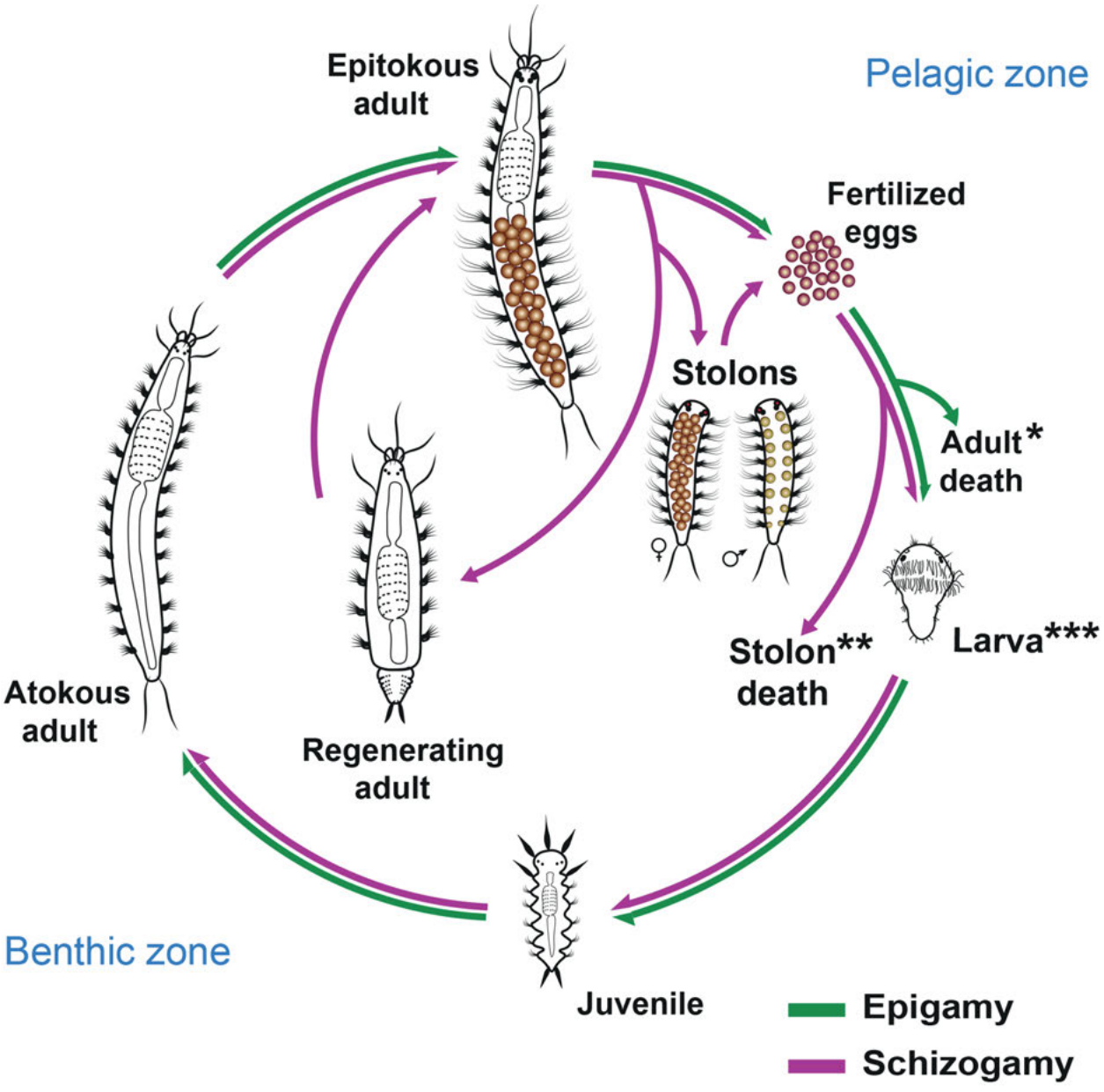


Fig. 7.13.2.15: Schematic representation of the epigamic and schizogamic syllid life cycles. The fertilized egg quickly develops into a planktotrophic or lecithotrophic trochophora larva. The larva then gives rise to a juvenile that grows and, eventually, reaches sexual maturity. When sexually mature, the atokous adult develops gonads and gametes and goes through the morphological changes associated with epigamy and schizogamy. Then when fully mature, either the epitokous adult (epigamy) or the detached stolon (schizogamy) goes to the pelagic zone, where swarming and spawning take place. In schizogamy, the tailless adult regenerates the lost posterior body and is able to produce new stolons (figure modified after Ponz-Segrelles et al. 2020).

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midbody backward, parapodia acquire notopodia with thin, curved notoaciculae and fascicles of very long capillary (natatory) chaetae that are laterally flattened; (3) genital glands develop in the modified segments, which store spermatozoa or oocytes and consequently, the modified segments are enlarged, and may also acquire a different color, and the body shortens as the modified segments are compressed; and (4) members of the Autolytinae genus *Epigamia* undergo more dramatic changes, losing the gut (Gidholm 1966, Nygren 2004). Along with these structural changes, there are also behavioral changes; individuals become more active and swim and may form large concentrations of planktonic reproductive individuals (Fig. 7.13.2.16). Sexual products are usually released through the nephridia, but there are some cases where the body wall of females breaks open to discharge the oocytes. In other polychaete families, which also reproduce by epigamy (Nereididae, Phyllodocidae, Glyceridae, Scalibregmatidae, Nephtyidae, Spionidae, Amphinomidae, Eunicidae, and Opheliidae according Rouse and Pleijel 2001), individuals usually die after spawning, but in at least some species of syllids, it has been confirmed that they resume their benthic lives after reproduction (Gidholm 1966, Daly 1975, Garwood 1982, Tsuji and Hill 1983, Fischer and Fischer 1995). Garwood (1982) showed that most specimens of a population of *Streptosyllis websteri* Southern, 1914 spawned twice during the reproductive season, at the beginning of their third year of life. By contrast, Sardá and San Martín (1992) studied a population of *Streptosyllis verrilli* (Moore, 1907) and found that this species only spawns once, during the ninth or tenth month of life, in a short reproductive season, and then dies; the population of this species fluctuates strongly throughout the year, from a minimum after the reproductive period in summer to a maximum in Autumn.

Fertilized eggs are presumed to float in the water column, where they develop. During spawning, some individuals produce green colored bioluminescence

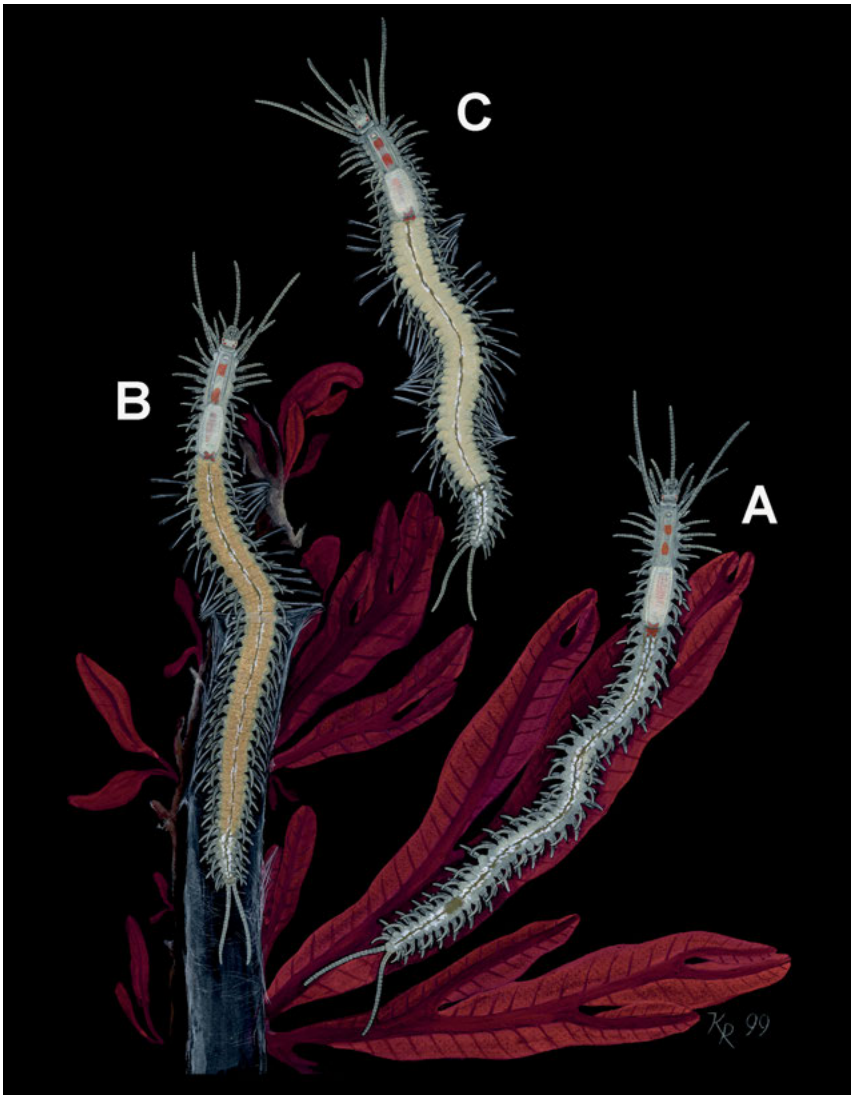


Fig. 7.13.2.16: Process of epigamy in *Eusyllis blomstrandi*. A, Benthic, nonepitokous specimen. B, Pre-epigamic specimen. C, Epigamic specimen. Drawing by K. Rehbinder, included in Fischer (2016).

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(Tsuji and Hill 1983, Zörner and Fischer 2007), and in *Odontosyllis*, the eyes have a maximum sensitivity to the green part of the visible spectrum (Glasby 2000). Recently, the transcriptome of several reproductive bioluminescent *Odontosyllis enopla* Verril, 1900 was analyzed, and the luciferase gene and several other genes related to periodicity were identified (Brugler et al. 2018).

Some species of *Syllides* brood ventrally (Heacox and Schroeder 1978) as does at least three species of *Perkinsyllis* San Martín, López & Aguado, 2009 (Hartmann-Schröder 1979, San Martín et al. 2009, San Martín and Hutchings 2006, Fukuda and Nogueira 2013). Another kind of brooding was reported for *Nudisyllis pulligera* Krohn, 1852 by Pierantoni (1905) in which the eggs and developing embryos and juveniles are attached to the dorsal cirri. Ponz-Segrelles et al. (2020) observed the brooding process in *N. pulligera* and noted that that two or three juveniles develop from each egg without any larval stage (Fig. 7.13.2.19). *Amblyosyllis anae* Aguado, Capa, Lago-Bacia et al., 2019 does not develop natatory chaetae during reproduction, and the eggs are deposited in gelatinous masses (Pernet 1998); similar reproduction has been examined in *Anoplosyllis edentula* Claparède, 1868 (Cognetti-Varriale 1971).

In Exogoninae, the males bear natatory chaetae (Figs. 7.13.2.17A and 7.13.2.18C, D) and the females do not discharge their eggs into the water column; they brood them until hatching or even retain the juveniles up until an advanced state. They can brood dorsally (Fig. 7.13.2.17B–E) or ventrally (Fig. 7.13.2.17F–I). In dorsal brooding, Kuper and Westheide (1998) demonstrated that in the genera *Prosphaerosyllis* and *Salvatoria*, the eggs are attached by means of tiny notochaetae, which penetrate the egg; this has also been shown in species of the genera *Erinaceusyllis* and *Cicese* (San Martín 2003, 2005, Díaz-Castañeda and San Martín 2001). By contrast, in *Exogone*, *Parapionosyllis*, *Sphaerosyllis*, and *Brania*, eggs are attached ventrally by means of adhesive glands on the nephridial openings; in these genera, the juveniles may even develop to an advanced state. This kind of reproduction with external gestation is related to small body size (Westheide 1984). In these genera of Exogoninae, the development is direct, and the attached embryos are without any kind of ciliation (Figs. 7.13.2.17G, H and 7.13.2.18A, B).

The other main kind of reproduction in syllids is schizogamy or stolonization (Fig. 7.13.2.15), which involves the detachment of part of the parent, which becomes free living for a limited time. The detached unit is called stolon and carries the gametes in its body; it generally bears natatory chaetae (Fig. 7.13.2.15) in most parapodia and usually has a well-differentiated head, with eyes, palps, and antennae (Figs. 7.13.2.4B and 7.13.2.19E, F), in various combinations. When mature, the stolon detaches from the parent and migrates into the water, at the surface or close to the bottom, for reproduction. It lacks a gut, does not feed, and dies after spawning. Schizogamy is present in Syllinae and Autolytinae as a convergent trait with independent phylogenetic origins (Nygren 1999, Aguado et al. 2007, 2012).

Schizogamy or stolonization can be subdivided into two different modes attending to the development and number of simultaneous stolons: Scissiparity, when only one stolon is produced at the same time, or Gemmiparity, when several stolons are produced simultaneously. Both modes, scissiparity and gemmiparity, are present in Autolytinae (gemmiparity in species of *Myrianida*) and Syllinae (gemmiparity in some species of *Parahaplosyllis*, *Ramisyllis*, *Trypanobia*, *Trypanedenta*, and *Trypanosyllis*; see Aguado et al. 2015a).

In scissiparity, the stolon is usually formed through the modification of the most posterior segments (Fig. 7.13.2.15). The stolon, once developed, detaches from the parental stock, which later regenerate the lost segments. Male and female stolons usually release gametes, spermatozoa fertilize the oocytes, and the embryonic and larval development occur in the plankton or in gelatinous masses attached to the female stolon body (see brooding modes below).

By contrast, in gemmiparity, the stolons are developed *de novo*. Aguado et al. (2015a) summarized the different kinds of gemmiparity in Autolytinae and Syllinae. In Autolytinae, the stolons are produced in a series or a chain, being the last one the most developed one and the first to be detached (several species in *Myrianida*). In Syllinae, the stolons can be developed collaterally (stolons in different developmental degree attached ventrally to the same area at the end of the body, e.g., *Trypanedenta* and *Parahaplosyllis*) (Fig. 7.13.2.33E), successively (each stolon is attached ventrally to different posterior segments, e.g., *Trypanobia*) (Fig. 7.13.2.33C), or at the tips of branches (in branching syllids, such as *Ramisyllis multicaudata*) (Johnson 1901, Potts 1911, Okada 1933, 1937, Glasby et al. 2012, Schroeder et al. 2017, Aguado et al. 2015a, Ponz-Segrelles et al. 2021).

There are several kinds of stolons, based on "head" shape and cephalic appendages. Stolons of some species of Syllinae from the Iberian Peninsula were studied by Estapé and San Martín (1991), and further descriptions of stolons were included in San Martín (2003). Aguado et al. (2012) suggested that the type of stolon may have an important evolutionary significance and stolons should be described along with the stocks, when possible.

In Syllinae, the different stolon types are as follows:

1. Acephalous (Figs. 7.13.2.20A and 7.13.2.29E). Found in some species of *Haplosyllis* and *Branchiosyllis*. Stolon

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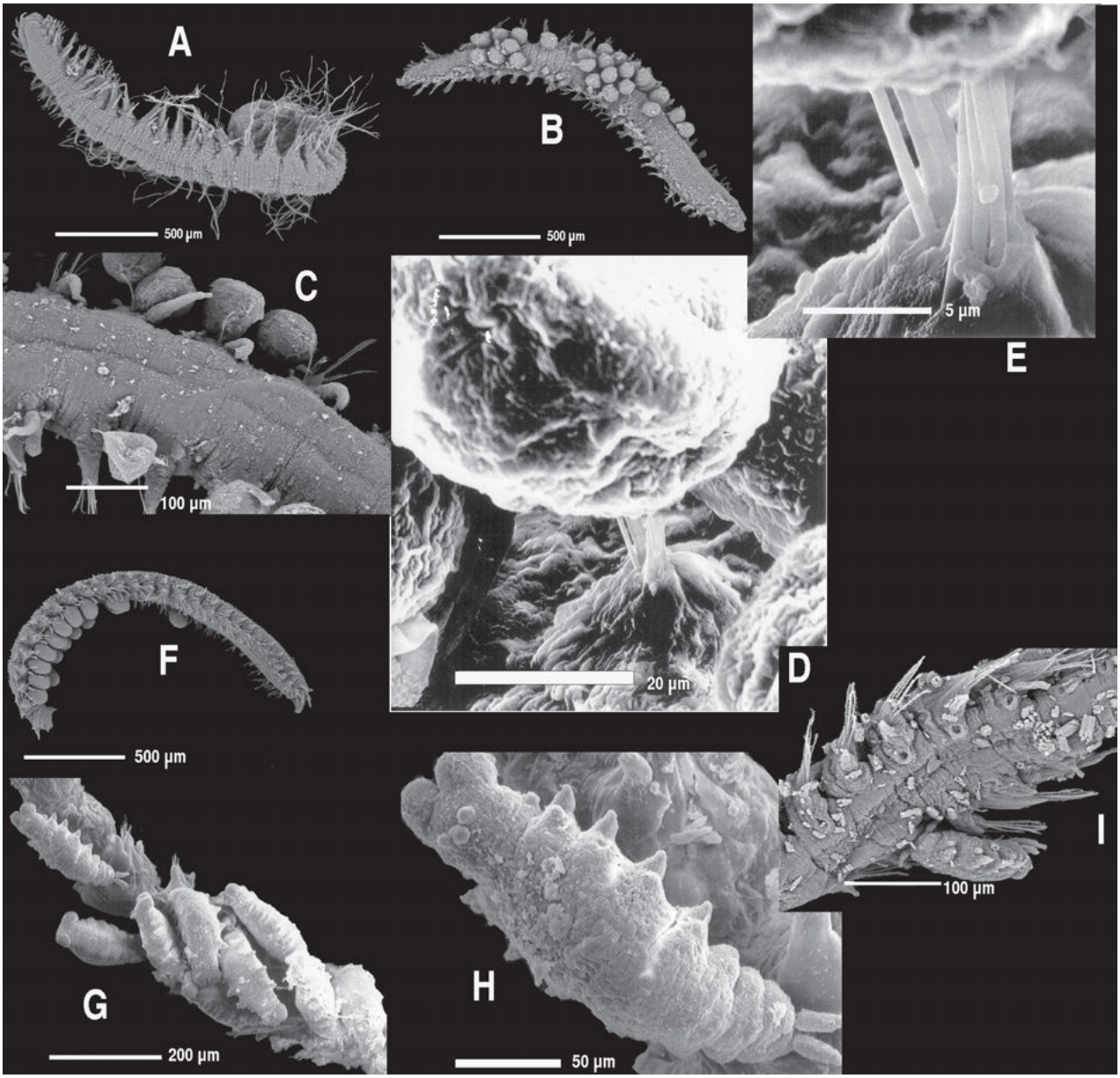


Fig. 7.13.2.17: SEM pictures showing epigamy and brooding in Exogoninae. A, Epigamic male with natatory chaetae. B–E, Dorsal brooding. F–I, Ventral brooding with development of juveniles. A, Epigamic male; B, female with embryos; C, detail of the eggs and the capillary notochaetae (*Erinaceusyllis hartmannschroederae* San Martín, 2005); D, E, close detail of capillary notochaetae insertion in egg (*Salvatoria vieitezi* (San Martín, 1984)); F, female carrying eggs (*Sphaerosyllis hirsuta* Ehlers, 1897); G, juveniles on a female (*Exogone verugera* (Claparède, 1868)); H, detail of one juvenile; I, juvenile on female, and nephridial opening after detachment of other juveniles (*Exogone africana* Hartmann-Schröder, 1974). A–C, F, I, after San Martín (2005); D, E, G, H, after San Martín (2003).

lacks head and appendages, and the natatory chaetae start from first chaetiger, which is not different to subsequent ones; on each segment, there is a photoreceptor organ on each side.

2. Acerous or *Tetraglene* (Figs. 7.13.2.20B and 7.13.2.33D). Found in species of *Trypanosyllis*, *Trypanedenta*, *Eurysyllis tuberculata* Ehlers, 1864, *Plakosyllis brevipes* Hartmann-Schröder, 1956 and Ramisyllis. The head is bilobed, lacks antennae, and has two pairs of eyes.
3. Dicerous or *Chaetosyllis* (Figs. 7.13.2.4B, 7.13.2.20C, D, and 7.13.2.29B, C). Found in many species of *Syllis*, *Megasyllis*, *Opisthosyllis*, *Alcyonosyllis*, and *Parasphaerosyllis*. It is the most common kind of stolon. The head is strongly bilobed and bears two small appendages, or antennae, a pair of dorsal, and a pair of ventral eyes.
4. Tricerous. Described by San Martín et al. (1997) in *Haplosyllides floridana* Augener, 1922. The rounded

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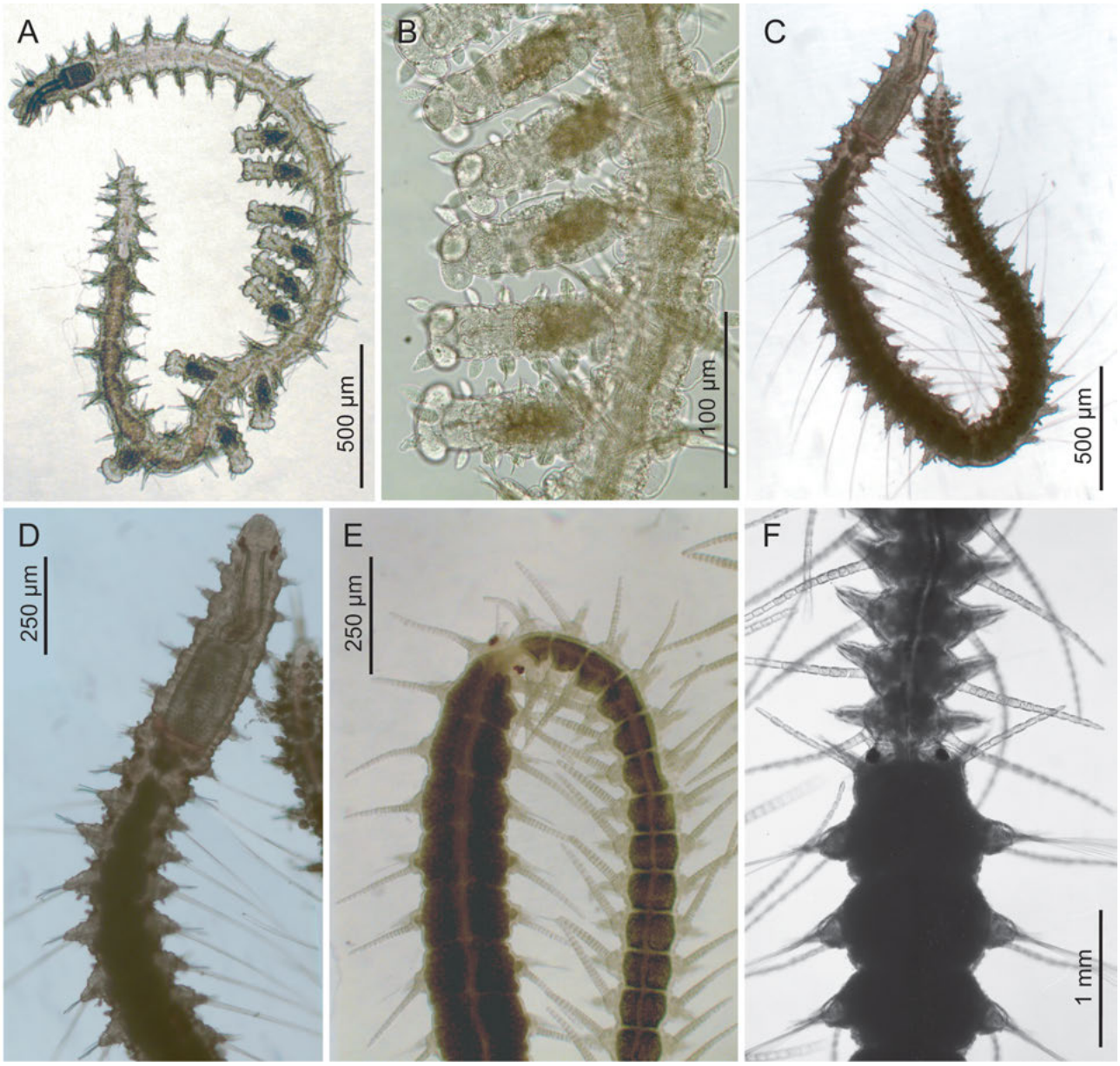


Fig. 7.13.2.18: A, B, *Parapionosyllis* sp. Brooding female with embryos. A, Entire animal; pharyngeal tube slightly protruded. B, Enlargement of highly differentiated embryos. C, D, *Erinaceusyllis* sp. Epigamic male with hair-like epitokous natatory chaetae. C, Entire animal. D, Enlargement of anterior part of specimen. E, F, Schizogamic females with stolons. E, *Syllis* sp. F, *Megasyllis pseudoheterosetosa* (Böggemann & Westheide, 2004). Mahé, Seychelles. A–D, G. Purschke, Osnabrück, E M.C.M. Müller, Osnabrück, F. W. Westheide, Osnabrück.

head has three small, papilliform antennae and lacking palps.

5. Tetracerous (Fig. 7.13.2.20E, F). Found in *Syllis amica* Quatrefages, 1865, *Syllis rosea* (Langerhans, 1879), *Syllis pulvinata* (Langerhans, 1881), and *Syllis cryptica* Ben-Eliahu, 1977. The head bears two moniliform antennae, two slender, separated palps, and a pair of eyes.
6. Pentacerous or *Ioida* (Figs. 7.13.2.20G, H). Found in *Syllis hyalina* Grube, 1863, *Syllis gracilis*, and *Syllis armillaris*. The palps are more developed than in the tetracerous stolon, although more ventrally inserted, and there are three moniliform antennae and four eyes.

In general, the stolons of Syllinae do not show any regionalization, being all segments quite similar in morphology (Fig. 7.13.2.20C, D). However, stolons of *Ramisyllis multicaudata* have been recently described with a clear sexual dimorphism (Schroeder et al. 2017). Stolons in Syllinae have usually biramous parapodia (counting with natatory notochaetae), except the first pair, dorsal cirri

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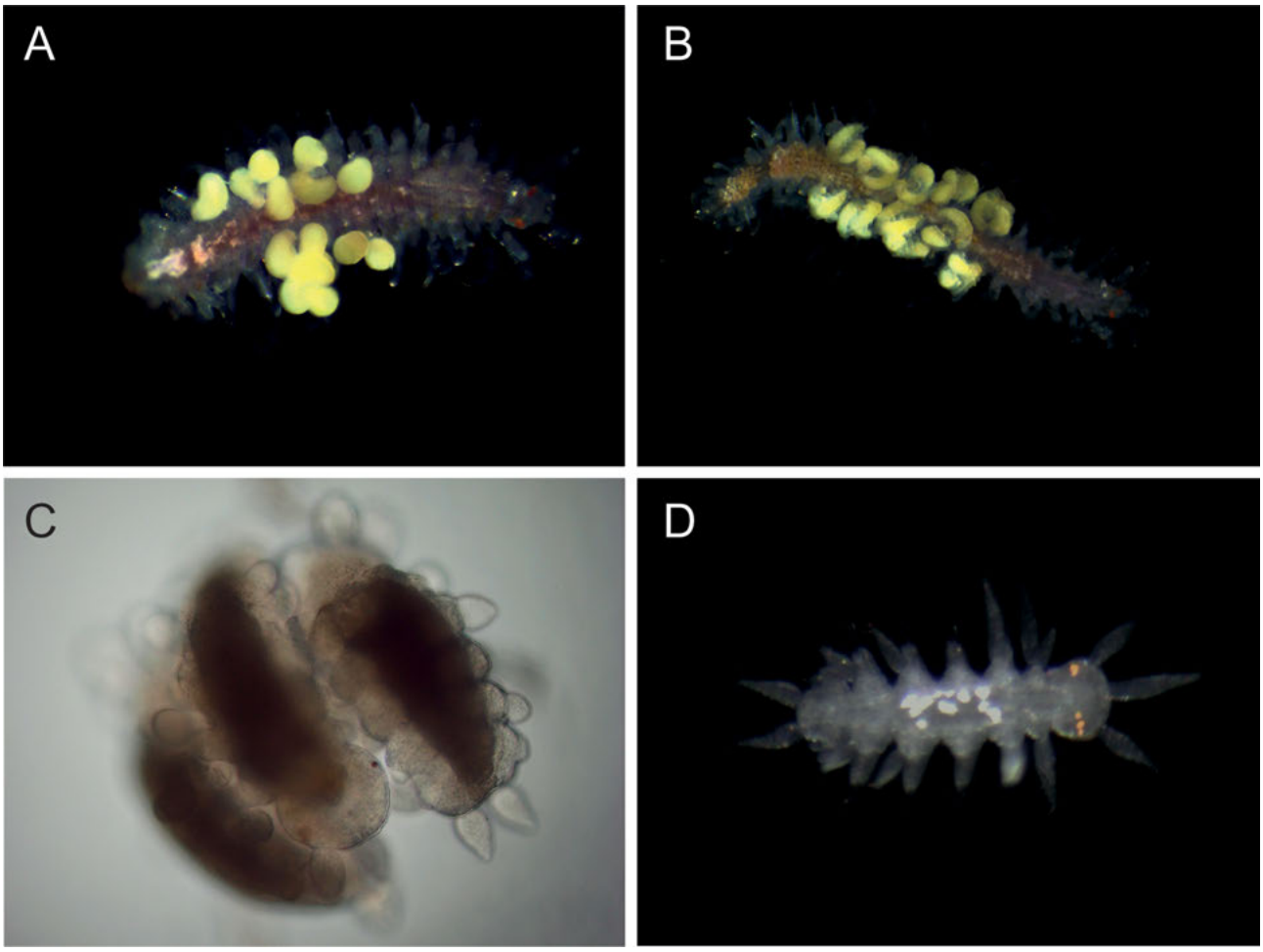


Fig. 7.13.2.19: Development of juveniles in *Nudisyllis pulligera* (after Ponz-Segrelles et al. 2020).

moniliform with few articles (smooth in *Megasyllis* and *Alcyonosyllis*), which are slender and weakly delineated.

In general, in Syllinae, stolons do not brood eggs, excepting one recently reported case. Langeneck et al. (2020) described how the female stolon of *Syllis rosea* (Langehans, 1879) take care of the eggs in a gelatinous mass.

In contrast to Syllinae, the stolons in Autolytinae show a regionalization and strong sexual dimorphism. The male stolon is named *Polybostrichus* and the female *Sacconereis*. Both stolons are complex and show a replication of the appendages of the stock.

The *Polybostrichus* (Fig. 7.13.2.21C) has a head with four large eyes, usually with one pair much bigger than the other; two long, bifurcated palps; and three antennae, the lateral ones short and frontally directedand the median antenna very long and coiled. The first segment is achaetous and lacks parapodia, with two pairs of cirri, of which the dorsal ones are very long and coiled. Several anterior segments are unmodified; behind these, there is a moderately long region with birameous segments with natatory chaetae; there is then a region of few segments at the posterior end, without natatory chaetae and, finally, the pygidium.

The *Sacconereis* (Fig. 7.13.2.21D) is less complex, although it has the same regions as the male stolons, the palps are shorter and not bifurcated, all three antennae and the dorsal cirri are moderately long, and some species develop one or more ventral sacs for brooding eggs. Using SEM, San Martín (2003) observed the presence of two semicircular, ciliated nuchal organs in the female stolons of two different Autolytinae species, and in contrast to male stolons, they have segmental ciliary bands, with cilia emerging from epidermal pores. The *Sacconereis* usually discharge eggs into the water column, with embryonic and larval development in the plankton, but in some cases, female stolons produce an external ovigerous sac (Fig. 7.13.2.21F), in which eggs are fertilized (Gidholm 1965, Qian and Chia 1989) (Fig. 7.13.2.21E). Some species retain embryos and larvae (Fig. 7.13.2.21G) (up to 500) in a brood

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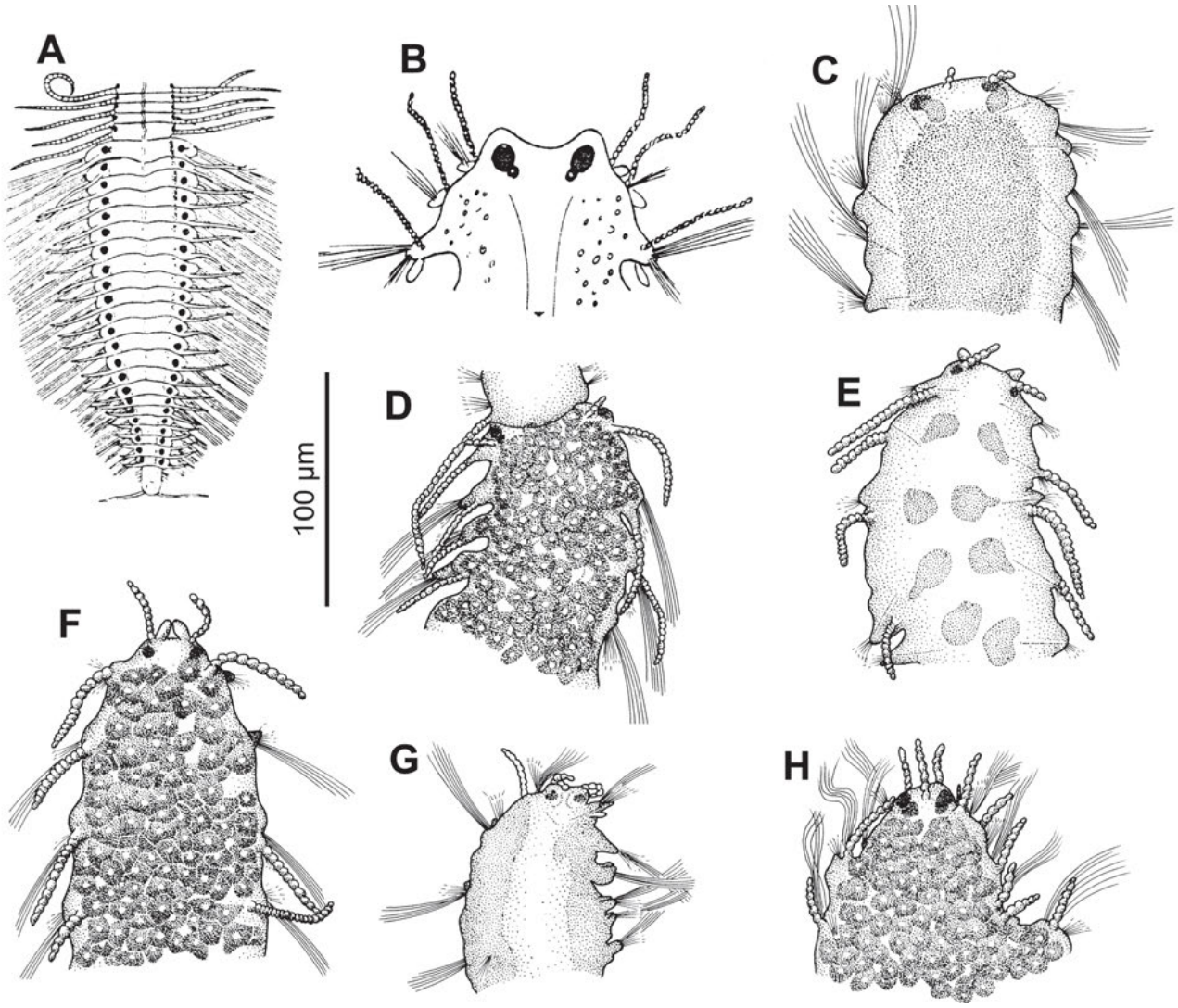


Fig. 7.13.2.20: Different stolons in the Syllidae. A, Acephalous (*Haplosyllis spongicola* (Grube, 1855)), attached to stock. B, Acerous, anterior end of a female (*Trypanosyllis zebra* (Claparède, 1864)). C, Dicerous, anterior end of a male. D, Same, female attached to stock (*Syllis prolifera* Krohn, 1852). E, Tetracerous, anterior end of male. F, Female (*Syllis pulvinata* (Langerhans, 1881)). G, Pentacerous, anterior end of male. H, Female (*Syllis armillaris* (O.F. Müller, 1776)). San Martín's original drawings modified by Jordi Corbera.

pouch, derived from the ovigerous sac, on the ventral side of body (Glasby 2000). Britayev et al. (1998) and Britayev and San Martín (2001) described a case where the female stolon of a species of *Proceraea* from the North Pacific deposited eggs one by one inside the thecae of the hydrozoan *Abietinaria turgida*, where its larvae develop, feeding on the polyp, with their prostomium orientated into the coenosarc, inducing the polyp to develop an accessory theca before death. The juvenile syllid is protected within this theca until its preadult stage, when it leaves the perisarc and has a free-living lifestyle, crawling through the hydrozoan colony, feeding on the polyps.

The mechanisms that trigger the stolonization are still not clear. Several authors (Durchon 1957, Franke 1980, 1983, 1986, Heacox and Schroeder 1982, among others) proposed a system of two control regions (prostomium and proventricle) secreting antagonistic hormones (stolonizing hormone and inhibitory hormone, respectively). Franke (1986) explained that the reproduction in *Syllis prolifera* is stimulated by a hormonal cycle in the prostomium that controls the inhibitory stolonization hormone, which originates in the proventricle. The stolonization starts when the level of that hormone decreases during the summer, as hormone levels are related to summer moonlight periods. More recently, in a comparative transcriptomic study in *Syllis magdalena* Wesenberg-Lund, 1962, Álvarez-Campos et al. (2019) suggested the gonads at the posterior part of the body as an additional control

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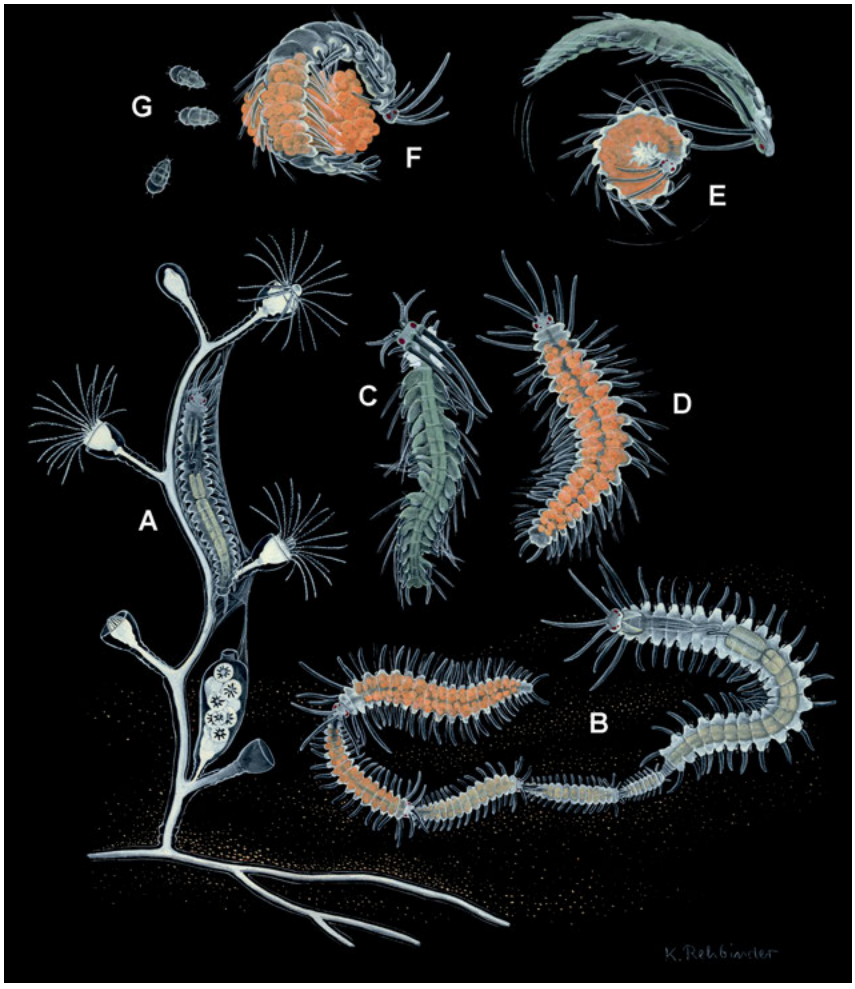


Fig. 7.13.2.21: Life cycle of *Myrianida prolifera*. A, Stock animal living on hydroids. B, Stolonizing female. C, Male stolon. D, Female stolon. E, Matting dance, the male keeping in touch with the female by a pair of head tentacles and wrapping mucous strings with embedded sperm around the female. F, Brooding female in the plankton. G, Hatched larvae. After Fischer (2016), K. Rehbinder's original drawing, after a film (Fischer et al. 1992).

region and proposed several neurohormone candidates involved in stolonization.

Some studies revealed that the absence of the proventricle or the proventricle region (e.g., by dissection and extraction) triggers successive stolonization events (without regeneration) and masculinization (i.e., only masculine stolons are developed) (Durchon 1975, Hauenschild 1953, Heacox and Schroeder 1982, Junqua 1957, Weidhase et al. 2016, Wissocq 1963).

The cycle from one stolonization to another takes approximately 1 month in *Syllis prolifera*. It has been shown that some species of *Syllis* can change sex between stolonizations. Durchon (1951) found that, in *Syllis amica*, 20% of studied individuals had a second stolonization and that 40% of these individuals underwent a natural sex change, there being a higher tendency toward sex change in females than in males. Recently, Ponz-Segrelles et al. (2020), in a comparative transcriptomic study of *S. prolifera* and *Nudisyllis pulligera*, revealed that females are more similar to nonreproducing specimens in terms of gene expression than males. Previously, Ponz-Segrelles et al. (2018) showed that there is a differential expression of certain genes (stem cell markers) in females and males of *Typosyllis antoni*.

Wissocq (1966) explained that in *Haplosyllis spongicola*, gametes may also originate in nonmodified segments, and that they migrate to the stolon, during the process of stolonization. Schiedges (1979a, b) demonstrated that photoperiod is the external stimulus of reproduction in some species of *Myrianida* (as *Autolytus*). Female stolons swim to the light and stay near surface, and male stolons are attracted by a female sexual pheromone. This pheromone induces the male stolon to rapid swimming movements while releasing spermatozoa to fertilize eggs (Gidholm 1965).

Other reproductive modes have also been described in the family, such as hermaphroditism (Goodrich 1930, Westheide 1990a) and viviparity, as in *Syllis vivipara* Krohn, 1869 (see Goodrich 1900); *Dentatisyllis mangalis* Russell, 1995; *Dentatisyllis mortoni* Ding, Licher & Westheide, 1998; *Parexogone hebes* (Webster & Benedict, 1884) (see Pocklington and Hutchenson 1983); *Parexogone*

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meridionalis (Cognetti, 1955) (see San Martín 1984a); *Syllis garciai* (see Aguado and San Martín 2006); and *Syllis unzima* Simon, San Martín & Robinson, 2014 (see Simon et al. 2014).

The larvae development has been studied in detail for some species of Syllinae and Exogoninae (Cazaux 1969, Heacox 1980, Franke 1980, Giangrande 1997, Simon et al. 2014, among others).

Syllids have a great capacity for regenerating tissues and segments (Ribeiro et al. 2018), and it is common to find specimens in different states of regeneration. Posterior regeneration is widely distributed, whereas complete anterior regeneration (including the proventricle) is more limited (Ribeiro et al. 2018, 2020, 2021). Sometimes some regenerating specimens have been erroneously identified as stolons, especially in the genera *Sphaerosyllis* and *Exogone* (see Michel 1909). *Procerastea halleziana* reproduces asexually by fragmentation and rapid regeneration (Langhammer 1928); fragmentation is induced by strong contractions of the segmentary longitudinal muscles, which break off at specific points that define megasepta and correspond to strong constrictions of the gut (Okada 1929); each fragment regenerates anterior and posterior parts (Caullery 1925, Berrill 1952, Glasby 2000, Ribeiro et al. 2018). It is common to find numerous specimens of *Syllis gracilis* regenerating both anteriorly and posteriorly, suggesting that they also fragment their bodies and later regenerate as a natural way to colonize a favorable substratum and thereafter reproduce sexually. Similarly, a recently described species, *Syllis malaquini* Ribeiro, Ponz-Segrelles, Helm, Egger & Aguado, 2020 (Ribeiro et al. 2020), is able to reproduce asexually by architomic fission as well as sexually by schizogamy (Ribeiro et al. 2020). The complete anterior regeneration seems to occur in those species that are able to reproduce asexually by fission (Ribeiro et al. 2020, 2021). Lattig and Martin (2011a) described a species of *Haplosyllis* in which detached and regenerating fragments, filled with gametes, could be mistaken with stolons.

The process of regeneration has been recently studied by Weidhase et al. (2017) and Ribeiro et al. (2018, 2019, 2020, 2021). Ribeiro et al. (2019), in a comparative transcriptomic study of *Syllis gracilis* and *Sphaerosyllis hystrix*, found that posterior regeneration and normal postembryonic development are more similar between each other in terms of gene expression, whereas anterior regeneration is a distinct process.

Phylogeny and taxonomy

In early classifications, syllids were included in the Nereidoidea, but they were later considered to be a separate family. Fauchald (1977) included syllids within the order Phyllodocida, suborder Nereidiformia, close to Antonbruunidae, Calamyzidae, Hesionidae, Nereidae, and Pilargidae. Pettibone (1982) placed them in the order Phyllodocida, superfamily Nereididacea. More recently, Glasby (1993) considered a superfamily Nereidoidea composed of the families Chrysopetalidae, Hesionidae, Nautiniellidae, Nereididae, Pilargidae, and Syllidae. The families Calamyzidae and Levidoridae were considered by that author as members of the Syllidae. Levidoridae was subsequently included in the syllid subfamily Autolytinae (San Martín 2003, Nygren 2004), whereas the Calamyzidae have recently been moved to the family Chrysopetalidae (Aguado et al. 2013). Rouse and Fauchald (1997) carried out a cladistic analysis of the polychaetes and placed the Syllidae within a clade named Palpata, Aciculata, and Phyllodocida, with Pilargidae and Sphaerodoridae as the phylogenetically closest families, but also close to Hesionidae and Nereididae. The relationships between Syllidae and Sphaerodoridae were investigated by Aguado et al. (2007), who showed that the sphaerodorids should not be included within syllids.

There have been several studies dealing with the organization of groups within the syllids. The first systematic general organization of the Syllidae was that of Malaquin (1893). Fauvel (1923a) adopted the classification of Malaquin (1893) while proposing some changes and provided keys for the identification of genera and species from France, as well as descriptions of species. San Martín (2003) reviewed all the knowledge on the family to date, proposed some changes to the taxonomy and systematics, and produced diagnoses of subfamilies and genera, with keys to the identification of all taxa from the Iberian Peninsula.

The family is currently divided into five subfamilies. Traditionally, the authorship of the first four subfamilies is attributed to Rioja (1925). However, Langerhans (1879) had previously proposed three tribes: Syllideae Grube, 1850; Exogoneae Langerhans, 1879; and Autolyteae Langerhans, 1879; and later, Malaquin (1893) added the tribe Eusylleae. The first author to use subfamily categories was Fauvel (1923a, b), followed by Rioja (1925). The first four subfamilies should be assigned as follows: Eusyllinae Malaquin, 1893; Syllinae Grube, 1850; Exogoninae Langerhans, 1879; and Autolytinae Langerhans, 1879.

Aguado and San Martín (2009) found an additional and well-supported monophyletic group and described as a fifth subfamily, the Anoplosyllinae. The subfamily Eusyllinae (sensu Fauvel) was shown as para- or polyphyletic, depending on the study (Nygren and Sundberg 2003, Aguado et al. 2007, Aguado and San Martín 2009). However, Aguado et al. (2012) reorganized this subfamily

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to form a monophyletic group after combined morphological and molecular phylogenetic analysis.

Hartman (1965) proposed the subfamily Eurysyllinae for the genus *Eurysyllis*, considering *Plakosyllis* as a synonym. This subfamily was also accepted in Hartmann-Schröder (1971b, 1996). However, both of these genera have the typical reproduction of the subfamily Syllinae, and they appear to be close to other genera of Syllinae, and the validity of this subfamily has not received general acceptance.

Aguado and Bleidorn (2010) investigated the relationships within the Syllidae, through different alignment programs, parameters, and methodologies. The family Syllidae was found to be monophyletic, with Anoplosyllinae as the sister group to the rest of the syllids. The low support values for a monophyletic Syllidae obtained by previous studies (Aguado et al. 2007) were explained by the presence of a hypervariable region (V4) in the 18S DNA gene. The secondary structure of this gene was explored by the first time for syllids, and its information was considered to be very valuable to the interpretation of the evolution of the group. More recently, a phylogenetic analysis of complete mitochondrial genomes supported previous results about the systematics of the complete Syllidae, and revealed that the mitochondrial gene order was highly variable within the family, with the highest variability within Syllinae (Aguado et al. 2016).

In terms of the evolution of reproductive modes, epigamy was found to be the primitive condition, whereas schizogamy has appeared twice, in the Syllinae and Autolytinae, respectively (Nygren and Sundberg 2003, Aguado et al. 2007, 2012). In addition, Aguado et al. (2007, 2012) proposed an evolutionary hypothesis for the different brooding types found in the family.

Nygren (2004) undertook a phylogenetic revision of the subfamily Autolytinae and proposed a new classification for this group. San Martín (2005) dealt with the subfamily Exogoninae from Australia, reviewing all the brooding modes in the group and proposing possible hypotheses about their evolutionary relationships. San Martín and Hutchings (2006) published a monograph of the Eusyllinae from Australia, including revised diagnoses for most of the genera assigned to that group. The Australian Syllinae was revised by San Martín et al. (2008a, b, 2010) and the genus *Pionosyllis* by San Martín et al. (2009). Licher (1999) wrote a large and valuable revision of the genus *Typosyllis*, elucidating many aspects of its difficult taxonomy. Aguado and San Martín (2008) revised and redescribed some of the more problematic genera in the Syllidae and clarified the interpretation of some morphological features in these taxa. The phylogenetic relationships of *Megasyllis*, *Alcyonosyllis*, and *Paraopisthosyllis* were explored by Aguado and Glasby (2015). Aguado et al. (2015a) proposed a phylogenetic hypothesis for the "ribbon clade" within Syllinae that was later supported by Álvarez-Campos et al. (2018). Lastly, Riberio et al. (2020) provided the most recent phylogenetic analysis of Syllinae.

The classification of the Autolytinae proposed by Nygren (2004) has been followed in this study as have the generic diagnoses proposed by San Martín (2005), San Martín and Hutchings (2006), San Martín et al. (2008a, b, 2009, 2010), and Aguado and San Martín (2007). The species proposed by Licher (1999) as belonging to the genera *Typosyllis* and *Syllis* have all been assigned to the genus *Syllis*, following San Martín (1984a, 1992, 2003) and Álvarez-Campos et al. (2015a, b).

Aguado et al. (2012) explained the phylogenetic relationships within the monophyletic Syllidae, defined by the presence of the proventricle. The family was early divided into different evolutionary lines: (1) *Anguillosyllis* and (2) a large clade including the rest of syllids. This large clade was divided into Anoplosyllinae (without pharyngeal armature) and a second clade (defined by the presence of pharyngeal armature), including several monophyletic groups: the subfamilies Autolytinae, Exogoninae, Eusyllinae, and Syllinae and some independent genera. These authors also showed that several genera may be not monophyletic and need further studies. A schematic synthesis of the phylogeny of the Syllidae is shown in Figure 7.13.2.22 based on Aguado et al. (2012, 2015a) and Ribeiro et al. (2020).

Phylogenetic methods and molecular markers are being used to reveal that several species previously considered "cosmopolitan" are in fact complexes of species (Westheide and Hass-Cordes 2001, Álvarez-Campos et al. 2017). Similarly, several groups have been reorganized, and the species revealed more restricted distributions than previously thought (Aguado et al. 2019).

A list of genera and their distribution between the subfamilies and those considered as *incertae sedis* is shown in Tab. 7.13.2.1 (after Aguado et al. 2012).

Anoplosyllinae Aguado & San Martín, 2009

Diagnosis: Body cylindrical, size from small to minute. Palps basally fused, without medial scar. Three antennae, usually long, extending beyond palps; four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri. Nuchal organs consist of two dorsolateral, densely ciliated grooves between the prostomium and the peristomium. Peristomium with

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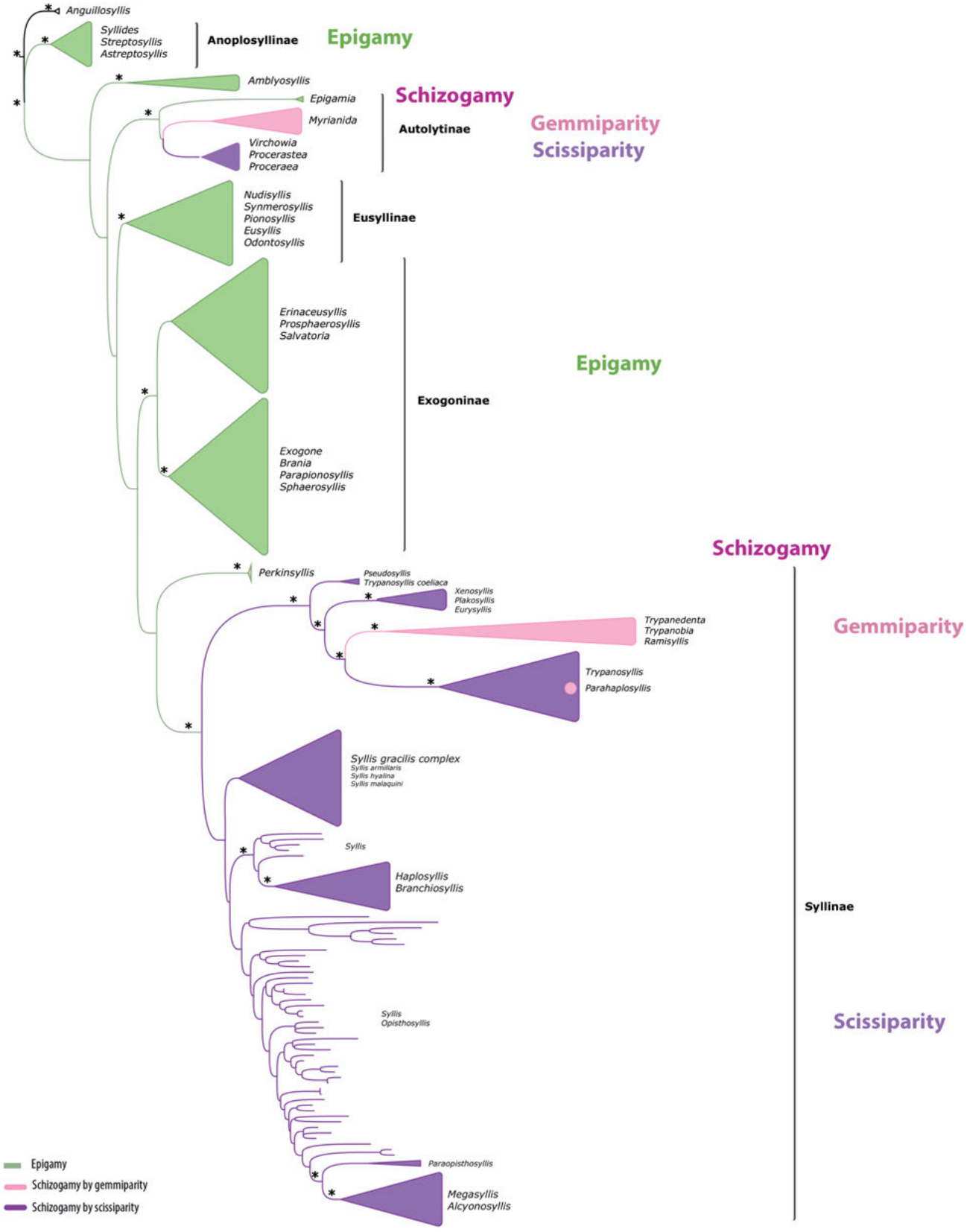


Fig. 7.13.2.22: Schematic phylogenetic tree of the family Syllidae. Relationships based on Aguado et al. (2012, 2015a) and Ribeiro et al. (2020). Reproductive modes shown by colors. *Well-supported clades. Some genera (e.g., *Syllis, Opisthosyllis,* and *Trypanosyllis*) are paraphyletic.

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Tab. 7.13.2.1: All the current valid genera of the family Syllidae organized into the five subfamilies and one group "incertae sedis" for those genera whose phylogenetic relationships are still not clear (after Aguado et al. 2012).

Taxonomic rank	**Subfamily**	**Subfamily**	**Subfamily**	**Subfamily**	**Subfamily**	**–**
Name of group	**Anoplosyllinae**	**Autolytinae**	**Exogoninae**	**Syllinae**	**Eusyllinae**	**Incertae sedis**
Included genera	*Anoplosyllis* *Streptospinigera* *Astreptosyllis* *Streptosyllis* *Syllides*	*Acritagasyllis* *Epigamia* *Erseia* *Imajimaea* *Levidorum* *Myrianida* *Pachyprocerastea* *Paraproceraea* *Paraprocerastea* *Planicirrata* *Proceraea* *Procerastea* *Virchowia*	*Brania* *Cicese* *Erinaceusyllis* *Exogone* *Parapionosyllis* *Parexogone* *Prosphaerosyllis* *Salvatoria* *Sphaerosyllis*	*Alcyonosyllis* *Branchiosyllis* *Dentatisyllis* *Eurysyllis* *Haplosyllis* *Inermosyllis* *Karroonsyllis* *Megasyllis* *Nuchalosyllis* *Opisthosyllis* *Parahaplosyllis* *Paraopisthosyllis* *Parasphaerosyllis* *Plakosyllis* *Pseudosyllis* *Ramisyllis* *Rhopalosyllis* *Syllis* *Tetrapalpia* *Trypanedenta* *Trypanobia* *Trypanospina* *Trypanosyllis* *Xenosyllis*	*Eusyllis* *Nudisyllis* *Odontosyllis* *Opisthodonta* *Pionosyllis* *Synmerosyllis*	*Amblyosyllis* *Anguillosyllis* *Bollandiella* *Brachysyllis* *Brevicirrosyllis* *Clavisyllis* *Dioplosyllis* *Guillermogonita* *Haplosyllides* *Lamellisyllis* *Miscellania* *Murrindisyllis* *Neopetitia* *Nooralia* *Palposyllis* *Paraehlersia* *Psammosyllis* *Perkinsyllis* *Streptodonta* *Westheidesyllis*

bright, hyaline granules, in some genera. Pharynx straight, relatively short, unarmed. Antennae, tentacular cirri, and anterior dorsal cirri smooth; remaining dorsal cirri smooth or annulated, with articles strongly marked by constrictions. Ventral cirri present, elongated from midbody to posteriorly, medially inserted in posterior parapodia. Compound heterogomph chaetae, and dorsal and ventral simple chaetae on some or all parapodia. Reproduction by epigamy.

The subfamily consists of 5 genera and about 44 species.

Anoplosyllis Claparède, 1868

Anoplosyllis Claparède, 1868: 214.

Type species: *Anoplosyllis edentula* Claparède, 1868.

Diagnosis: Body small (<5 mm in length), with up to 30 chaetigers. Pharyngeal tube shorter than proventricle. Antennae, tentacular cirri, and dorsal cirri all smooth, club shaped, tapered basally, longer than parapodial lobes. One species broods eggs in gelatinous masses. Cosmopolitan; 2 species (Fig. 7.13.2.23A).

Astreptosyllis Kudenov & Dorsey, 1982

Astreptosyllis Kudenov & Dorsey, 1982: 575.

Type species: *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982.

Diagnosis: Antennae, tentacular cirri, and dorsal cirri of two anterior chaetigers not annulated, club shaped, slender basally and distally slightly inflated, longer than body width; from chaetiger 3 onward, dorsal cirri annulated, articles elongated to pyriform, with dark, glandular inclusions. Dorsal simple chaetae thick, provided with distal, longitudinally striated hood. Reproduction unknown. Only known from Australia; 2 species (Fig. 7.13.2.23B).

Streptosyllis Webster & Benedict, 1884

Streptosyllis Webster & Benedict, 1884: 711.

Type species: *Streptosyllis arenae* Webster & Benedict, 1884.

Diagnosis: Dorsal cirri smooth or indistinctly annulated, club shaped to elongated, sometimes with glandular inclusions. Compound chaetae include homogomph to hemigomph forms, with blades falcigerous. Aciculae in some anterior parapodia distinctly enlarged (Fig. 7.13.2.9G). Cosmopolitan; 17 species (Figs. 7.13.2.23C and 7.13.2.24A–D).

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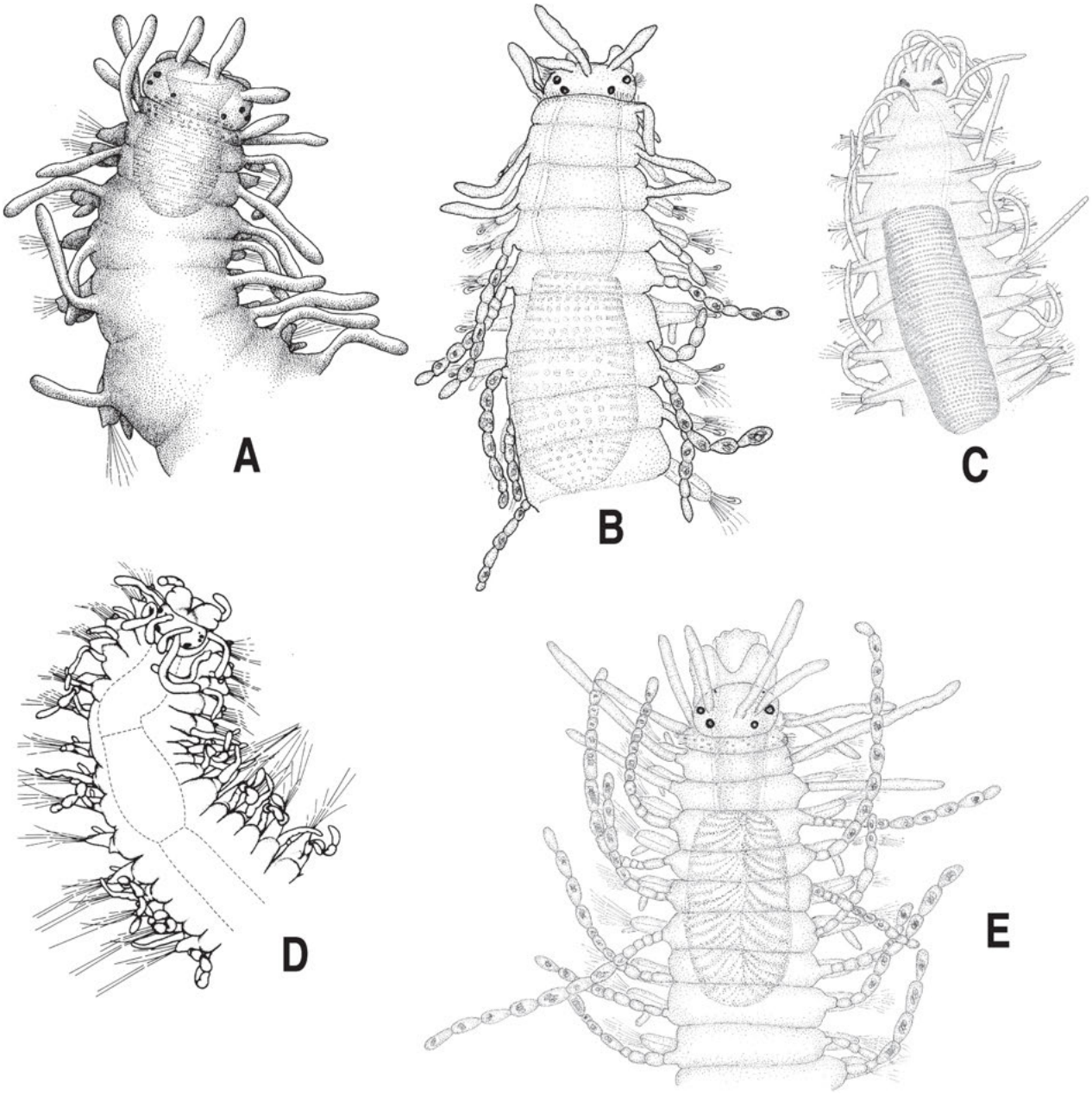


Fig. 7.13.2.23: Anterior ends of species of the five genera of the Anoplosyllinae. A, *Anoplosyllis edentula* Claparède, 1868. B, *Astreptosyllis similiseta* Hartmann-Schröder, 1986. C, *Streptosyllis arenae* Webster & Benedict, 1884. D, *Streptospinigera alternocirrus* Ohwada, 1988. E, *Syllides tam* San Martín & Hutchings, 2006. A, after San Martín (2003); B, E, after San Martín and Hutchings (2006); D, after Ohwada (1988). A, San Martín's original drawing modified by Jordi Corbera. B, E, San Martín's original. C, Aguado's original drawing.

Two recent papers on this genus are Faulwetter et al. (2008), which also includes some comments about the related genera, and Musk et al. (2016), which includes an amendment to the diagnosis of the genus.

Streptospinigera Kudenov, 1983

Streptospinigera Kudenov, 1983: 84–85.

Type species: *Streptospinigera heteroseta* Kudenov, 1983.

Diagnosis: Antennae, tentacular cirri, and anterior dorsal cirri smooth, club shaped, smooth, and elongated in midbody and abruptly becoming strongly annulated on posterior parapodia in some species. Compound chaetae include falcigerous and spinigerous forms. Blades of falcigers thick on anterior parapodia, abruptly becoming slender thereafter. Spiniger-like chaetae present from midbody backward, with slender shafts. Dorsal simple

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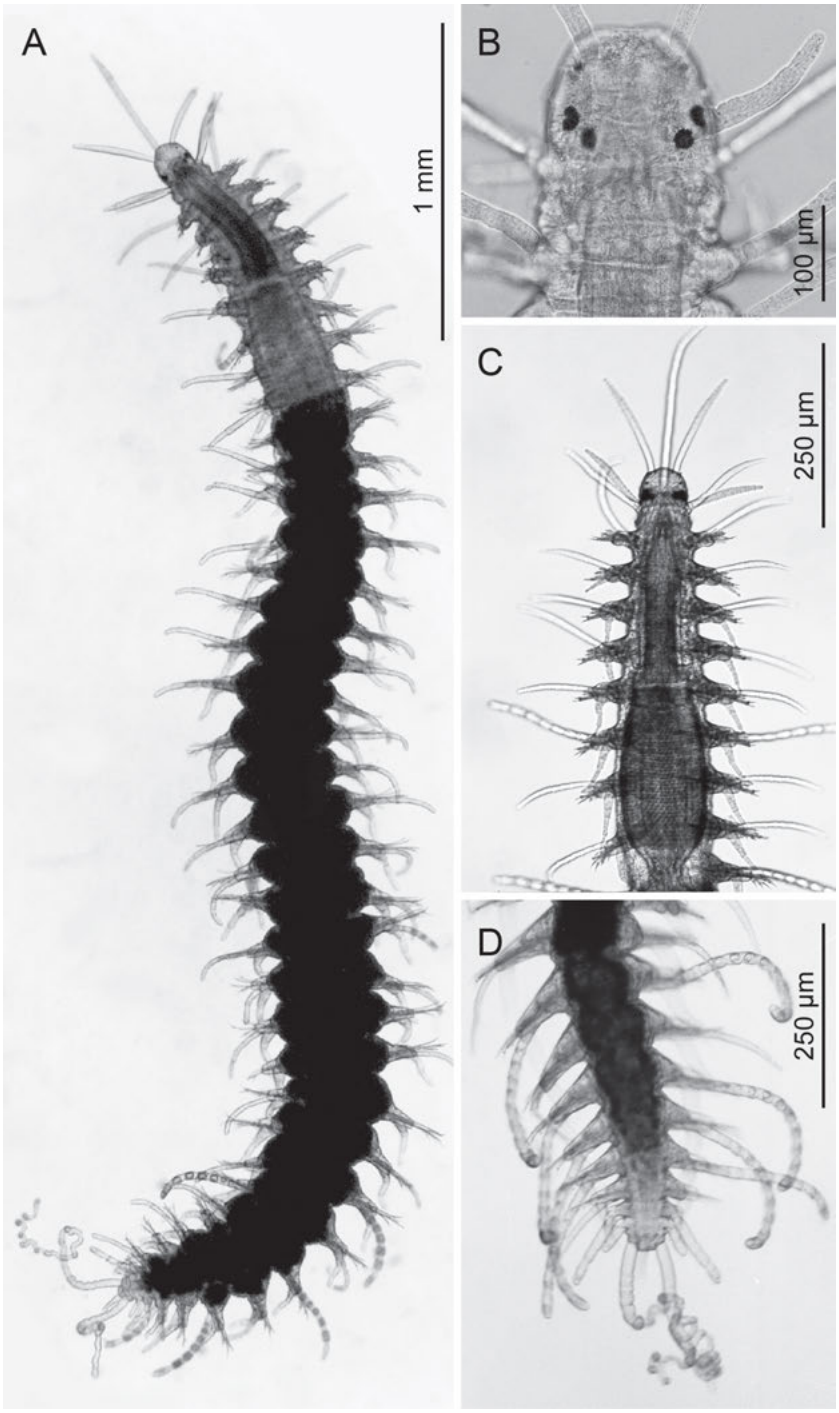


Fig. 7.13.2.24: *Streptosyllis*. Micrographs from living specimens. A, B, *S. websteri* Southern, 1914. Sylt, North Sea. A, entire animal. B, Anterior end showing the three pairs of pigmented eyes. C, D, *Streptosyllis aequiseta* Hartmann-Schröder, 1981. Seychelles. C, Anterior region, pharyngeal tube unarmed, long, barrel-shaped proventricle. D, posterior end. Originals A G. Purschke, B K. Psathaki, C, D W. Westheide, Osnabrück.

chaetae present from anterior parapodia, distally falcate, thick on anterior parapodia, abruptly becoming slender, capillary. Aciculae distally break shaped to truncate, some anterior ones thicker than the rest. Gulf of México, Japan, Arctic and subarctic, Mediterranean; 4 species (Fig. 7.13.2.23D).

A recent paper on this genus is Olivier et al. (2013).

***Syllides* Örsted, 1845**

Syllides Örsted, 1845a: 408.

Type species: *Syllides longocirrata* Örsted, 1845.

Diagnosis: Antennae, tentacular cirri, and dorsal cirri of chaetigers 1 and 2 not annulated, club shaped to fusiform; dorsal cirri from chaetiger 3 onward, distinctly annulated, with glandular inclusions in some articles. Compound

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chaetae heterogomph with slender blades usually bidentate. Reproduction by epigamy; some species brood eggs ventrally. Cosmopolitan; about 19 species Figure 7.13.2.23E.

Autolytinae Langerhans, 1879

Diagnosis: Body cylindrical, size from medium to large. Palps fused, usually ventrally folded. Three antennae, usually long, extending beyond palps (one genus without antennae); four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri, typically long and slender. Two nuchal lappets (Fig. 7.13.2.7B) (indistinct in some genera). Pharynx slender, usually long and convoluted with trepan (two genera unarmed). Dorsal cirri smooth, sometimes with a distinct cirrophore. Ventral cirri absent. Dorsal simple chaetae bayonet shaped. Reproduction by schizogamy (one genus by epigamy). The subfamily consists of 13 genera and about 109 species.

Nygren (2004) revised the whole subfamily.

***Acritagasyllis* Lucas, San Martín & Sikorski, 2010**

Acritagasyllis Lucas, San Martín & Sikorski, 2010: 252. Modified by Rivolta et al. (2015).

Type species: *Acritagasyllis longichaetosus* Lucas, San Martín & Sikorski, 2010

Diagnosis: Anterior and midbody segments fused in groups of two to three. Prostomium conical, without eyes. Two antennae, median antenna absent. Palps absent. Two spherical nuchal lappets. Single pair of tentacular cirri. Antennae, tentacular cirri, and dorsal cirri smooth. Ventral cirri fused all along their length to parapodial lobes. Pharynx slender, convoluted, opening in a crown of soft papillae and a trepan, with nine large teeth, alternating with 2–3 small teeth. Compound chaetae with long, thin, slender and delicate blades. Dorsal simple chaetae bayonet shaped with filiform tip. Reproduction by anterior scissiparity. Off Norway; only the type species is known (Fig. 7.13.2.25A).

***Epigamia* Nygren, 2004**

Epigamia Nygren, 2004: 163.

Type species: *Autolytus noroi* Imajima & Hartman, 1964.

Diagnosis: Two rows of cilia per segment. Nuchal lappets extending to at least chaetiger 1 and sometimes as far as chaetiger 6. Dorsal cirri commonly alternating in length; cirrophores equal, shorter than or of the same length as parapodial lobes. All appendages cylindrical, with one exception, in which dorsal cirri are flattened on some parapodia. Pharynx with single to multiple sinuations. Trepan with various types of denticulation, in one to three rings. Compound chaetae with bidentate blades. Dorsal bayonet chaetae subdistally denticulated. Reproduction by epigamy. Polar, subpolar, and temperate seas; about nine species (Fig. 7.13.2.25B).

***Erseia* Nygren, Sundkvist, Mikac & Pleijel, 2010**

Erseia Nygren, Sundkvist, Mikac & Pleijel, 2010: 42.

Type species: *Erseia oligochaeta* Nygren, Sundkvist, Mikac & Pleijel, 2010.

Diagnosis: Nuchal lappets extending to anterior part of tentacular segment. All appendages cylindrical. Dorsal bayonet chaetae probably absent. Pharynx with single, small sinuation. Trepan with a single large dorsal tooth and 25–28 small teeth in one ring. Reproduction by schizogamy by anterior scissiparity. Adriatic Sea; only the type species is known.

***Imajimaea* Nygren, 2004**

Imajimaea Nygren, 2004: 105.

Type species: *Autolytus japonensis* Imajima & Hartman, 1964.

Diagnosis: Nuchal lappets extending to the end of tentacular segment or end of chaetiger 1. Dorsal cirri from chaetiger 3 of equal length; cirrophores present on tentacular cirri and first dorsal cirri, otherwise absent. Anterior appendages cylindrical or flask shaped, dorsal cirri cylindrical or ovoid to egg shaped. Compound chaetae with bidentate blades. Pharynx with single to multiple sinuation anterior and lateral to proventricle. Trepan arranged in one ring, with equal teeth, or with two large lateral teeth in combination with irregularly sized and arranged teeth. Compound chaetae with bidentate blades. Pseudosimple chaetae present on chaetigers 1–4, in all chaetigers, or absent; simple chaetae uni- or bidentate, with small distal tooth. Dorsal bayonet chaetae, subdistally denticulated. Reproduction by schizogamy by anterior scissiparity. NE Atlantic, Japan, and Kuwait; 4 species (Fig. 7.13.2.25C).

Interesting paper is Nygren and Pleijel (2010).

***Levidorum* Hartman, 1967**

Levidorum Hartman, 1967: 84.

Type species: *Levidorum scotiarum* Hartman, 1967.

Diagnosis: Ciliation absent on one species, unknown on others. Nuchal lappets absent. Without antennae, tentacular cirri, or dorsal cirri. Pharynx with single sinuation anterior and lateral to proventricle. Trepan with five equal teeth. All chaetae pseudosimple, knob-like. Bayonet chaetae absent. Reproduction by schizogamy, by anterior scissiparity. Mediterranean and Gulf of México; 4 species (Fig. 7.13.2.25D).

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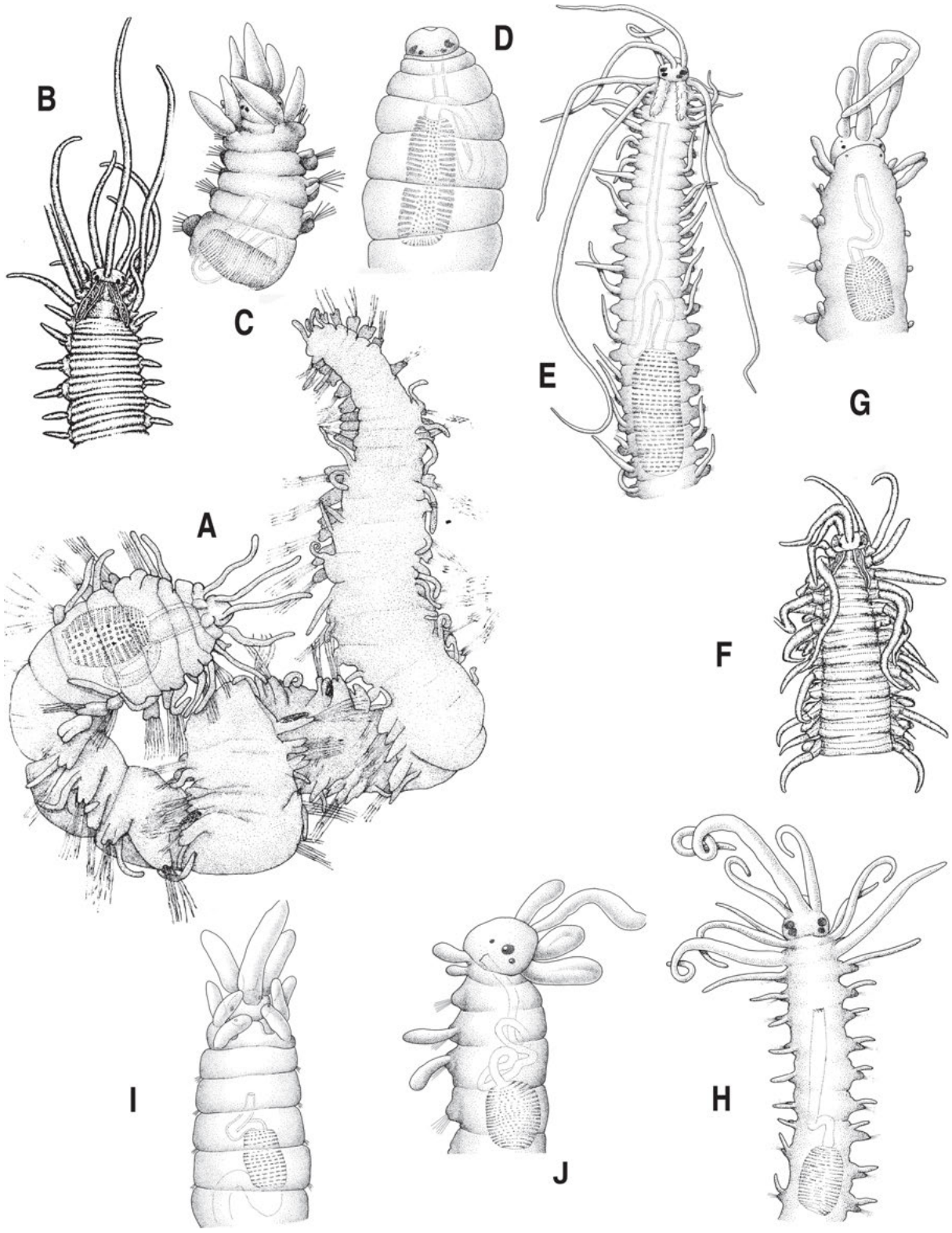


Fig. 7.13.2.25: Anterior ends of species of different genera of the Autolytinae. A, *Acritagasyllis longichaetosus* Lucas, San Martín & Sikorski, 2010. B, *Epigamia noroi* (Imajima & Hartman, 1964). C, *Imajimaea draculai* (San Martín & López, 2002). D, *Levidorum pori* (Ben-Eliahu, 1977). E, *Myrianida longoprimicirrata* (López, San Martín & Jiménez, 1997). F, *Paraproceraea tamana* (Imajima, 1966). G, *Paraprocerastea crocantinae* San Martín & Alós, 1989. H, *Proceraea picta* Ehlers, 1864. I, *Procerastea halleziana* Malaquin, 1893. J, *Virchowia clavata* Langerhans, 1879. A, after Lucas et al. (2010); B, after Imajima (1966b); C–D, F, after Imajima (1966); G–J, after San Martín (2003). A, C, D, E, G, H, I, J, San Martín's original drawing modified by Jordi Corbera; H, Sardà's original drawing modified by Jordi Corbera; I, Alós original drawing modified by Jordi Corbera.

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Perkins (1987) considered this genus as belonging to a different family (Levidoridae), and described two new species.

Myrianida Milne Edwards, 1845

Myrianida Milne Edwards, 1845: 180.
Podonereis Blainville, 1818
Autolytus Grube, 1850
Diploceraea Grube, 1850
Sacconereis J. Müller, 1853
Crithida Gosse, 1855
Sylline Grube, 1860
Monocerina Costa, 1861
Eucerastes Quatrefages, 1865
Autolytides Malaquin, 1893
Type species: *Myrianida fasciata* Milne Edwards, 1845.
Diagnosis: One or two rows of cilia per segment. Nuchal lappets extending to end of peristomium or as far as end of chaetiger 12. Cirri (cirrophores plus cirrostyles) may be equal in length or alternating. Appendages cylindrical or thick and swollen, slightly flattened or flattened. Pharynx with single to multiple sinuations. Trepan with various types of denticulation, in one ring. Compound chaetae with bidentate blades (Fig. 7.13.2.9M). Dorsal bayonet chaetae thin, subdistally denticulate (Fig. 7.13.2.9N). Reproduction by schizogamy, gemmiparous, or scissiparous (Figs. 7.13.2.2B and 7.13.2.21). Cosmopolitan; about 42 species (Fig. 7.13.2.25E).

Recent papers on this genus are Álvarez-Campos et al. (2014b), Çinar (2015), and Aguirre et al. (2015).

Pachyprocerastea Nygren, 2004

Pachyprocerastea Nygren, 2004: 100.
Type species: *Procerastea hydrozoicola* Hartmann-Schröder, 1992.
Diagnosis: Only anterior half of body annulated. Nuchal lappets short, extending over anterior part of peristomium. Cirrophores only present on tentacular cirri and first dorsal cirri. All appendages cylindrical. Pharynx with sinuation anterior to proventricle. Details of trepan unknown. Compound chaetae on ventral position and some pseudosimple chaetae on parapodia, with small, diffuse denticulation along "fusion line." Dorsal bayonet chaetae, thick, distally denticulate. Reproduction by schizogamy, by anterior scissiparity. New Caledonia; only the type species is known, associated on calcified hydrocorals and hydrozoans.

Paraproceraea Nygren, 2004

Paraproceraea Nygren, 2004: 104.
Type species: *Autolytus (Autolytus) tamanus* Imajima, 1966.
Diagnosis: Anterior segments triannulated in appearance. Nuchal lappets extend to half way along chaetiger 3. All appendages cylindrical. Pharynx with sinuation anterior and lateral to anterior half of proventricle. Trepan with 90 small subequal teeth. Compound chaetae with bidentate blades. Dorsal bayonet chaetae subdistally denticulate. Reproduction unknown. Japan; only the type species is known (Fig. 7.13.2.25F).

Paraprocerastea San Martín & Alós, 1989

Paraprocerastea San Martín & Alós, 1989: 872.
Type species: *Paraprocerastea crocantinae* San Martín & Alós, 1989.
Diagnosis: Ciliation unknown. Nuchal lappets unknown. Antennae, tentacular cirri, and dorsal cirri of first chaetiger, moderately long, more or less club shaped; remaining dorsal cirri small, egg shaped. All chaetae pseudosimple, with fine denticulation present along "fusion line" on some, bidentate with small distal tooth. Bayonet chaetae thick, distally denticulated. Pharynx with single minute sinuation anterior to proventricle. Trepan arranged in one ring, with 19–23 equal teeth. Reproduction unknown. Mediterranean coast of Spain; only the type species is known (Fig. 7.13.2.25G).

Planicirrata Nygren, 2004

Planicirrata Nygren, 2004: 102.
Type species: *Myrianida proceraeae* Hartmann-Schröder & Rosenfeldt, 1990.
Diagnosis: Nuchal lappets reaching end of tentacular segment. Dorsal cirri lanceolate, flattened. Pharynx with three sinuations. Trepan with about 30 small, equal teeth. Compound chaetae with bidentate blades, small distal tooth. Dorsal bayonet chaetae thick, distally expanded. Reproduction by schizogamy, by anterior scissiparity. Antarctica; only the type species known.

Proceraea Ehlers, 1864

Proceraea Ehlers, 1864: 256.
Amytis Savigny, 1822
Polynice Savigny, 1822
Nereisyllis Blainville, 1828
Polybostrichus Örsted, 1843
Stephanosyllis Claparède, 1864
Pteroautolytus Ehlers, 1907
Regulatus Imajima, 1966
Type species: *Proceraea picta* Ehlers, 1864
Diagnosis: Color pattern often characteristic of species. Ciliation only present on prostomium, nuchal lappets, and ventrally on a few segments. Nuchal lappets extend to from half way along persitomium to the end of chaetiger 2. Cirrophores present only on tentacular cirri and first

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dorsal cirri. Anterior appendages cylindrical, dorsal cirri cylindrical, or ovoid to egg shaped. Pharynx with single to multiple sinuations. Trepan arranged in two rings, either one large tooth alternating with one small or one large alternating with two small or two large alternating with one small or one large alternating with two to four small (Fig. 7.13.2.14D). Number of teeth 18, 24, 27, or 34–44. Compound chaetae with bidentate blades. Dorsal bayonet chaetae thick, distally denticulated (thin, subdistally denticulated in one species) (Fig. 7.13.2.9O). Reproduction schizogamy, by anterior scissiparity. Cosmopolitan; about 33 species (Figs. 7.13.2 and 7.13.2.25H).

Recent papers on this genus are Martin et al. (2014, 2017).

Procerastea Langerhans, 1884

Procerastea Langerhans, 1884: 249.

Type species: *Procerastea nematodes* Langerhans, 1884.

Diagnosis: Nuchal lappets extending at most to end of peristomium. Dorsal cirri only present on first chaetiger; appendages club shaped or cylindrical. Pharynx with single small sinuation, or with one to several sinuations, anterior to proventricle. Trepan arranged in one ring, with 6–30 equal teeth. Compound chaetae present from chaetiger 1, chaetiger 2, or absent. Pseudosimple chaetae present on chaetigers 1–4, or in all chaetigers. Both simple and compound chaetae uni- or bidentate, with small distal tooth. Bayonet chaetae thick, distally expanded and denticulate. Reproduction by schizogamy by anterior scissiparity. Cosmopolitan; 5 species (Fig. 7.13.2.25I).

Virchowia Langerhans, 1879

Virchowia Langerhans, 1879: 582.

Autosyllis Imajima & Hartman, 1964

Type species: *Virchowia clavata* Langerhans, 1879.

Diagnosis: Ciliation present on prostomium. Nuchal lappets extending to between end of chaetiger 1 and end of chaetiger 3. Cirri (cirrophores and cirrostyles) alternate in length and shape. Appendages cylindrical or club shaped. Pharynx with single to multiple sinuations anterior and lateral to proventricle. Trepan arranged in a single ring, with equal or unequal teeth. Compound chaetae with small distal tooth, sometimes minute; blade serration absent or present; in one species, blades and shafts fused forming pseudosimple chaetae. Dorsal bayonet chaetae thick, distally expanded with distal denticulation. Reproduction by schizogamy, by anterior scissiparity. Cosmopolitan; 6 species (Fig. 7.13.2.25J).

Exogoninae Langerhans, 1879

Diagnosis: Body cylindrical, size from minute to small. Palps fused along their entire length or at least to half length. Three antennae, usually short (one species, *Exogone acerata* San Martín & Parapar, 1990, lacking antennae). Four lensed eyes and sometimes two anterior eyespots (a few genera with only two eyes). One or two pairs of tentacular cirri, typically short. Nuchal organs in two dorsolateral, densely ciliated grooves between prostomium and peristomium. Pharynx straight, with a middorsal, anterior tooth, sometimes far from anterior margin. Dorsal cirri typically short to papilliform, smooth. Reproduction by epigamy and brooding of eggs, some genera brood dorsally by means of capillary notochaetae (Fig. 7.13.2.17B–E), other genera brood ventrally, attaching eggs and juveniles on to the nephridial pore (Figs. 7.13.2.17F–I and 7.13.2.18A, B).

The subfamily consists of 9 genera and about 210 species.

Some papers on the whole subfamily are Nogueira et al. (2001, 2004), Ruiz-Ramírez and Salazar-Vallejo (2001), San Martín (2005), Ding and Westheide (2008), Abd-Elnaby (2010), and Soto and San Martín (2017b).

Brania Quatrefages, 1866

Brania Quatrefages, 1866: 18.

Type species: *Exogone pusilla* Dujardin, 1851.

Diagnosis: Palps fused basally for about 2/3 of their length, with the remaining distal 1/3 free. Two pairs of tentacular cirri and dorsal cirri on all parapodia, appendages bottle shaped, truncated or bowling-pin shaped. Parapodial glands present, sometimes inside dorsal cirri. Pharynx with an anterior tooth. Compound chaetae with unidentate blades with subdistal spines and rounded tips; aciculae with rounded, slightly hollow tips. Dorsal simple chaetae usually subdistally serrated. Ventral simple chaetae sigmoid, usually unidentate. Ventral brooding. Cosmopolitan in temperate and tropical waters; 9 species. Several species described as *Brania* belong in fact to *Salvatoria* (Fig. 7.13.2.26A).

Cicese Díaz-Castañeda & San Martín, 2001

Cicese Díaz-Castañeda & San Martín, 2001: 712–714.

Type species: *Cicese sphaerosylliformis* Díaz-Castañeda & San Martín, 2001.

Diagnosis: Body covered with papillae, usually small, short, scarce, sometimes also distributed on cirri and parapodia. Peristomium large, covering posterior margin of prostomium, forming two dorsolateral wings covering nuchal organs; two pairs of tentacular cirri. Dorsal cirri present on chaetiger 2. Antennae, tentacular cirri, and dorsal cirri spindle shaped to pyriform, with bulbous bases and slender tips. Middorsal pharyngeal tooth small, located near anterior margin, surrounded by a crown of papillae around opening. Compound chaetae

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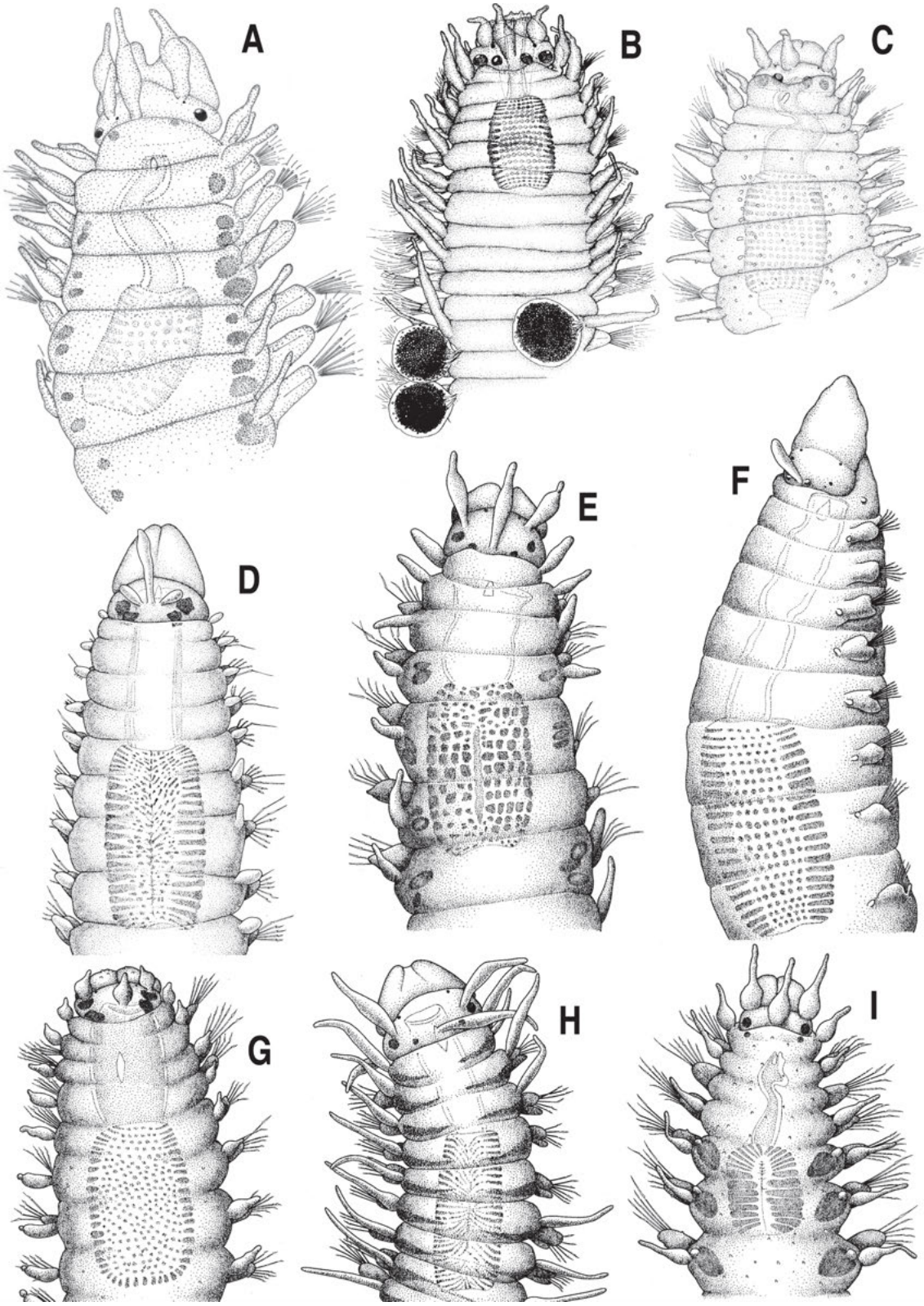


Fig. 7.13.2.26: Anterior ends of species of the 9 genera of Exogoninae. A, *Brania furcelligera* (Augener, 1913). B, *Cicese sphaerosylliformis* Díaz-Castañeda & San Martín, 2001. C, *Exogone dispar* (Webster, 1879). D, *Erinaceusyllis bidentata* (Hartmann-Schröder, 1974). E, *Parapionosyllis brevicirra* Day, 1954. F, *Parexogone hebes* (Webster & Benedict, 1884). G, *Prosphaerosyllis xarifae* (Hartmann-Schröder, 1960). H, *Salvatoria vieitezi* (San Martín, 1984). I, *Sphaerosyllis hystrix* Claparède, 1863. A, C: after San Martín (2005); B: after Díaz-Castañeda and San Martín (2001); D, E–I: after San Martín (2003). A–C, San Martín's original drawings; D–I, San Martín's original drawing modified by Jordi Corbera.

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heterogomph, with bidentate blades of differing sizes; capillary dorsal and ventral simple chaetae present. Proventricle long and wide, barrel shaped, with numerous, slender muscle cell rows (15–22). Dorsal brooding. México (Pacific coast); only the type species is known (Fig. 7.13.2.26B).

***Erinaceusyllis* San Martín, 2005**

Erinaceusyllis San Martín, 2005: 73.

Type species: *Sphaerosyllis erinaceus* Claparède, 1863.

Diagnosis: Body covered with papillae, usually small, short, scarce, sometimes also distributed on cirri and parapodia. Peristomium usually large, covering posterior margin of prostomium, sometimes forming two dorsolateral wings covering nuchal organs; single pair of tentacular cirri. Dorsal cirri present or absent on chaetiger 2. Antennae, tentacular cirri, and dorsal cirri spindle shaped to pyriform, with slightly bulbous bases and short to moderately long tips. Pharyngeal tooth small, conical to rhomboidal, located near anterior margin, sometimes near middle of pharynx; pharynx usually without papillae around opening, but papillae present on larger species. Proventricle long and wide, barrel shaped, with numerous, slender muscle cell rows (15–22). Compound chaetae heterogomph, with blades long or short, sometimes long and slender, bidentate, bidentate, and/or unidentate. Dorsal brooding. Cosmopolitan; about 16 species (Figs. 7.13.2.26C and 7.13.2.27A).

***Exogone* Oersted, 1845**

Exogone Oersted, 1845b: 20
Cystonereis Kölliker in Koch, 1846
Exogona Dujardin, 1851
Microsyllis Claparède, 1863
Exotokas Ehlers, 1864

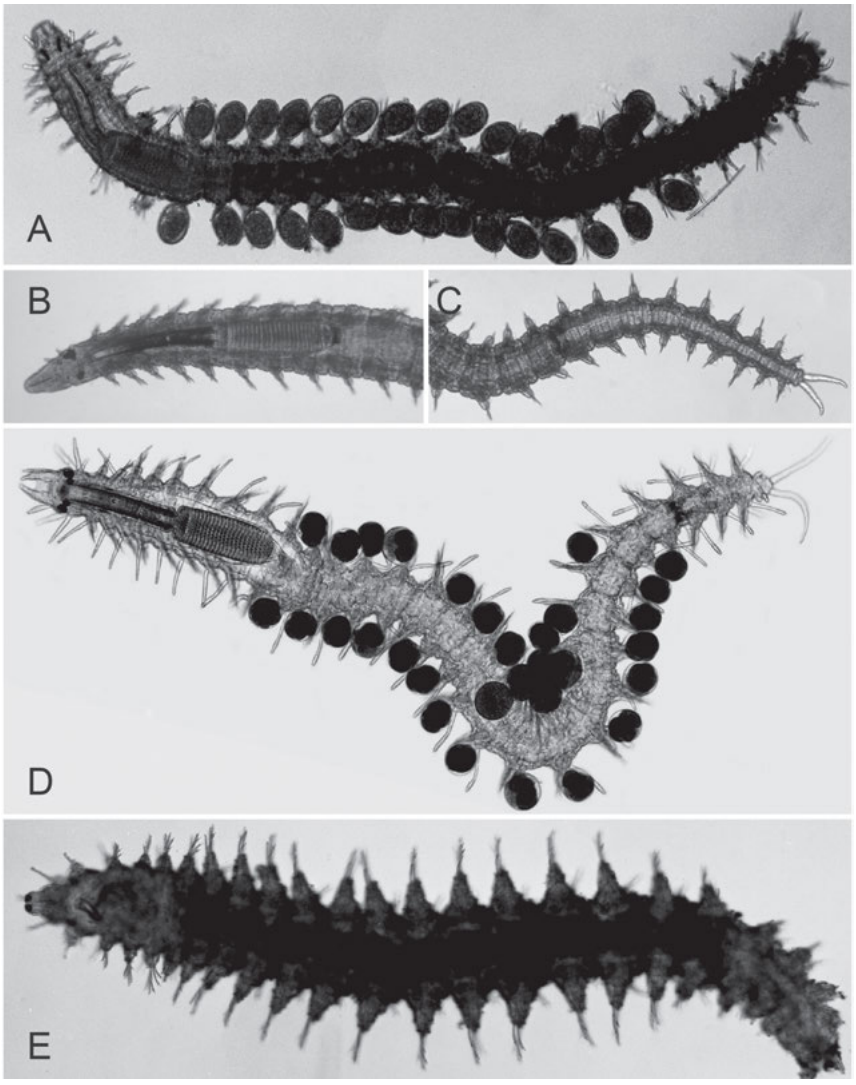


Fig. 7.13.2.27: Light micrographs of 4 species of Exogoninae. A, *Erinaceusyllis* sp., Toliara, West Coast of Madagascar, brooding female, length about 2.5 mm. B, C, *Parexogone seychellensis* Böggemann & Westheide, 2004. B, Anterior end; C, posterior end; D, *Salvatoria* cf. *opisthodentata* (Hartmann-Schröder, 1979) brooding female; E, *Sphaerosyllis capensis* Day, 1953. Mahé, Seychelles, length about 2 mm. Originals W. Westheide, Osnabrück.

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Oophylax Ehlers, 1864
Spermosyllis Claparède, 1864
Sylline Claparède, 1864
Gossia Quatrefages, 1865
Syllia Quatrefages, 1865
Schmardia Quatrefages, 1866
Paedophylax Claparède, 1868
Paedophyllax Claparède, 1868
Exogonita Hartman & Fauchald, 1971
Type species: *Exogone naidina* Oersted, 1845.
Diagnosis: Body surface smooth. Palps well developed, completely fused to each other or with terminal notch. One pair of tentacular cirri. Dorsal cirri usually small, papilliform to oval, present on all segments or absent on chaetiger 2. Pharynx with anterior tooth and with anterior margin surrounded by soft lobes. Compound chaetae and dorsal and ventral simple chaetae usually present; blades sometimes fused to shafts or absent, forming pseudosimple chaetae; typically, one to two spiniger-like chaetae (Fig. 7.13.2.9J) and several short falcigers, with proximal tooth larger than distal (Fig. 7.13.2.9K), on each parapodium. Ventral brooding. Cosmopolitan; about 44 species (Fig. 7.13.2.26D).

Papers on this genus are Pascual et al. (1996), San Martín et al. (1996), Paresque et al. (2014), Fukuda and Nogueira (2014), Fukuda et al. (2019), and Nascimento et al. (2020).

Parapionosyllis Fauvel, 1923

Parapionosyllis Fauvel, 1923a: 289.
Type species: *Pionosyllis gestans* Pierantoni, 1903.
Diagnosis: Body surface smooth. Palps partially fused with distal half or 1/3 separated. One pair of tentacular cirri, bottle or bowling-pin shaped, located lateroventrally. Dorsal cirri present on all parapodia, short, bowling-pin shaped. Parapodial glands present. Pharynx with an anterior tooth, surrounded by soft papillae. Compound chaetae with unidentate blades with a subdistal spine and rounded tips; aciculae with rounded, slightly hollowed tips. Dorsal simple chaetae usually subdistally serrated. Ventral simple chaetae sigmoid, usually unidentate. Ventral brooding. Temperate and tropical waters; 20 species (Fig. 7.13.2.26E).

An interesting paper on this genus is Riera et al. (2006).

Parexogone Mesnil & Caullery, 1918

Parexogone Mesnil & Caullery, 1918: 125.
Spermosyllis Claparède, 1864
Exogonella Hartman, 1961
Type species: *Paedophylax hebes* Webster & Benedict, 1884.
Diagnosis: Body surface smooth. Palps well developed, completely fused to each other or with terminal notch. One pair of tentacular cirri. Dorsal cirri papilliform to oval, present or absent on chaetiger 2. Pharynx with anterior tooth, anterior margin surrounded by soft lobes. Compound chaetae with heterogomph articulations, falcigers all similar in shape and blade length, sometimes pseudospinigers (elongate falcigers) with shaft tips simple, blades relatively similar to falcigers but longer. Dorsal simple chaetae similar throughout body, tips unidentate or bidentate, the latter with both teeth similar. Ventral simple chaetae on posterior parapodia. Ventral brooding; some species viviparous. Cosmopolitan; about 20 species (Figs. 7.13.2.26F and 7.13.2.27B, C).

Prosphaerosyllis San Martín, 1984

Sphaerosyllis (Prosphaerosyllis) San Martín, 1984c: 377.
Type species: *Sphaerosyllis xarifae* Hartmann-Schröder, 1960.
Diagnosis: Body with dorsal and ventral papillae, also present on cirri and parapodia, usually covered by detritus; sometimes, some dorsal or ventral papillae long (macropapillae). Palps fused along their length, short, slightly ventrally folded, with small papillae. Prostomium usually partially covered dorsally by peristomium, some species with prostomium retractable within peristomium. One pair of tentacular cirri, located ventrolaterally. Antennae, tentacular cirri, and dorsal cirri short, pyriform to bulbous, with spherical bases and short tips that are usually retractile into their bases, especially in midbody and posterior parapodia; tips sometimes papilliform and short. Dorsal cirri present on all parapodia. Parapodial glands absent. Pharynx long and wide, usually without papillae around opening; pharyngeal tooth romboidal to oval, located behind anterior margin of pharynx, sometimes midway along pharynx. Proventricle long and wide, similar in size to pharynx, with numerous, slender muscle cell rows. Compound chaetae heterogomph with short, unidentate falcate blades; dorsal and ventral simple, capillary, unidentate chaetae on some parapodia. Acicula usually single, acuminate, sometimes slightly modified. Dorsal brooding. Cosmopolitan; about 30 species (Fig. 7.13.2.26G).

Recent papers dealing with this genus are Olivier et al. (2012) and Faulwetter et al. (2011a).

Salvatoria McIntosh, 1885

Salvatoria McIntosh, 1885: 188.
Grubea Quatrefages, 1866
Protogrubea Czerniavsky, 1881a
Grubeosyllis Verrill, 1900

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Brania in part Fauvel 1923; in part Kudenov & Harris, 1995; not Quatrefages 1866
Pseudobrania San Martín, 1984a
Type species: *Salvatoria kerguelensis* McIntosh, 1885.
Diagnosis: Body surface smooth. Palps well developed, joined along their length by dorsal membrane, more or less distinct. Two pairs of tentacular cirri. Antennae, tentacular cirri, and dorsal cirri usually spindle shaped, proportionally long and slender in comparison with those of other genera of the subfamily, usually slightly bulbous at their base and ending with an elongate, acute tip; dorsal cirri on all segments or absent on chaetiger 2. Parapodial glands absent. Pharynx wide, usually without papillae around the opening, although some larger species have crown of small papillae; pharyngeal tooth typically romboidal to ovate, located anywhere from near anterior margin to about midway along pharynx. Proventricle proportionally long and wide, massive, with numerous, slender muscular rows. Compound chaetae heterogomph, with blades bidentate, subdistal tooth sometimes small, appearing as unidentate; some parapodia with dorsal and ventral simple capillary chaetae. Acicula usually single, acuminate with long, filiform tip; without point in some species, appearing distally rounded. Dorsal brooding. Cosmopolitan; about 32 species (Figs. 7.13.2.12B, 7.13.2.13A, B, 7.13.2.26H, and 7.13.2.27D).

Sphaerosyllis Claparède, 1863

Sphaerosyllis Claparède, 1863: 45.
Type species: *Sphaerosyllis hystrix* Claparède, 1863.
Diagnosis: Body with dorsal and ventral papillae, sometimes extending to cirri and parapodia. Prostomium without eyespots, usually partially covered dorsally by peristomium. Palps fused along their entire length. One pair of tentacular cirri, located lateroventrally, directed anteriorly. Antennae, tentacular cirri, and dorsal cirri short, pyriform to bulbous or flask shaped, with spherical bases and short, slender tips; dorsal cirri absent on chaetiger 2. Pharynx slender, provided with small, soft papillae around opening; pharyngeal tooth conical, on anterior margin. Proventricle usually short, with few (12–20/23) large muscle cell rows. Parapodial glands usually present and distinct, with fibrillar, hyaline, or granular material. Compound, heterogomph chaetae with short, unidentate blades; dorsal and ventral simple, unidentate chaetae on some parapodia. Aciculae usually single, thick, distally bent at right angle; sometimes with another straight, slender acicula in anterior parapodia. Ventral brooding. Cosmopolitan; about 38 species (Figs. 7.13.2.26I and 7.13.2.27E).

Recent papers on this genus are Musco et al. (2005), Núñez et al. (2009), Faulwetter et al. (2011b), del Pilar-Ruso and San Martín (2012), and Surugiu and San Martín (2017).

Syllinae Grube, 1850

Diagnosis: Body cylindrical or dorsoventrally flattened, size from small to large or very large. Palps basally fused or free (one genus, *Karroonsyllis*, with palps fused almost for their entire length). Nuchal organs in two dorsolateral, densely ciliated grooves between prostomium and peristomium (one genus with nuchal lappets, *Nuchalosyllis* Rullier & Amoureux, 1979). Three antennae, usually long, extending beyond palps. Four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri, typically long and slender (*Karroonsyllis* with single pair). Dorsal cirri typically long, annulated (*Eurysyllis* and *Plakosyllis* with short dorsal cirri formed by a single article). Pharynx straight, typically with a middorsal, anterior tooth (some genera with unarmed pharynx, *Inermosyllis*, *Xenosyllis*). Reproduction by scissiparous or rarely, gemmiparous schizogamy (Figs. 7.13.2.4, 7.13.2.15, 7.13.2.18E, F, .11.6.29B, C, E, and 7.13.2.33C–E, 7).

The subfamily comprises 24 genera and about 395 species.

Alcyonosyllis Glasby & Watson, 2001

Alcyonosyllis Glasby & Watson, 2001: 44–45.
Type species: *Alcyonosyllis phili* Glasby & Watson, 2001.
Diagnosis: Palps basally fused. Antennae, tentacular cirri, anal cirri, and dorsal cirri smooth. Pharynx with middorsal tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae. Chaetae all simple, with two to three hooked chaetae with subdistal boss, per parapodium; capillary dorsal and ventral simple chaetae absent. Only known from the tropical Indo-Pacific, associated with octocorals; about 8 species (Figs. 7.13.2.28A and 7.13.2.29A–C).

Recent papers on this genus are San Martín and Nishi (2003), Glasby and Aguado (2009), Álvarez-Campos et al. (2013), and Aguado and Glasby (2015).

Branchiosyllis Ehlers, 1887

Branchiosyllis Ehlers, 1887: 148.
Type species: *Branchiosyllis oculata* Ehlers, 1887.
Diagnosis: Body cylindrical, dorsoventrally flattened, or laterally compressed. Palps basally fused. Antennae, tentacular cirri, anal cirri, and dorsal cirri distinctly annulated. Parapodia with branchiae or digitiform lobes in some species. Pharynx with an anterior tooth, surrounded by crown of about 10 soft papillae. Compound chaetae falcigers; blades of some or all chaetae rotated

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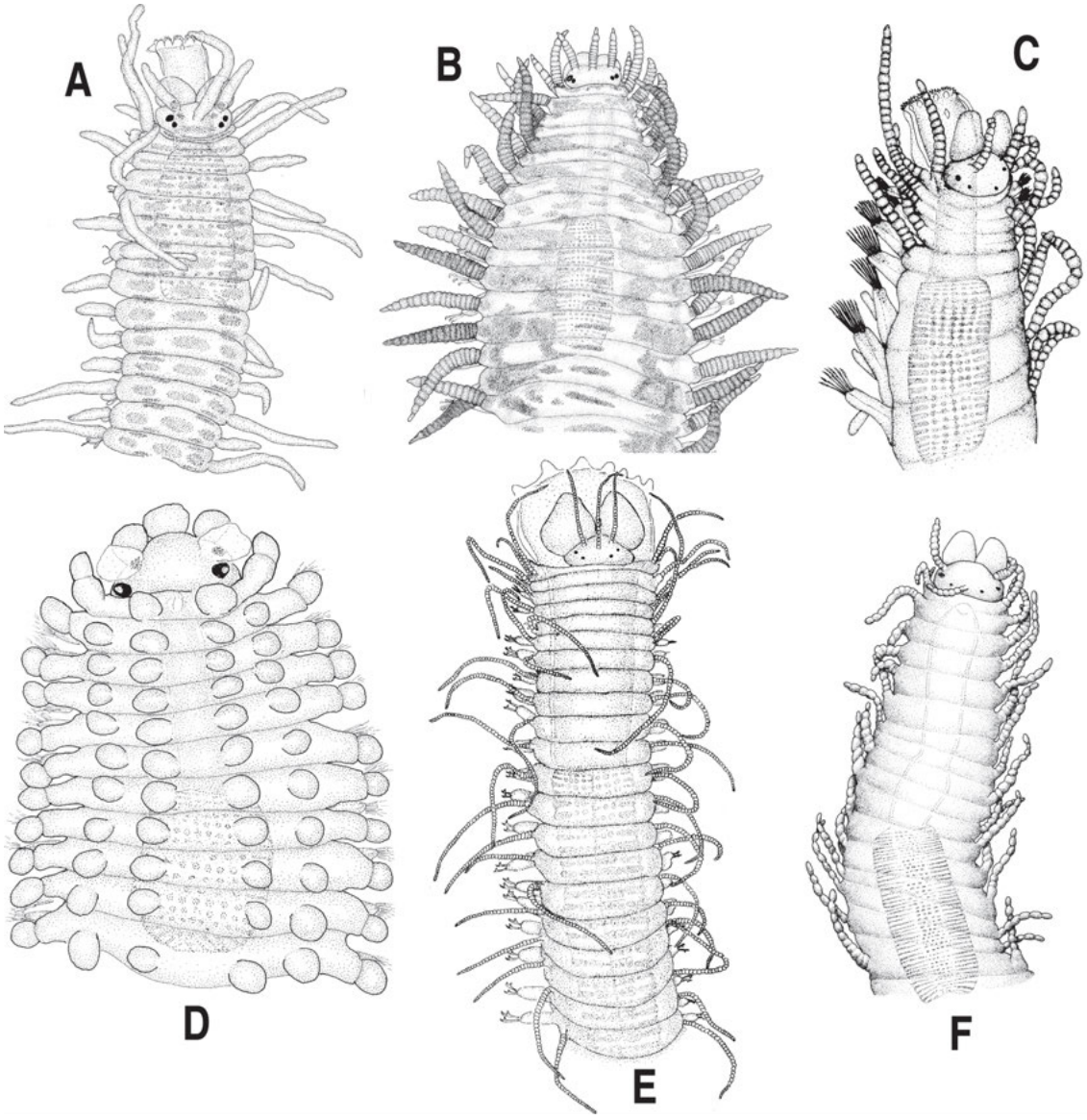


Fig. 7.13.2.28: Anterior ends of species of 6 genera of the Syllinae. A, *Alcyonosyllis glasbyi* San Martín & Nishi, 2003. B, *Branchiosyllis baringabooreen* San Martín, Hutchings & Aguado, 2008. C, *Dentatisyllis morrocoyensis* San Martín & Bone, 1999. D, *Eurysyllis tuberculata* Ehlers, 1864. E, *Haplosyllis spongicola* (Grube, 1855). F, *Inermosyllis balearica* (San Marín, 1982). A, After San Martín and Nishi (2003); B, D, after San Martín et al. (2008b); C, after San Martín and Bone (1999); E, after Lattig et al. (2007); F, after San Martín (2003). A–E, San Martín's original drawings; F, San Martín's original drawing modified by Jordi Corbera.

180°, claw shaped (ungulae). Capillary simple chaetae absent. Acerous stolons. Circumtropical; 29 species (Figs. 7.13.2.28B and 7.13.2.29D, E).

Several recent papers increased the knowledge of this genus all around the world, as Ruiz-Ramírez and Harris (2008), Góngora-Garza et al. (2011), Álvarez-Campos et al. (2012), San Martín et al. (2013), Paresque et al. (2016a), Lucas et al. (2017a), and Nascimento et al. (2019).

Dentatisyllis Perkins, 1981

Dentatisyllis Perkins, 1981: 1166.

Type species: *Syllis carolinae* Day, 1973.

Diagnosis: Palps basally fused. Antennae, tentacular cirri, anal cirri, and dorsal cirri distinctly annulated. Pharynx with middorsal tooth, located on anterior rim; anterior margin of pharynx with crown of soft papillae and a trepan. Compound chaetae with falcigerous blades, spiniger-like blades present in some species; capillary dorsal and ventral simple chaetae present. Circumtropical; 9 species (Fig. 7.13.2.28C).

Some additional papers are Ding et al. (1998) and San Martín and Bone (1999).

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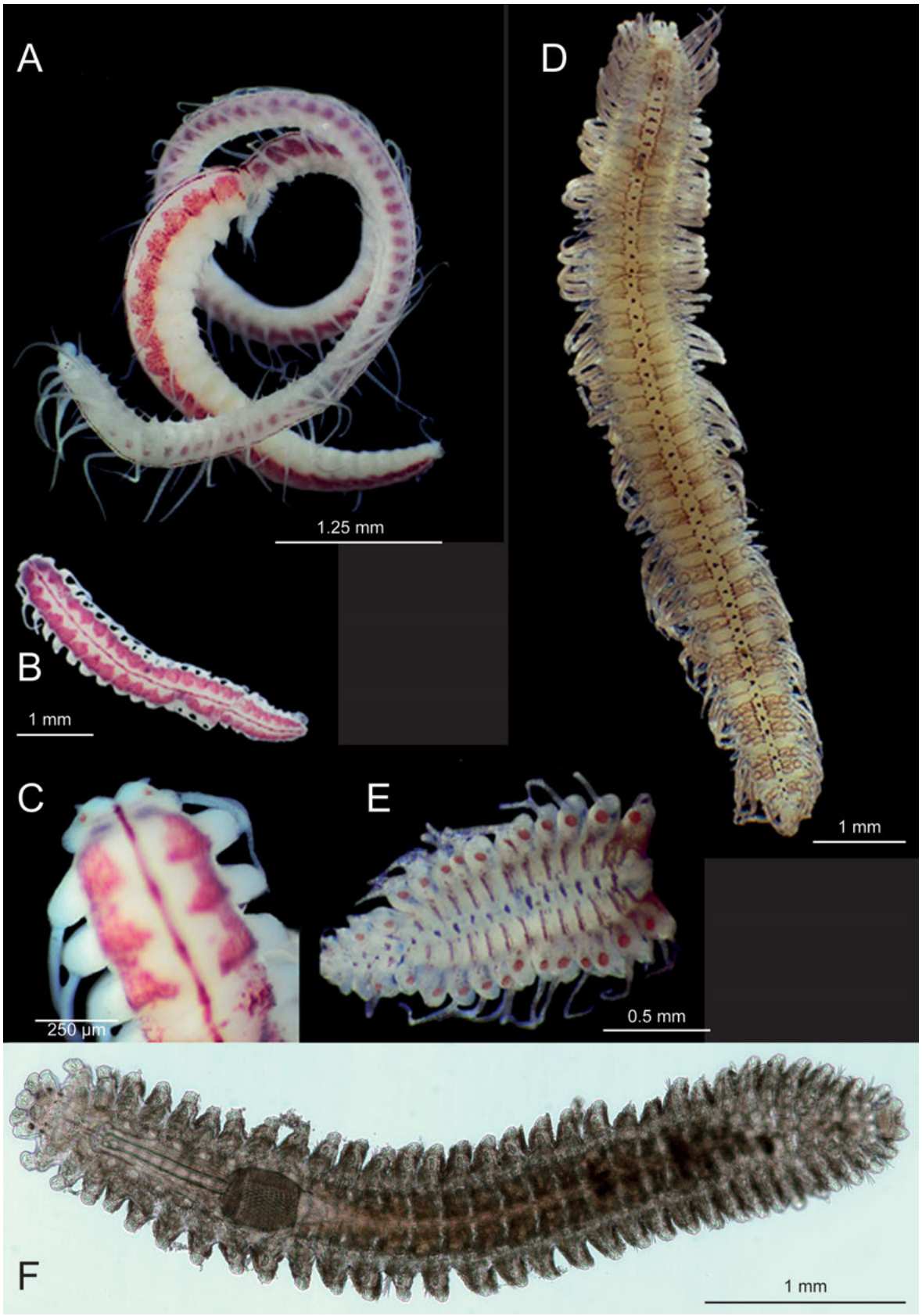


Fig. 7.13.2.29: A, *Alcyonosyllis aidae* Álvarez-Campos, San Martín & Aguado, 2013, entire animal. B, *Alcyonosyllis aidae* stolon. C, same, detail of anterior end. D, *Branchiosyllis tagalog* Álvarez-Campos, San Martín & Aguado, 2012, entire animal. E, *Branchiosyllis tagalog* stolon. F, *Eurysyllis tuberculata* Ehlers, 1864. Entire animal, Roscoff, France. Original G. Purschke, Osnabrück.

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***Eurysyllis* Ehlers, 1864**

Eurysyllis Ehlers, 1864: 264.
Polymastus Claparède, 1864
Type species: *Eurysyllis tuberculata* Ehlers, 1864.
Diagnosis: Body small, strongly dorsoventrally flattened. Palps fused, inserted ventrally. Dorsum with four longitudinal rows of spherical tubercles, similar in size and shape to antennae and dorsal cirri, four tubercles present on each segment except peristomium, which has two. Antennae, tentacular cirri, and dorsal cirri each reduced to single spherical article. Pharynx with anterior tooth, surrounded by crown of about 10 soft papillae and trepan of minute, indistinct teeth. Compound chaetae with short falcigers; some simple capillary chaetae on posterior parapodia. Acerous stolons. Cosmopolitan in temperate and tropical waters; 8 species (Figs. 7.13.2.28D and 7.13.2.29F).

Interesting recent paper is by De Chiara et al. (2017).

***Haplosyllis* Langerhans, 1879**

Syllis (Haplosyllis) Langerhans, 1879: 527.
Hemisyllis Verrill, 1900
Trypanosyllis (Trypanoseta) Imajima & Hartman, 1964
Geminosyllis Imajima, 1966d
Type species: *Syllis spongicola* Grube, 1855.
Diagnosis: Body cylindrical. Palps basally fused. Antennae, tentacular cirri, anal cirri, and dorsal cirri annulated. Pharynx with tooth, located on anterior rim; anterior margin of pharynx with crown of soft papillae (Fig. 7.13.2.14B), sometimes with a an additional crown of soft denticles. Chaetae all simple, usually 1–3 thick chaetae per parapodium (Fig. 7.13.2.9F). Acerous stolons in some species (Fig. 7.13.2.18A), dicerous in others. Cosmopolitan in tropical and temperate waters; usually associated with sponges or gorgonians; about 49 species (Fig. 7.13.2.28E).

This genus received little attention before the present century, but after the papers of Martin et al. (2002, 2003), Sardá et al. (2002), Lattig et al. (2007), numerous papers described many species all around the world, as Lattig and Martin (2009, 2011a, b), Lattig et al. (2010a, b), Paresque and Nogueira (2014), Paresque et al. (2016a), and Cepeda et al. (2017), which greatly increased the number of know species. Probably it is a non-monophyletic group, which could be divided in several different genera.

***Inermosyllis* San Martín, 2003**

Inermosyllis San Martín, 2003: 326.
Pseudosyllides Augener, 1927
Type species: *Pseudosyllides curacaoensis* Augener, 1927.
Diagnosis: Body cylindrical. Palps basally fused. Antennae, tentacular cirri, and dorsal cirri moniliform, or indistinctly annulated basally on some species. Pharynx unarmed, opening surrounded by crown of soft papillae. Compound chaetae falcigerous and capillary dorsal and ventral simple chaetae on some parapodia. Reproduction unknown. Tropical areas and Mediterranean; 4 species (Fig. 7.13.2.28F).

***Karroonsyllis* San Martín & López, 2003**

Karroonsyllis San Martín & López, 2003: 192.
Type species: *Karroonsyllis exogoneformis* San Martín & López, 2003.
Diagnosis: Body of meiofaunal size, cylindrical. Palps long and broad, fused along their entire length, except for terminal notch. Nuchal organs as ciliated grooves inserted in ventrolateral position. Antennae, the one pair of tentacular cirri, and dorsal cirri annulate, with few articles. Pharynx beginning on segments 4–5, with dorsal, conical tooth, and crown of soft papillae. Compound chaetae, and simple dorsal and ventral capillary chaetae on posterior parapodia. Australia; only the type species is known (Fig, 7.13.2.30A).

***Megasyllis* San Martín, Hutchings & Aguado, 2008**

Megasyllis San Martín, Hutchings & Aguado, 2008a: 5.
Type species: *Syllis corruscans* Haswell, 1885.
Diagnosis: Some species large (more than 30 mm) usually brightly colored. Palps large, broad, basally fused. Segments bi- or triannulate in large specimens, weakly annulate in small ones. Antennae, tentacular cirri, and anterior dorsal cirri weakly to distinctly articulated; remaining dorsal cirri irregularly wrinkled to smooth, slender, long to moderate in length; sometimes all cirri smooth. Large species with longer dorsal cirri arising more dorsally than shorter ones. Young specimens with all appendages smooth; antennae and anterior cirri becoming progressively more articulated with age. Pharynx similar in length or shorter than proventricle, provided with a crown of numerous, soft papillae and one single tooth, placed anteriorly, sometimes slightly back from pharyngeal rim; several species with a distinct pigmented band on pharynx. Compound chaetae heterogomph strongly bidentate falcigers, typically both teeth similar, acute; sometimes proximal tooth larger that distal one. Solitary dorsal and ventral simple capillary chaetae on posterior parapodia; dorsal simple chaetae very thin, distinctly more slender than shafts of compound chaetae. Aciculae straight to slightly acuminate. Dicerous stolons. Tropical and subtropical areas; 14 species (Fig. 7.13.2.30B).

Some recent papers on this genus are San Martín et al. (2014) and Aguado and Glasby (2015).

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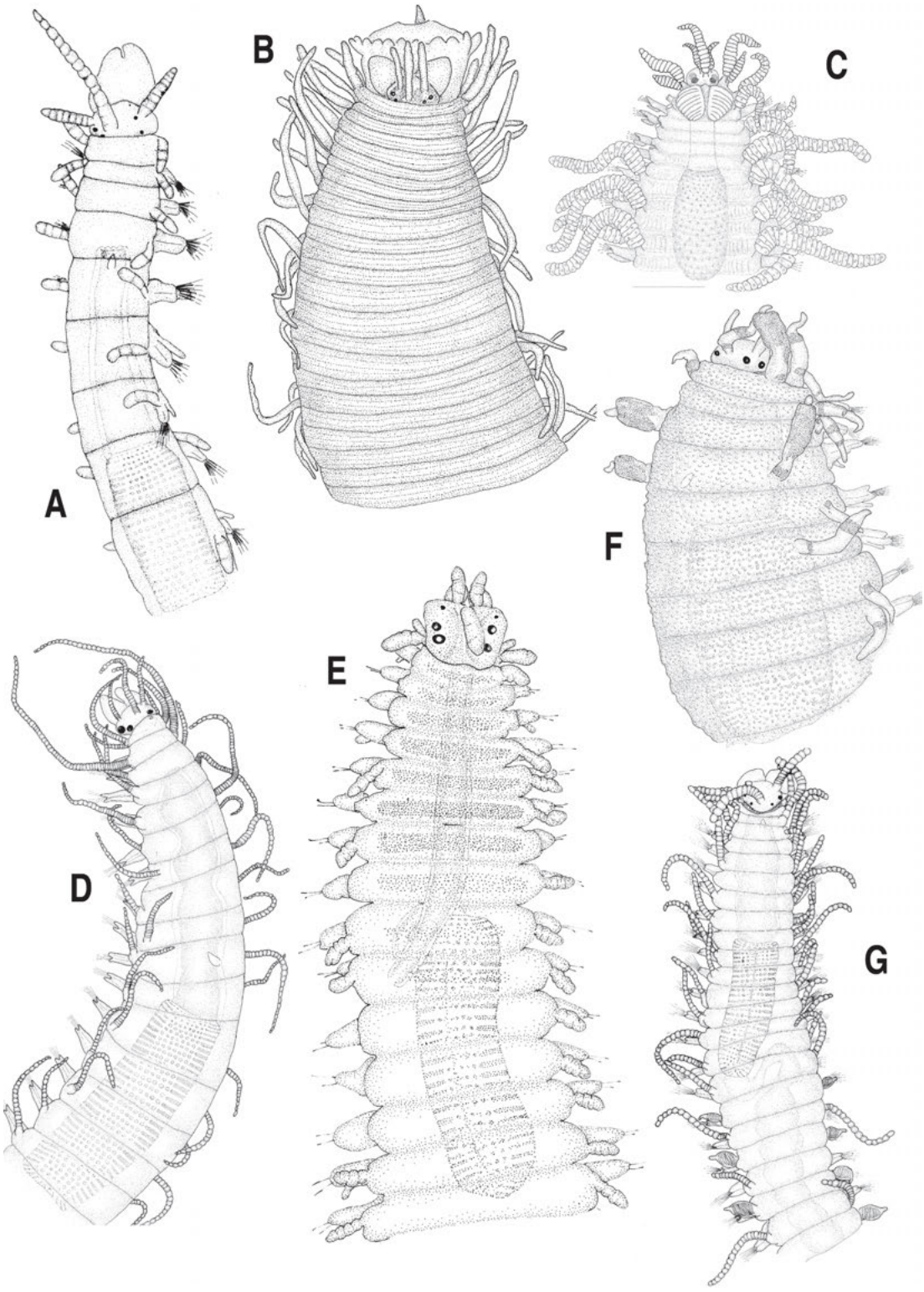


Fig. 7.13.2.30: Anterior ends of species of seven more genera of the Syllinae. A, *Karroonsyllis exogoneformis* San Martín & López, 2003. B, *Megasyllis corruscans* (Haswell, 1855). C, *Nuchalosyllis lamellicornis* Rullier & Amoureux, 1979. D, *Opisthosyllis japonica* Imajima, 1966. E, *Parahaplosyllis brevicirra* Hartmann-Schröder, 1990. F, *Paraopisthosyllis ornaticirra* San Martín & Hutchings, 2006. G, *Parasphaerosyllis indica* Monro, 1937. A, after San Martín and López (2003); B, D, after San Martín et al. (2008a); D, after Aguado and San Martín (2008); E, after San Martín et al. (2008b); F, after San Martín and Hutchings (2006); G, after San Martín et al. (2010). A, B, D–G, San Martín's original drawings; C, Aguado's original drawing.

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Nuchalosyllis Rullier & Amoureux, 1979

Nuchalosyllis Rullier & Amoureux, 1979: 164.

Type species: *Nuchalosyllis lamellicornis* Rullier & Amoureux, 1979.

Diagnosis: Body flattened, ribbon shaped. Palps basally fused. A pair of prominent nuchal epaulettes, with several transversal lamellae. Antennae, tentacular cirri, dorsal cirri, and anal cirri distinctly annulated. Compound chaetae falcigerous. Stolons probably dicerous. Brazil; two species (Fig. 7.13.2.30C).

A recent paper on this genus is Fukuda and Nogueira (2012).

Opisthosyllis Langerhans, 1879

Opisthosyllis Langerhans, 1879: 541.

Type species: *Opisthosyllis brunnea* Langerhans, 1879.

Diagnosis: Palps basally fused. Some species with an occipital flap, derived from first chaetiger. Antennae, tentacular cirri, anal cirri, and dorsal cirri distinctly annulated. Pharynx with tooth, typically inserted behind middle of pharynx; anterior margin of pharynx with crown of soft papillae. Compound chaetae falcigerous; capillary dorsal and ventral simple chaetae present. Stolons dicerous. Circumtropical; 19 species (Fig. 7.13.2.30D).

Papers on this genus are Lee and Rho (1994a, b), Aguado et al. (2005), San Martín et al. (2008a), and Paresque et al. (2016b).

Parahaplosyllis Hartmann-Schröder, 1990

Parahaplosyllis Hartmann-Schröder, 1990: 45.

Type species: *Parahaplosyllis brevicirra* Hartmann-Schröder, 1990.

Diagnosis: Body dorsoventrally flattened. Palps short, separate. Antennae inserted on anterior margin of prostomium. Antennae, tentacular cirri, and dorsal cirri short, rough, indistinctly annulated, similar in length to parapodial lobes. Pharynx long, slender, and curved, with an anterior tooth and a trepan. Only simple chaetae, a single dorsal capillary chaeta and a thick, hooked simple chaeta, distally bidentate, with a curved spur (Fig. 7.13.2.8F). Stolons probably dicerous. Australia and Philippines, 2 species (Fig. 7.13.2.30E).

Papers dealing with this genus are San Martín et al. (2010) and Álvarez-Campos et al. (2013).

Paraopisthosyllis Hartmann-Schröder, 1991

Paraopisthosyllis Hartmann-Schröder, 1991: 27.

Basidiosyllis San Martín, López & Aguado 2009

Type species: *Opisthosyllis brevicirra* Hartmann-Schröder, 1979.

Diagnosis: Body robust, cylindrical, broad anteriorly, tapered posteriorly, with many segments. Dorsal and ventral surfaces covered with numerous, small papillae. Palps basally fused, broad, ventrally folded. Antennae, tentacular cirri, anal cirri, and dorsal cirri smooth, enlarged, club shaped to foliaceous. Dorsal cirri usually with distinct cirrophores, those of anterior segments alternating in size in some species, larger cirri arising more dorsally. Pharynx wide, with pharyngeal tooth inserted far from anterior rim. Proventricle wide, voluminous. Compound chaetae and dorsal and ventral simple chaetae on posterior parapodia. Australia, Philippines, and Brazil; 10 species (Fig. 7.13.2.30F).

Revision of this genus is done in Paresque et al. (2016b).

Parasphaerosyllis Monro, 1937

Parasphaerosyllis Monro, 1937: 273.

Type species: *Parasphaerosyllis indica* Monro, 1937.

Diagnosis: Body cylindrical. Palps basally fused. Antennae, tentacular cirri, anal cirri, and anterior dorsal cirri distinctly annulate, from midbody, alternating between long, strongly annulate and short, lemon-shaped cirri, with a single, inflated article. Pharynx with tooth, located on anterior rim; anterior margin of pharynx with crown of soft papillae. Compound chaetae with falcigerous blades; capillary dorsal and ventral simple chaetae present. Stolons dicerous. Circumtropical; 5 species (Fig. 7.13.2.30G).

Papers dealing with this genus are Imajima (1966d), Capa et al. (2001), San Martín et al. (2008b), and Cañete (2017).

Plakosyllis Hartmann-Schröder, 1956

Plakosyllis Hartmann-Schröder, 1956: 87.

Type species: *Plakosyllis brevipes* Hartmann-Schröder, 1956.

Diagnosis: Body dorsoventrally flattened. Palps separate, inserted ventrally. Antennae inserted on anterior margin of prostomium. Antennae, tentacular cirri, and dorsal cirri reduced to single spherical article. Pharynx with anterior dorsal tooth, with crown of about 10 soft papillae. Compound chaetae short falcigers. Stolons acerous. Cosmopolitan in temperate and tropical waters; 4 species (Figs. 7.13.2.6C and 7.13.2.31A).

Papers dealing with this genus are Perkins (1981), San Martín et al. (2008b), and Salcedo-Oropeza et al. (2011).

Pseudosyllis Grube, 1863

Pseudosyllis Grube, 1863: 44. Álvarez-Campos et al. 2017: 511.

Trypanosyllis Claparède, 1864 (partim)

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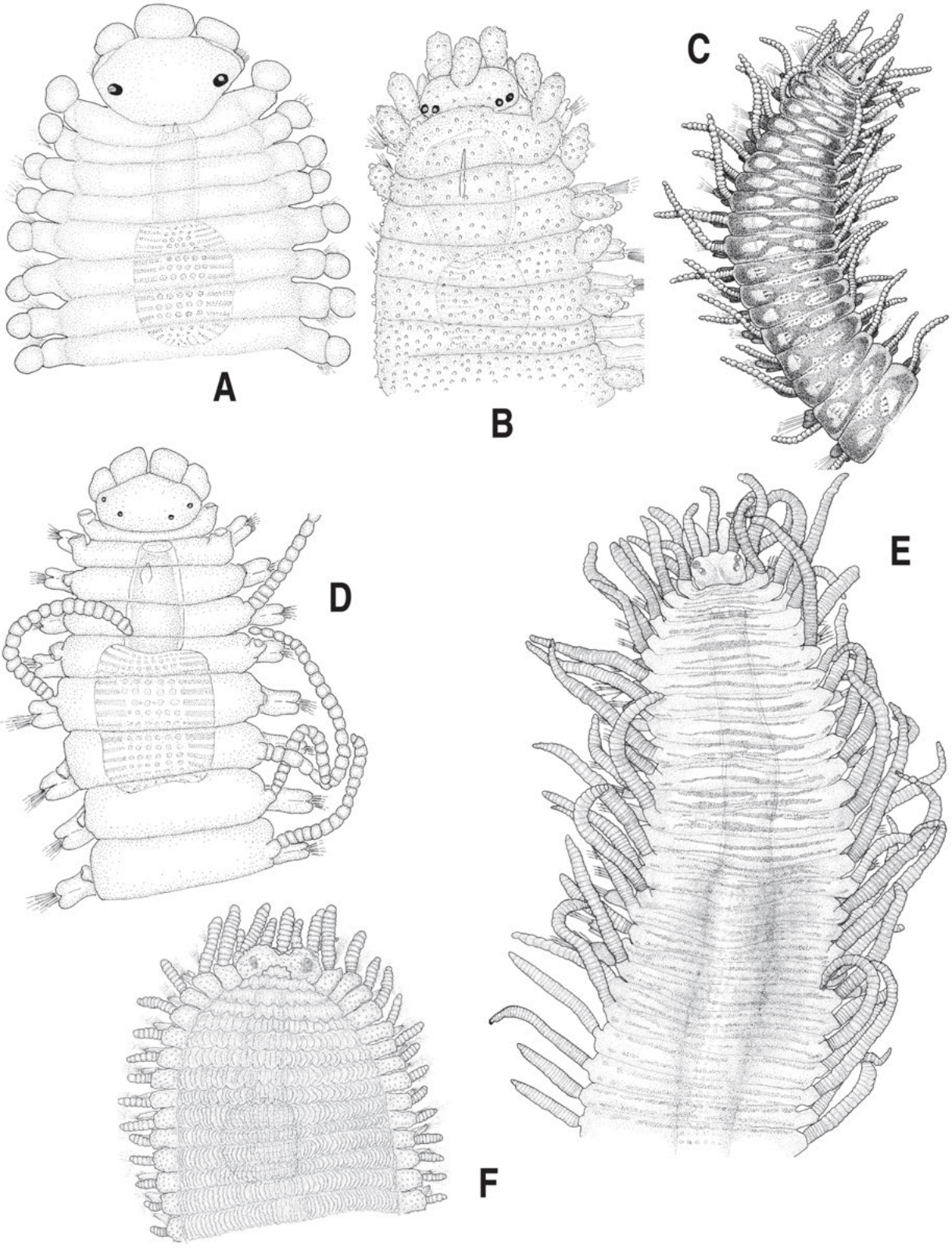


Fig. 7.13.2.31: Anterior ends of species of a further 6 genera of the Syllinae. A, *Plakosyllis brevipes* Hartmann-Schröder, 1956. B, *Rhopalosyllis hamulifera* Augener, 1913. C, *Syllis variegata* Grube, 1860. D, *Tetrapalpia dorsoaciculata* (Hartmann-Schröder, 1991). E, *Trypanosyllis zebra* (Grube, 1860). F, *Xenosyllis moloch* San Martín, Hutchings & Aguado, 2008. A, B, D, F, after San Martín et al. (2008b); C, after San Martín (2003); E, after San Martín et al. (2008a). A, B, D–F, San Martín's original drawings; C, San Martín's original drawing modified by Jordi Corbera.

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Type species: *Pseudosyllis brevipennis* Grube, 1863.
Diagnosis: Body of medium to small size, without color pattern. Short appendages, relatively thick, with few articles. Bidentate chaetae with similar teeth; with spines along margin, distalmost spines reaching the distalmost tooth. Pharynx with a middorsal tooth and a trepan of 8–10 teeth, surrounded by a crown of soft papillae. Proventricle shorter than pharynx, occupying two or three segments. Reproduction by single tetraglene stolon. Only type species known, but probably several species described into *Trypanosyllis* could belong in fact to *Pseudosyllis* (Figs. 7.13.2.6A and 7.13.2.32C).

Ramisyllis Glasby, Schroeder & Aguado, 2012

Ramisyllis Glasby *et al*. 2012: 483.
Type species: *Ramisyllis multicaudata* Glasby, Schroeder & Aguado, 2012.
Diagnosis: Dendriform body flattened ventrally. Palps free. Antennae, the two pairs of tentacular cirri and dorsal cirri articulate, with alternation of thick and slender cirri on (mid and) posterior segments. Pharynx slender, middorsal tooth present in juveniles, lost in adults. Only simple chaetae present, tomahawk shaped. Stolons produced on length body of worm within the sponge. Australia; only the type species is known.

Recent papers on this genus are Aguado et al. 2015a, Schroeder et al. 2017 and Ponz-Segrelles et al. 2021).

Rhopalosyllis Augener, 1913

Rhopalosyllis Augener, 1913: 245.
Type species: *Rhopalosyllis hamulifera* Augener, 1913.
Diagnosis: Body cylindrical, covered with numerous, small papillae, on prostomium, dorsal and ventral surfaces, parapodia, and anal cirri. Palps basally fused, rounded, sometimes ventrally folded. Antennae, tentacular cirri, and dorsal cirri indistinctly annulated short, oval to spindle shaped, covered with papillae. Pharyngeal tooth long and slender. Compound chaetae present; some chaetae on posterior segments with shafts and blades fused to form thick, bidentate hooks; dorsal and ventral simple chaetae present on most posterior parapodia. Stolons type unknown. Australia; only the type species is known (Fig. 7.13.2.31B).

A paper dealing with this genus is San Martín et al. (2008b).

Syllis Savigny *in* Lamarck, 1818

Syllis Savigny *in* Lamarck, 1818: 318.
Ioida Johnston, 1840
Trichosyllis Schmarda, 1861
Gnathosyllis Schmarda, 1861
Isosyllis Ehlers, 1864
Aporosyllis Quatrefages, 1865
Pagenstecheria Quatrefages, 1865
Thoe Kinberg, 1866
Chaetosyllis Malmgren, 1867
Typosyllis Langerhans, 1879
Langerhansia Czerniavsky, 1881
Reductotyposyllis Hartmann-Schröder, 1974
Type species: *Syllis monilaris* Savigny *in* Lamark, 1818.
Diagnosis: Body cylindrical. Palps basally fused. Antennae, tentacular cirri, anal cirri, and dorsal cirri distinctly annulate. Pharynx with tooth, located on anterior rim or slightly behind; anterior margin of pharynx with crown of soft papillae (Fig.7.13.2.14A). Compound chaetae falcigerous (Fig. 7.13.2.9A–C), sometimes with pseudo-spinigers (Fig. 7.13.2.9D) sometimes with thick pseudosimple chaetae (Figs. 7.13.2.9E and 7.13.2.10E). Capillary dorsal and ventral simple chaetae present (Fig. 7.13.2.8). Stolons dicerous, tetracerous or pentacerous (Fig. 7.13.2.20C–H). Cosmopolitan; more or less, around 170 species (Figs. 7.13.2.31C and 7.13.2.32B, C).

Álvarez-Campos et al. (2015a) redescribed the type species of the genus (which also is the type genus of the family Syllidae) and designated a Neotype. According to the phylogenetic analyses in Aguado et al. (2015c), Álvarez-Campos et al. (2015b), and Ribeiro et al. (2020), the genus is not monophyletic and needs further reorganization. Recent additions to the knowledge of this genus among others are Tovar-Hernández et al. (2002, 2008), Salcedo-Oropeza et al. (2012), Simon et al. (2014), Aguado et al. (2015c), Álvarez-Campos et al. (2015b), San Martín et al. (2017b), Ba-Akdah et al. (2018), Sedick and Simon (2019), Lucas et al. (2020), Ribeiro et al. (2020), and Soto et al. (2020). A very important paper is Licher (1999).

Tetrapalpia San Martín, Hutchings & Aguado, 2008

Tetrapalpia San Martín, Hutchings & Aguado, 2008b: 151.
Type species: *Opisthosyllis dorsoaciculata* Hartmann-Schröder, 1991.
Diagnosis: Palps free, with distinct gap between them; each palp bilobed with lobes fused for most of their length. Antennae, tentacular cirri, anal cirri, and dorsal cirri distinctly annulate. Pharyngeal tube shorter than proventricle; tooth inserted just behind anterior margin of pharynx. Compound chaetae with short falcigerous blades; capillary chaetae present. Stolon type unknown. Australia; only the type species is known (Fig. 7.13.2.31D).

Trypanosyllis Claparède, 1864

Trypanosyllis Claparède, 1864: 558.
Parautolytus Ehlers, 1900
Parapterosyllis Hartmann-Schröder, 1960

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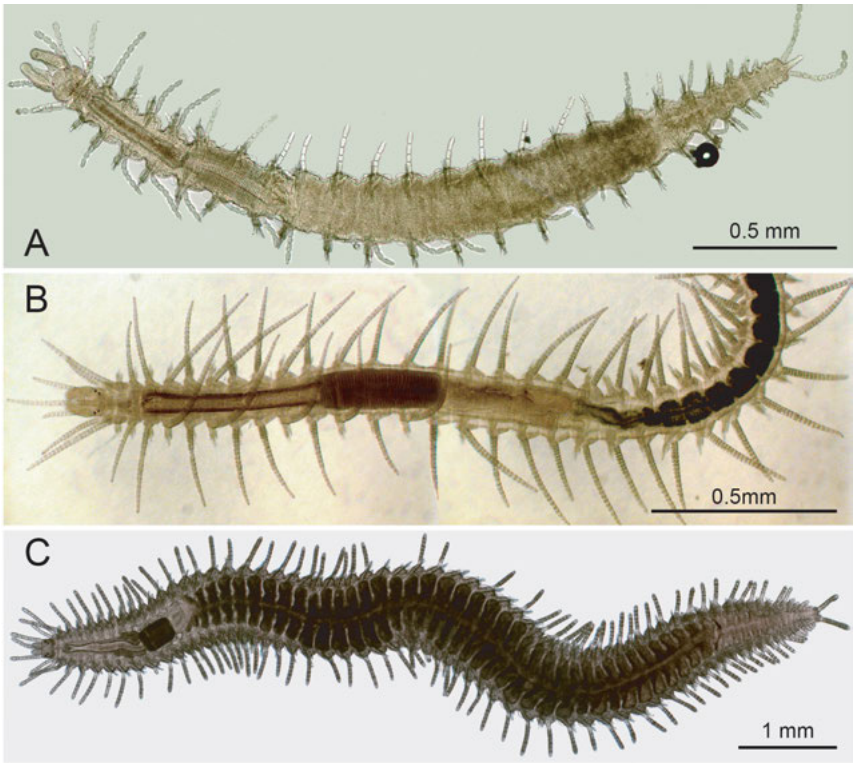


Fig. 7.13.2.32: A, *Syllis* cf. *pontxioi* San Martín & López, 2000, entire animal, juvenile with short cirri and unpaired anal cirrus. B, Adult of unidentified *Syllis* sp., species with comparatively long parapodial and tentacular annulated cirri; note long pharyngeal tube and proventricle extending over 12 chaetigers. C, *Pseudosyllis brevipennis* Grube, 1863, adult, entire animal. Micrographs from living specimens, Roscoff, France. Originals G. Purschke, Osnabrück.

Type species: *Syllis zebra* Claparède, 1864.
Diagnosis: Body dorsoventrally flattened, with numerous short segments. Dorsum with transverse bands of minute spinose papillae on some species (only distinct under SEM). Palps completely free. Antennae, tentacular cirri, and dorsal cirri annulate. Pharynx with a trepan, with or without middorsal tooth. Most species with compound chaetae with falcigerous blades, and simple dorsal and ventral capillary chaetae. In a few species, a few pseudosimple chaetae are present because of fusion of the blades and shafts. Stolons acerous (Fig. 7.13.2.14B). Cosmopolitan; 45 species (Figs. 7.13.2.31E and 7.13.2.33A, B).

This genus has been recently reviewed by Álvarez-Campos et al. (2017, 2018). Other papers dealing with this genus are Çinar (2007), Nogueira and Fukuda (2008), San Martín et al. (2008a), Salcedo-Oropeza et al. (2011), Paresque et al. (2016a), and Lucas et al. (2019).

Trypanedenta Imajima & Hartman, 1964

Trypanosyllis Claparède, 1864 (*partim*)
Trypanosyllis (*Trypanedenta*) Imajima & Hartman, 1964: 125.
Trypanedenta Álvarez Campos, Giribet, San Martín, Rouse & Riesgo, 2017
Type species: *Trypanosyllis gemmipara* Johnson, 1901.
Diagnosis: Flattened body, variable in size. Unidentate or bidentate chaetae, without serration in margin or with a few, minute spines. Pharynx with a trepan of about 10 teeth, surrounded by a crown of soft papillae. Reproduction by gemmiparity with clusters of several simultaneous tetraglene stolons with two pairs of eyes, without antennae. 3 species (Figure 7.13.2.33C, D). North Pacific Ocean and Antarctica.

Trypanobia Imajima & Hartman, 1964

Trypanosyllis (*Trypanobia*) Imajima & Hartman, 1964: 128.
Trypanobia Aguado et al., 2015b
Type species: *Trypanosyllis asterobia* Okada, 1933.
Diagnosis: Mid- to large-sized body, ribbon-like, strongly dorsoventrally flattened, with numerous short segments. Prostomium with four eyes and three antennae. Palps completely separate, ventrally directed. Two pairs of tentacular cirri. Antennae, tentacular cirri, and dorsal cirri distinctly articulated. Pharynx with trepan. Pharyngeal tooth absent. Chaetae all thick, simple; simple capillary chaetae absent. 5 species. Pacific Ocean (Fig. 7.13.2.33E).

Trypanospina Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018

Trypanospina Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018: 234.
Type species: *Trypanospina martini* Álvarez-Campos et al., 2018.
Diagnosis: Small-sized body, with numerous short segments. Numerous minute verrucae covering dorsal and ventral surface, densely distributed mainly in the

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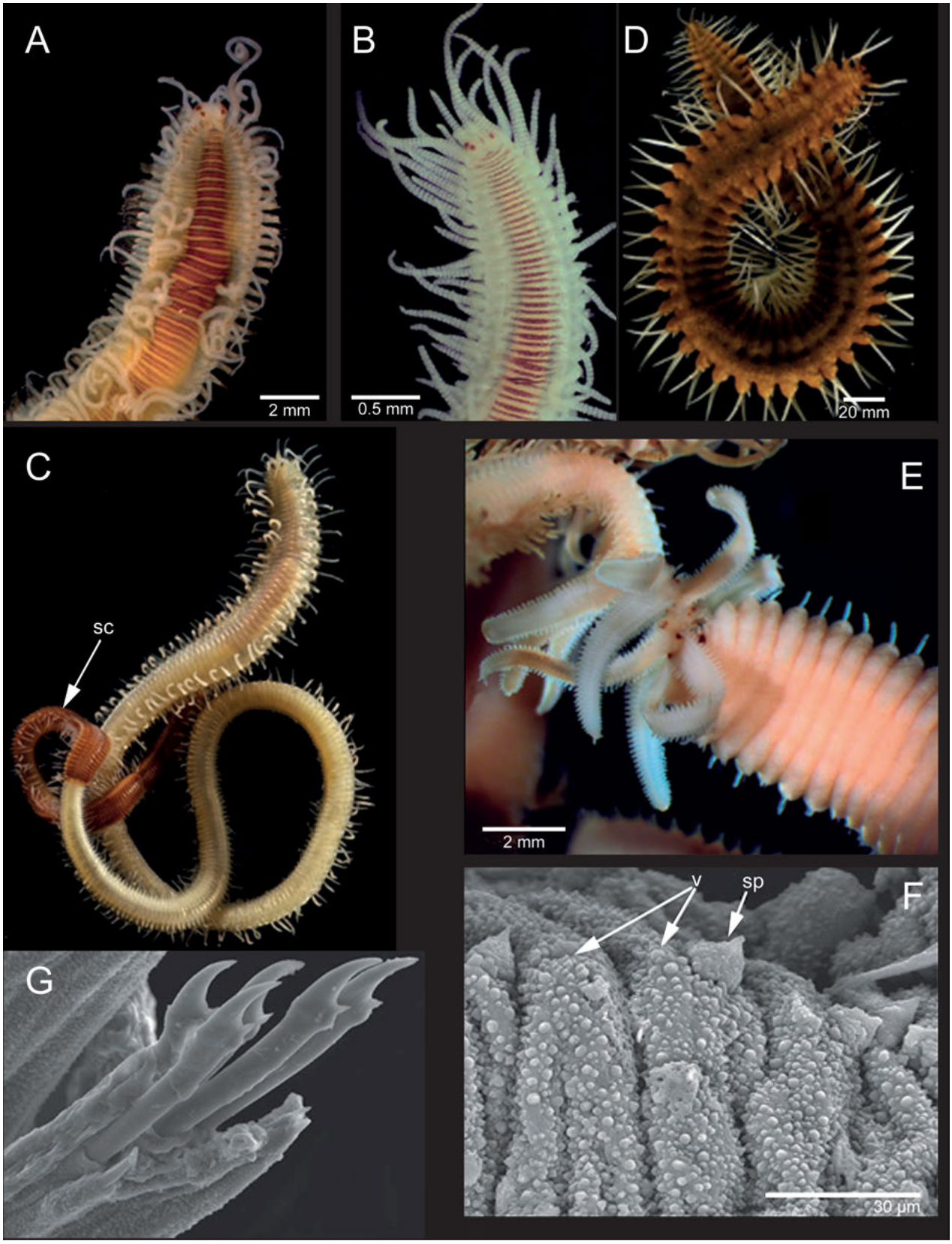


Fig. 7.13.2.33: A, *Trypanosyllis luzonensis* Pillai, 1965. B, *Trypanosyllis leivai* Álvarez-Campos, Riesgo & San Martín in Álvarez-Campos, Giribet, San Martín, Rouse & Riesgo, 2017. C, *Trypanedenta gemmipara* (Johnson, 1901). D, *Trypanedenta gemmipara*, stolon. E, *Trypanobia asterobia* Okada, 1933, cluster of stolons. F, *Trypanospina martini* Álvarez-Campos, Taboada, San Martín, Leiva & Riesgo, 2018, detail of verrucae (v) and spines (s) on dorsum. G, *Trypanospina martini*, posterior chaetae. From Álvarez-Campos et al. (2017, 2018).

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dorsum; some bigger spines on the posterior part of each segment as well as on the cirrophores. Simple unidentate thick chaetae, all similar throughout body, slightly curved, with a short triangular basal spur. Pharynx with a trepan composed by about 11 teeth, surrounded by a crown of soft papillae. Only type species known. Philippines (Fig. 7.13.2.33F, G).

Xenosyllis Marion & Bobretzky, 1875

Xenosyllis Marion & Bobretzky, 1875: 26.
Type species: *Syllis scabra* Ehlers, 1864.
Diagnosis: Body dorsoventrally flattened, with numerous, short segments Palps free from each other, positioned ventrally. Prostomium and lateral margins of each segment with papillae; dorsal surface with longitudinal striations. Tentacular segment reduced, covered by small lobe with papillae, dorsally. Antennae, tentacular cirri, anal cirri, and dorsal cirri short, annulated, covered with papillae. Pharynx long, unarmed. Compound chaetae falcigerous and capillary simple chaetae present. Temperate waters of Atlantic Ocean and Australia; 3 species (Fig. 7.13.2.31F).

Recent paper dealing with this genus is San Martín et al. (2008b).

Eusyllinae Malaquin, 1893

Diagnosis: Body cylindrical, size from minute to large. Palps basally fused or free at bases. Three antennae, usually long, extending beyond palps. Four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri, typically long and slender. Nuchal organs in two dorsolateral, densely ciliated grooves between prostomium and peristomium. Species of some genera with an occipital flap between prostomium and peristomium. Dorsal cirri typically long, slender, smooth, or pseudoarticulated. Pharynx straight, typically with a middorsal, anterior tooth (some genera without middorsal tooth or tooth located posteriorly in pharynx) and/or an arc of denticles, which may be orientated posteriorly. Reproduction by epigamy (Fig. 7.13.2.15); one genus (*Nudisyllis* Knox & Cameron, 1970) broods eggs attached to dorsal cirri (Fig. 7.13.2.19). The subfamily comprises 6 genera and about 112 species.

A large paper on this subfamily is San Martín and Hutchings (2006).

Eusyllis Malmgren, 1867

Eusyllis Malmgren, 1867: 40.
Claparedia Quatrefages, 1865
Desmosyllis Verrill, 1900
Synsyllis Verrill, 1900
Eudontosyllis Knox, 1960
Type species: *Eusyllis blomstrandi* Malmgren, 1867.
Diagnosis: Palps either entirely free or basally fused. Antennae, tentacular cirri, and dorsal cirri nonannulate sometimes rugose, with pseudoarticulate appearance. Pharynx with middorsal tooth, usually large and conspicuous, and incomplete ventral arc of small denticles, directed anteriorly (Fig. 7.13.2.14C). Compound chaetae and dorsal and ventral simple chaetae on some parapodia. Epigamic specimens (Fig. 7.13.2.16) sometimes strongly modified and phosphorescent. Cosmopolitan; about 24 species (Fig. 7.13.2.34A).

This genus has been recently revised by Brusa et al. (2013). Interesting paper on this genus are Fukuda et al. (2015) and Paresque et al. (2015).

Nudisyllis Knox & Cameron, 1970

Nudisyllis Knox and Cameron, 1970: 77.
Type species: *Nudisyllis tinihekea* Knox and Cameron, 1970.
Diagnosis: Body small, fragile. Palps separate. Dorsal cirri long, cylindrical, smooth, or slightly rugose. Pharyngeal tube shorter than proventricle; pharyngeal tooth located near anterior rim. Compound chaetae with both unidentate and bidentate blades on same parapodium, or all unidentate; bidentate blades having proximal tooth small, spine-like. Tips of aciculae tricuspidate or lancet shaped. Dorsal incubation of eggs in dorsal cirri reported in two species (Fig. 7.13.2.19). Atlantic and Pacific oceans and their adjacent seas; 4 species (Figs. 7.13.2.34B and 7.13.2.35A).

The genus was re-erected by San Martín et al. (2009).

Odontosyllis Claparède, 1863

Odontosyllis Claparède, 1863: 47.
Procome Ehlers, 1864
Eurymedusa Kinberg, 1866
Umbellisyllis Sars, 1869
Parautolytus Ehlers, 1900
Fauvelia Gravier, 1900b
Alluaudella Gravier, 1905
Hesperalia Chamberlin, 1919
Atelesyllis Pruvot, 1930
Pharyngeovalvata Day, 1951
Odontoautolytus Hartmann-Schröder, 1979
Synpalposyllis Hartmann-Schröder, 1983
Type species: *Syllis fulgurans* Audouin & Milne Edwards, 1833.
Diagnosis: Body of variable size, cylindrical, dorsally strongly convex, flattened ventrally. Palps broad, basally fused. Occipital flap present in many species, usually well developed, covering peristomium dorsally and prostomium partially. Dorsal cirri elongated, smooth,

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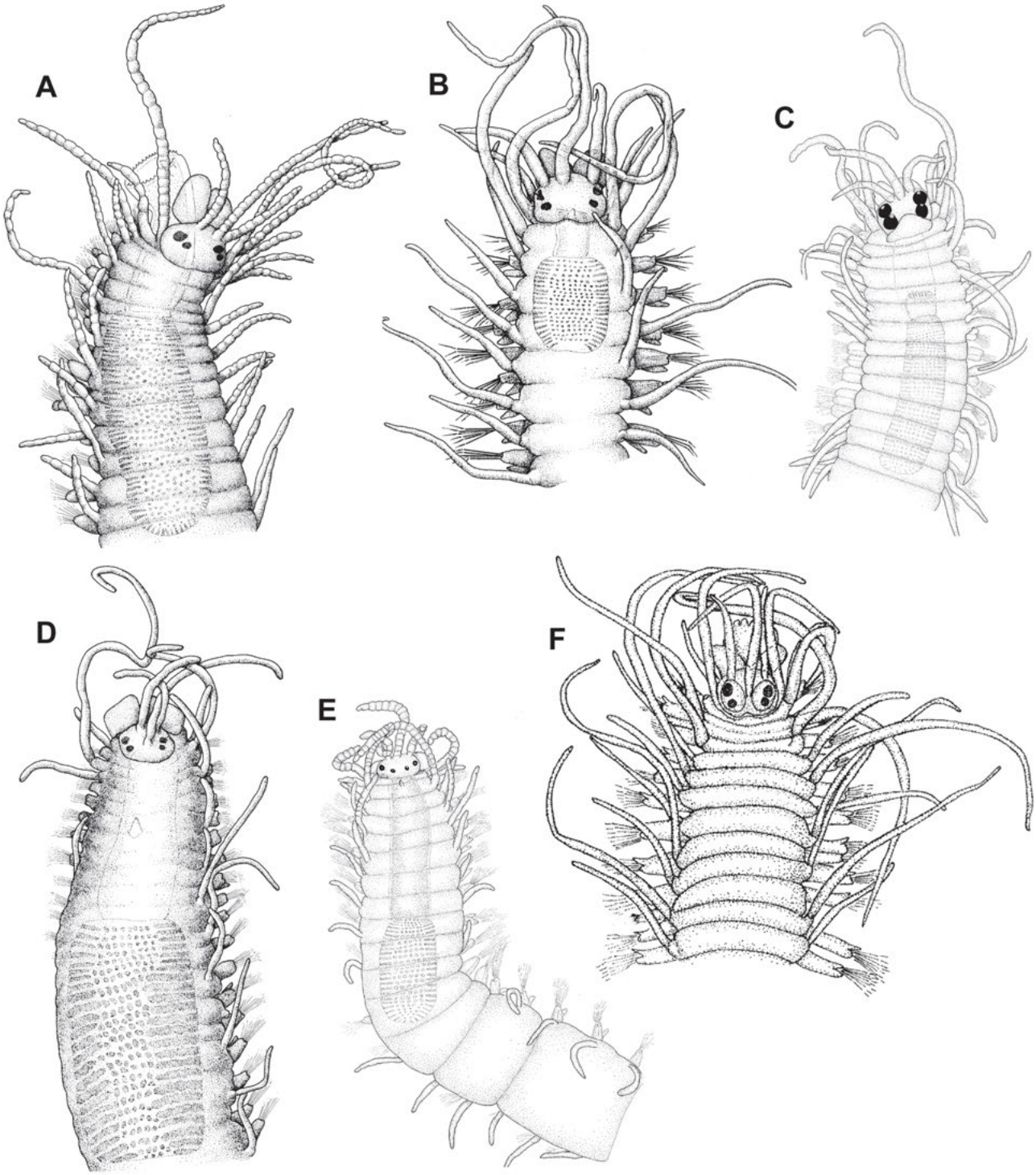


Fig. 7.13.2.34: Anterior ends of species of 6 genera of the Eusyllinae. A, *Eusyllis assimilis* Marenzeller, 1875. B, *Nudisyllis pulligera* (Krohn, 1852). C, *Odontosyllis australiensis* Hartmann-Schröder, 1979. D, *Opisthodonta morena* Langerhans, 1879. E, *Synmerosyllis yolandae* (San Martín & Hutchings, 2006). F, *Pionosyllis enigmatica* (Wesenberg-Lund, 1950). A, B, D, after San Martín (2003); C, E, after San Martín and Hutchings (2006); F, after San Martín et al. (2009). A, B, D, San Martín's original drawings modified by Jordi Corbera; C, E, F, San Martín's original drawings.

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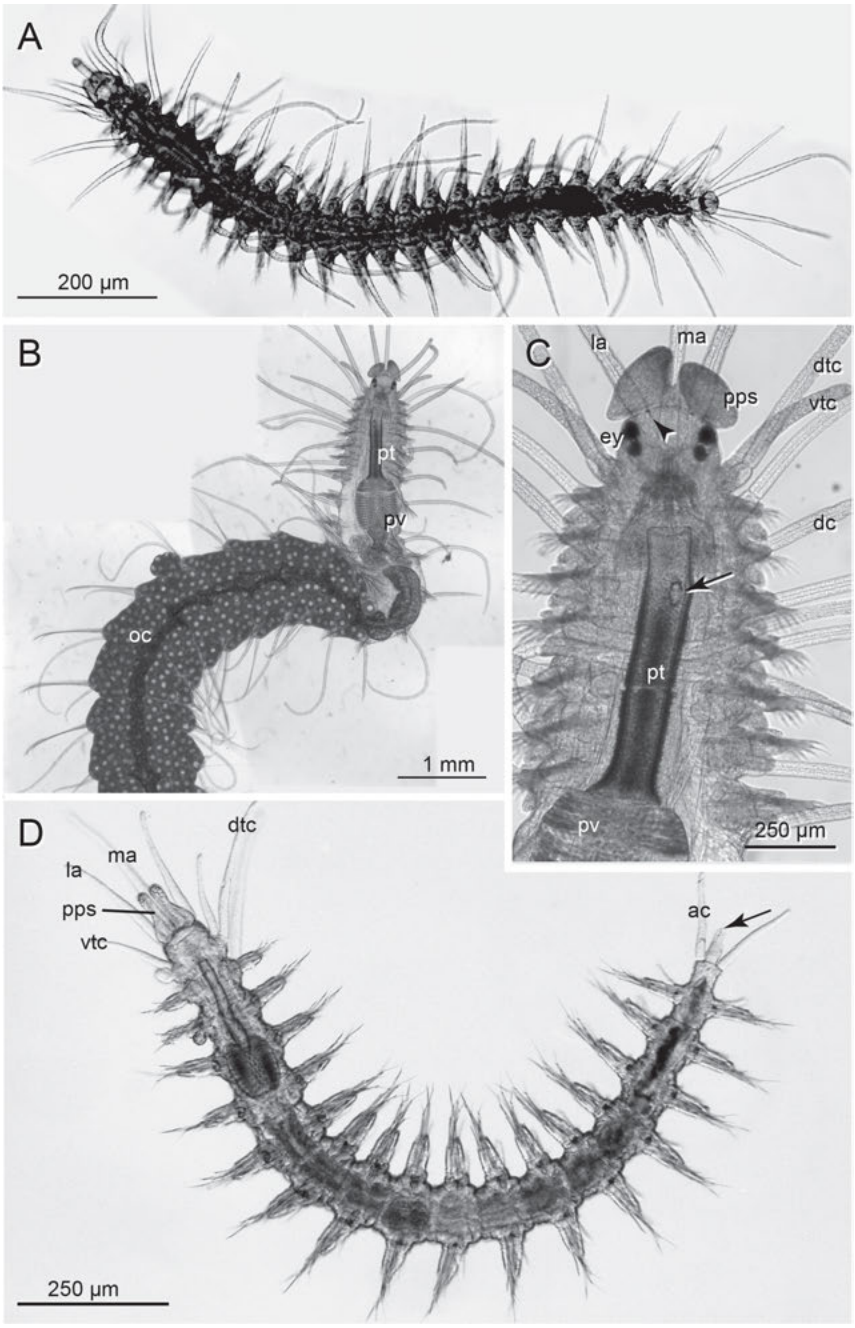


Fig. 7.13.2.35: Micrographs from living animals. A, *Nudisyllis samsonensis* (Hartmann-Schröder, 1980).Entire animal. B, C, *Opisthodonta* sp. B, Anterior end of mature female with numerous oocytes (oc), pv proventricle, pt pharyngeal tube. C, Enlargement of B, basally fused palps (pps), foliaceous and broadly extended, middorsal tooth subdistally inserted in anterior third of pharynx (arrow), arrowhead point to anterior minute eyes. D, *Neopetitia occulta* (Westheide & Hass-Cordes, 2001). Arrow points to unpaired median anal cirrus. ac, anal cirrus; dc, dorsal cirrus; dtc, dorsal tentacular cirrus; la, lateral antenna; ma, median antenna; pps, palps; vtc, ventral tentacular cirrus. Originals A, D. W. Westheide, Osnabrück, B, C G. Purschke, Osnabrück.

distally tapered, but sometimes short or indistinctly annulated. Pharyngeal tube distinctly shorter than proventricle, with several teeth pointing posteriorly, and two lateral plates. Proventricle usually long and wide. Compound chaetae usually with shafts distally spinose. Dorsal and ventral simple chaetae present on some parapodia. Epigamic specimens sometimes strongly modified and phosphorescent. Cosmopolitan; about 58 species (Fig. 7.13.2.34C).

Some recent papers on this genus are Fukuda and Nogueira (2006), Verdes et al. (2011), Fukuda et al. (2013), Paresque et al. (2015), Aguado et al. (2015b), and Salcedo-Oropeza et al. (2016).

Opisthodonta Langerhans, 1879

Opisthodonta Langerhans, 1879: 547.

Type species: *Opisthodonta morena* Langerhans, 1879.

Diagnosis: Palps basally fused, free for most of their length. Dorsal cirri long, cylindrical, smooth, or slightly rugose. Ventral cirri of anterior parapodia, ovate, foliaceous almost completely fused with parapodial lobe, with hyaline inclusions, possibly glandular. Pharyngeal

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tube with middorsal tooth, inserted on anterior third or middle of pharynx, and crown of soft papillae. Compound chaetae include falcigers, with long, thick proximal tooth and short distal tooth and sometimes a few chaetae with long, slender, spiniger-like blades. Dorsal simple chaetae apparently lacking. Tropical and temperate seas; 14 species (Figs. 7.13.2.34D and 7.13.2.35B, C).

Some papers dealing with this genus are San Martín et al. (2009) and Fukuda et al. (2015).

***Pionosyllis* Malmgren, 1867**

Pionosyllis Malmgren, 1867: 40.
Hesiosyllis Wesenberg-Lund, 1950
Type species: *Pionosyllis compacta* Malmgren, 1867.
Diagnosis: Body dorsally strongly convex. Palps basally fused. Antennae, tentacular cirri, and dorsal cirri smooth, sometimes rugose, long, filiform, similar throughout or alternating slightly in length. Pharynx and proventricle similar in size. Pharyngeal tooth anteriorly located. Compound chaetae with bidentate falcigerous blades, the two teeth similar in size; some dorsal anterior falcigers somewhat longer than others in some species; other species with some unidentate blades. Spines on margin of blades short to moderate. Dorsal and ventral simple chaeta on some posterior parapodia, bidentate, with both teeth similar; one species with filiform, unidentate dorsal simple chaetae. Aciculae straight, pointed, acute, usually protruding from parapodial lobes. Polar and subpolar seas, deep areas of temperate waters; 9 species (Fig. 7.13.2.34F).

San Martín et al. (2009) revised this genus.

***Synmerosyllis* San Martín, López & Aguado, 2009**

Synmerosyllis San Martín, López & Aguado, 2009: 1491.
Type species: *Pionosyllis lamelligera* Saint-Joseph, 1886.
Diagnosis: Segments of midbody fused, forming single segments from groups of two to three chaetigers. Palps free, divergent, slightly fused at bases. Antennae, tentacular cirri, and dorsal cirri of chaetiger 1 long, weakly annulated; dorsal cirri of remaining chaetigers much shorter, smooth. Ventral cirri of first chaetiger expanded, foliaceous, laminar. Pharynx longer than proventricle. Pharyngeal tooth positioned anteriorly. Compound chaetae falcigers with short to moderately long, bidentate blades; spines on margin short. Dorsal and ventral simple chaetae present on posterior parapodia. Tips of aciculae trifid. Temperate and tropical waters; 3 species (Fig. 7.13.2.34E).

Incertae sedis

Included here are 20 genera and 94 species whose phylogenetic position is uncertain; some could belong to the Eusyllinae and others to the Syllinae, but there are some other genera with very special and unusual characters. With two pairs of tentacular cirri unless otherwise stated.

***Amblyosyllis* Grube, 1857**

Amblyosyllis Grube, 1857: 186.
Cirrosyllis Schmarda, 1861
Pterosyllis Claparède, 1863
Nicotia Costa, 1864
Gattiola Johnston, 1865
Thylaciphorus Quatrefages, 1865
Pseudosyllides Czerniavsky, 1882
Type species: *Amblyosyllis rhombeata* Grube, 1857.
Diagnosis: Body dorsoventrally flattened, with specific number of segments. Intersegmental constrictions strongly marked, midbody segments typically trapezoidal in shape. Palps short, less than length of prostomium, basally fused, divergent, usually ventrally folded. Nuchal lappets present. Antennae, tentacular cirri, and dorsal cirri long, smooth to indistinctly annulated, fragile. Ventral cirri large, located lateroposteriorly to parapodial lobes, similar in length. Prepygidial segment without parapodia or chaetae, with two pairs of cirri. Pharynx long, slender, highly convoluted, with trepan formed of several teeth, lacking median tooth. Proventricle relatively small. Compound chaetae bidentate falcigers, other types of chaetae rarely present. Reproduction by epigamy and one species (*Amblyosyllis anae*) is known to brood eggs in a gelatinous mass. Cosmopolitan; about 22 species (Figs. 7.13.2.36A and 7.13.2.37).

Aguado et al. (2019) recently revised the genus and described several new species.

***Anguillosyllis* Day, 1963**

Anguillosyllis Day, 1963: 40.
Braniella Hartman, 1965
Type species: *Anguillosyllis capensis* Day, 1963.
Diagnosis: Body small, meiofaunal. Palps elongate, fused, with a distal notch, more or less marked. Without eyes. One pair of papilliform tentacular cirri. Antennae and tentacular cirri minute, papilliform. Dorsal cirri long, filiform. Pharyngeal tooth absent. Compound chaetae with elongated, slender blades. Reproduction by epigamy; one species (*Anguillosyllis lanai*) broods the eggs dorsally attached to parapodial lobes. Deep sea (183–5500 m); 20 species (Fig. 7.13.2.36C).

Macioleck (2020) revised the genus and described numerous new species. Other recent interesting papers are Aguado and San Martín (2008), Böggemann (2009), Böggemann and Purschke (2005), Barroso et al. (2017), and Fukuda and Barroso (2019).

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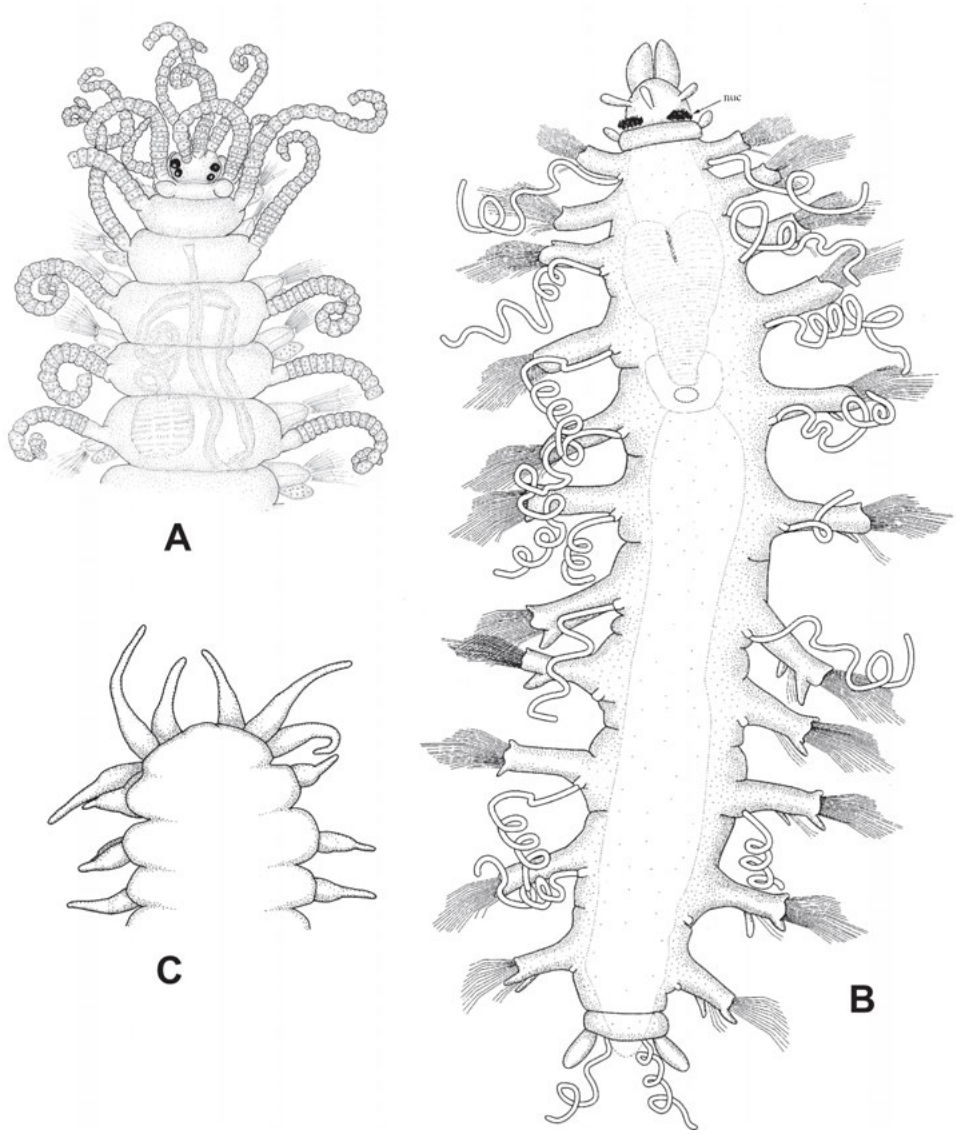


Fig. 7.13.2.36: Anterior ends of species of 3 genera considered i*ncertae sedis*. A, *Amblyosyllis multidenticulata* San Martín & Hutchings, 2006. B, *Anguillosyllis palpata* (Hartman, 1967). C, *Bollandiella antipathicola* (Glasby, 1994). A, After San Martín and Hutchings (2006); B, after Maciolek (2020); C, after Glasby (1994). A, San Martín's original drawing.

Bollandiella Glasby & Krell, 2009

Bollandiella Glasby & Krell, 2009: 355.
Bollandia Glasby, 1994
Type species: *Bollandia antipathicola* Glasby, 1994
Diagnosis: Body strongly arched dorsally, flat to concave ventrally. Dorsum, parapodia, and cirri ciliated. First two segments cephalized, fused together with peristomium. Antennae and palps absent. Three pairs of anterior appendages, probably representing one pair of peristomial cirri and two pairs of cirri associated with first two segments. Appendages conical with tapering ends. Pharynx sinuous, unarmed. Two simple neurochaetae per parapodium: one sigmoid, the other distally bent. Japan; parasitic on black corals; only the type species is known (Fig. 7.13.2.36C).

Brachysyllis Imajima & Hartman, 1964

Brachysyllis Imajima & Hartman, 1964: 108.
Type species: *Brachysyllis japonica* Imajima & Hartman, 1964.
Diagnosis: Body with 13 chaetigers plus a prepygidial achaetous segment. Segments more or less trapezoidal. Transverse rows of cilia covering dorsum and ventrum. Palps long, separate, with a small, subdistal papilla. Nuchal organs as ciliary rows. Antennae, tentacular cirri, anal cirri, and dorsal cirri long, filiform, and smooth. Ventral cirri long, filiform. Pharynx wide, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5–6), surrounded by a crown of distal pharyngeal papillae. Compound chaetae falcigerous, blades bidentate, and dorsal and ventral simple chaetae

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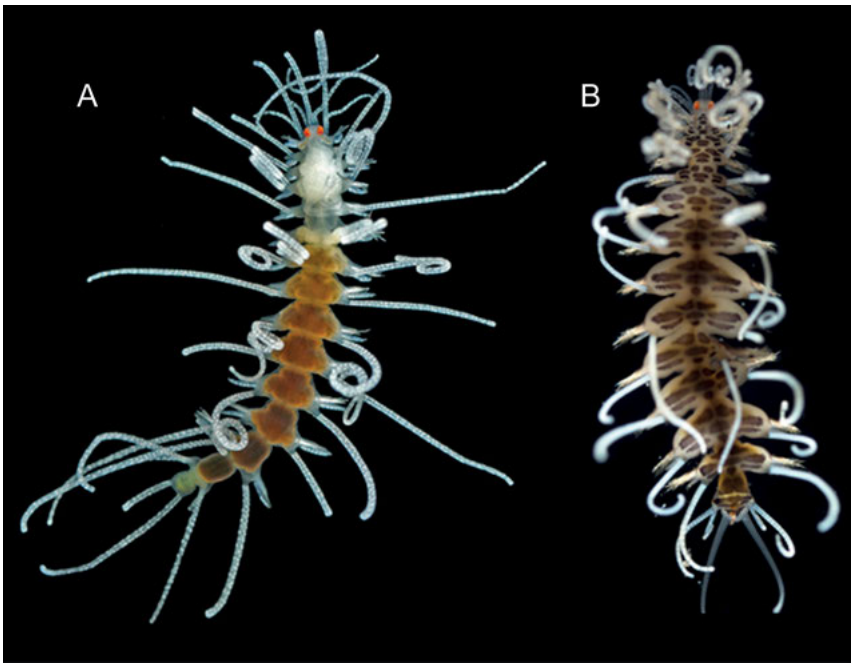


Fig. 7.13.2.37: A, *Amblyosyllis clarae* Aguado, Capa, Lago-Bacia et al. (2019). B, *Amblyosyllis ovei* Aguado, Capa, Lago-Bacia et al. (2019). Photos after Aguado et al. (2019).

absent. Aciculae bent distally. Reproduction by epigamy. Pacific Ocean; three species (Fig. 7.13.2.38A).

Recent papers dealing with this genus are Aguado and San Martín (2008) and Pleijel et al. (2012).

***Brevicirrosyllis* San Martín, López & Aguado, 2009.**

Brevicirrosyllis San Martín, López & Aguado, 2009: 1468.

Type species: *Pionosyllis weismanni* Langerhans, 1879.

Diagnosis: Palps basally fused. Antennae, tentacular dorsal cirri of first chaetiger long, smooth to rugose or pseudoannulate; remaining dorsal cirri short. Pharynx and proventricle similar in length; pharyngeal tooth located on anterior rim. Compound chaetae heterogomph or hemigomph bidentate falcigers, with moderately long or short bidentate blades; spines on margin short. Dorsal and ventral simple chaetae in posterior parapodia. Ventral simple chaetae hooded, expanded, usually with proximal tooth longer than distal tooth. Tips of aciculae acuminate. Reproduction by epigamy. Cosmopolitan in temperate and tropical seas; 5 species (Fig. 7.13.2.38B).

Papers dealing with this genus are San Martín and Hutchings (2006) and Fukuda et al. (2015). Probably is a member of the Eusyllinae.

***Clavisyllis* Knox, 1957**

Clavisyllis Knox, 1957: 493.

Type species: *Clavisyllis alternata* Knox, 1957.

Diagnosis: Body broad, subcylindrical. Nuchal organs form two straight epaulettes with a digitiform nuchal cirrus between them or curved epaulettes with knob-like tips. Antennae, dorsal tentacular cirri, and dorsal cirri large, ovoid, inflated, with cirrophores; ventral cirri triangular. Dorsal cirri, crowded and subtly alternating between lateral and dorsal segmental positions, to give the appearance of four longitudinal rows along the body. Pharynx with single tooth or trepan of 12–13 teeth. Compound falcigers with blades having distinct bidentate tips and long spines forming aristae distally. Australia and New Zealand; 2 species. Probably is a Syllinae (Fig. 7.13.2.38C).

Recent papers on this genus are Aguado and San Martin (2008) and Watson (2009).

***Dioplosyllis* Gidholm, 1962**

Dioplosyllis Gidholm, 1962: 253.

Type species: *Dioplosyllis cirrosa* Gidholm, 1962.

Diagnosis: Palps long, basally fused. Rows of transverse cilia covering dorsum and ventrum. Antennae, tentacular cirri, dorsal cirri, and anal cirri very long, filiform and smooth. Ventral cirri digitiform, inserted subdistally on parapodia. Pharyngeal tube long, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5–8), with a crown of distal pharyngeal papillae. Compound chaetae falcigerous, blades bidentate or tridentate, dorsal and ventral simple chaetae absent. Reproduction by epigamy. Florida, Canary Islands, and the Mediterranean Sea; 2 species (Fig. 7.13.2.38D).

See also Perkins (1981).

***Guillermogonita* Böggemann, 2009**

Guillermogonita Böggemann, 2009: 406.

Type species: *Guillermogonita abyssicola* Böggemann, 2009.

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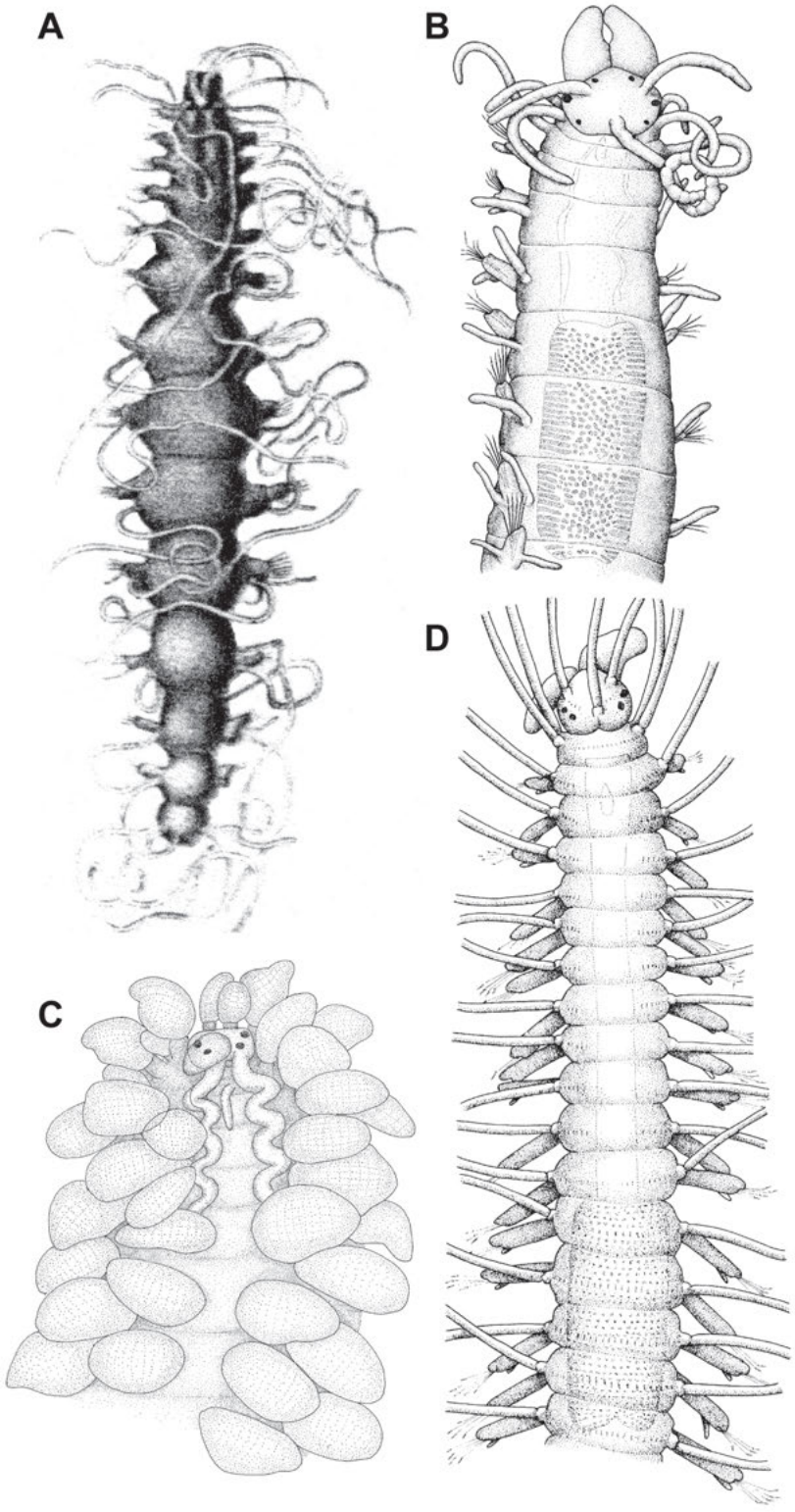


Fig. 7.13.2.38: Anterior ends or whole specimen of species of five more genera considered *incertae sedis*. A, *Brachysyllis infuscata* (Ehlers, 1901). B, *Brevicirrosyllis weismanni* (Langerhans, 1879). C, *Clavisyllis alternata* Knox, 1957. D, *Dioplosyllis cirrosa* Gidholm, 1962. A, After Ehlers (1901); B, after San Martín (2003); C, after Aguado and San Martín (2008). B, San Martín's original drawing modified by Jordi Corbera; C, Aguado's original drawing; D, Gidholm original drawing modified by Jordi Corbera.

Diagnosis: Body slightly flattened dorsoventrally. Palps free. No antennae. Pharynx unarmed. Proventricle without distinct muscle rings. Tentacular cirri short. Dorsal cirri smooth, oval to digitiform. Pharynx unarmed. Compound chaetae falcigerous, bidentate. Dorsal simple capillary chaetae on posterior parapodia. Angola and Guinea basins; only the type species is known (Fig. 7.13.2.39A).

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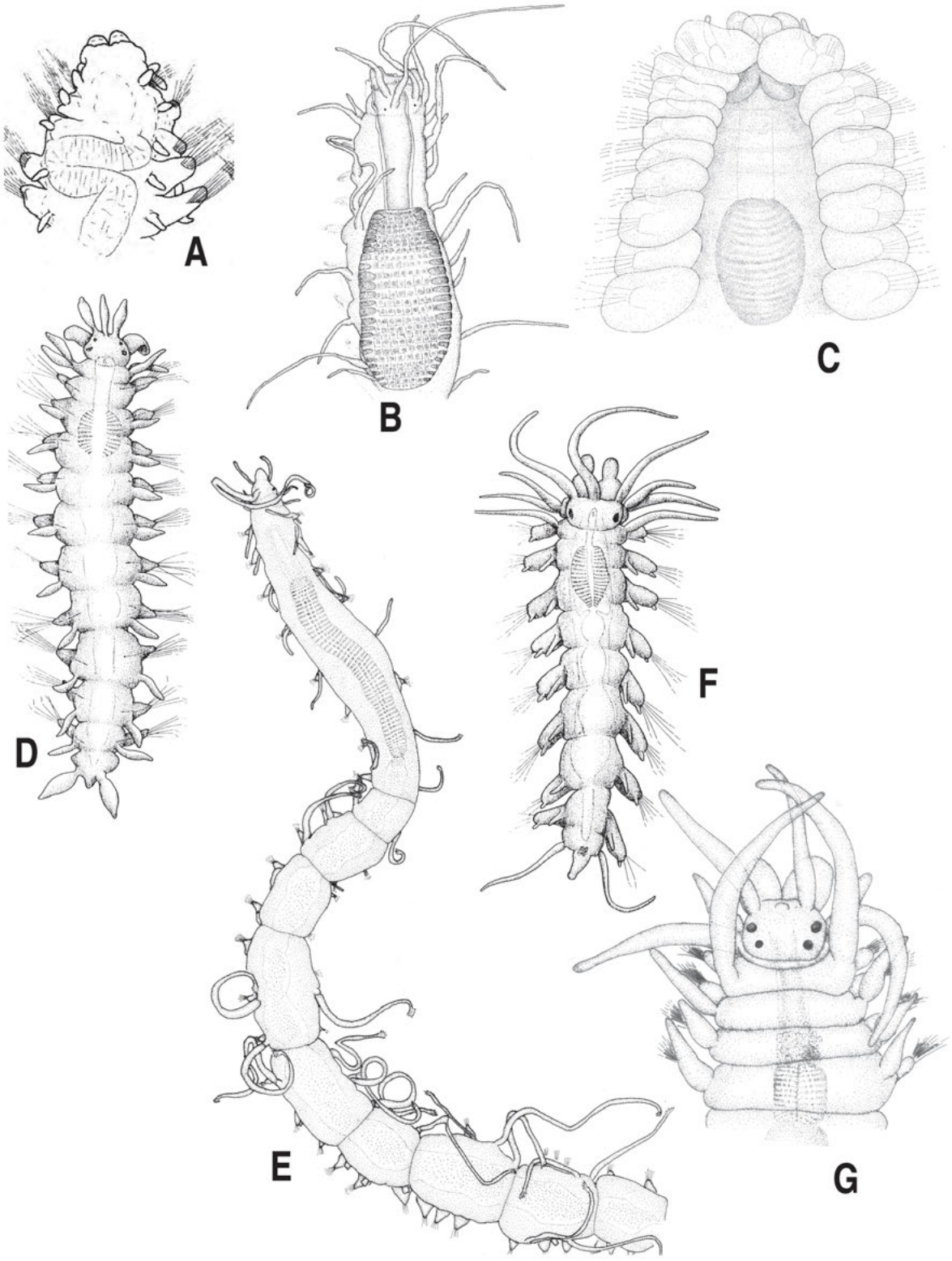


Fig. 7.13.2.39: Anterior ends or whole specimen of species of seven further genera considered *incertae sedis*. A, *Guillermogonita abyssicola* Böggemann, 2009. B, *Haplosyllides floridana* Augener, 1922. C, *Lamellisyllis comans* Day, 1960. D, *Miscellania dentata* Martin, Alós & Sardá, 1990. E, *Murrindisyllis kooromundroola* San Martín, Aguado & Murray, 2007. F, *Neopetitia amphophthalma* (Siewing, 1956). G, *Nooralia bulgannabooyanga* San Martín, 2002. A, After Böggemann (2009); B, after San Martín et al. (1997); C, after Aguado and San Martín (2008); D, F, after San Martín (2003); E, after San Martín et al. (2007); G, after San Martín (2005). B, E, G, San Martín's original drawings; C, Aguado's original drawing. D, Martín's original drawing modified by Jordi Corbera; F, Siewing's (1956) original drawing modified by Jordi Corbera.

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***Haplosyllides* Augener, 1922**

Haplosyllides Augener, 1922: 44.

Type species: *Haplosyllides floridana* Augener, 1922.

Diagnosis: Palps fused over almost their whole length. Antennae, tentacular cirri, dorsal cirri, and anal cirri smooth. Pharyngeal tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae and a layer of cilia; occasionally, large specimens without pharyngeal tooth. Chaetae simple, usually only two per parapodium. Reproduction by means of tricerous stolons. Caribbean Sea and the tropical Pacific; 3 species (Fig. 7.13.2.39B).

This genus was revised by Martin et al. (2009) because it reproduces by scissiparous schizogamy it could belong to the Syllinae. See also San Martín et al. (1997).

***Lamellisyllis* Day, 1960**

Lamellisyllis Day, 1960: 319.

Type species: *Lamellisyllis comans* Day, 1960.

Diagnosis: Palps basally fused. Dorsal pair of tentacular cirri foliaceous, ventral pair cirriform. Two prominent nuchal epaulettes. Dorsal cirri large, ovoid and foliaceous, with distinct cirrophores. Pharynx with middorsal tooth anteriorly located. Compound heterogomph falcigers with blades having long spines on cutting edge. South Africa; only the type species is known. Probably it is a Syllinae (Fig. 7.13.2.39C).

***Miscellania* Martín, Alós & Sardá, 1990**

Miscellania Martín, Alós & Sardá, 1990: 169.

Type species: *Miscellania dentata* Martín, Alós & Sardá, 1990.

Diagnosis: Body very small. Palps separate, ventrally folded. Tentacular cirri similar to antennae. Antennae, tentacular cirri, and dorsal cirri smooth. Dorsal cirri short, more or less fusiform. Pharynx short, with a middorsal tooth and an incomplete arc of minute denticles. Compound chaetae falcigers, and dorsal and ventral capillary simple chaetae present. Reproduction unknown. Mediterranean Sea and Atlantic; only the type species is known. Probably it is a Eusyllinae (Fig. 7.13.2.39D).

***Murrindisyllis* San Martín, Aguado & Murray, 2007**

Murrindisyllis San Martín, Aguado & Murray, 2007: 40.

Type species: *Murrindisyllis kooromundroola* San Martín, Aguado & Murray, 2007.

Diagnosis: Body surface with transverse ciliary bands. Anterior segments (about 9–10) fused as a single piece, including proventricular segments; midbody segments forming groups of two or three fused chaetigers. Palps completely fused and also fused to prostomium. Prostomium with two eyes. Antennae, tentacular cirri, and dorsal cirri smooth. Median antenna very long, coiled, lateral antennae much shorter. Dorsal cirri anteriorly short, longer after proventricle, very long on midbody, showing differences in length but without an obvious pattern, those of posterior parapodia short, papilliform. Dorsal cirri of midbody ending in wide expansion with five longitudinal rows of internal hollow cells forming a "hand-like" structure, and webbed. Pharynx short, unarmed, with 10 terminal papillae. Proventricle very long, about five to seven segments. Anterior and midbody parapodia with compound, heterogomph chaetae. Compound chaetae in anterior and midbody parapodia. Blades and shafts fused t first partially and then more completely in posterior part of body. Capillary dorsal and ventral chaetae on posterior parapodia. Australia; only the type species is known (Fig. 7.13.2.39E).

***Neopetitia* San Martín, 2003**

Neopetitia San Martín, 2003: 49.

Petitia Siewing, 1956: 414.

Type species: *Petitia amphophthalma* Siewing, 1956

Diagnosis: Body very small. Prostomium with single pair of eyes. Palps separate, biarticulate. Antennae, tentacular cirri, and first pair of dorsal cirri smooth, elongate; other dorsal cirri short, papilliform. Pharyngeal tube short, with a middorsal tooth. Compound chaetae, falcigers, and dorsal and ventral capillary simple chaetae present. Temperate and tropical waters; 3 species. Probably, it is a Eusyllinae. Recent papers on this genus are Westheide and Hass-Cordes (2001) and Riera et al. (2007) (Figs. 7.13.2.35D and 7.13.2.39F).

***Nooralia* San Martín, 2002**

Nooralia San Martín, 2002: 333.

Type species: *Nooralia bulgannabooyanga* San Martín, 2002.

Diagnosis: Palps basally fused. Antennae, tentacular cirri, and dorsal cirri of chaetiger one long, cylindrical to spindle shaped; other dorsal cirri short, lanceolate. Pharynx long, unarmed, with a crown of soft papillae on anterior rim. Compound chaetae with short unidentate or bidentate blades. Ventral simple chaetae apparently absent. Females brood eggs dorsally attached to compound notochaetae. Australia; only the type species is known (Fig. 7.13.2.39G).

***Palposyllis* Hartmann-Schröder, 1977**

Palposyllis Hartmann-Schröder, 1977: 87.

Type species: *Palposyllis prosostoma* Hartmann-Schröder, 1977.

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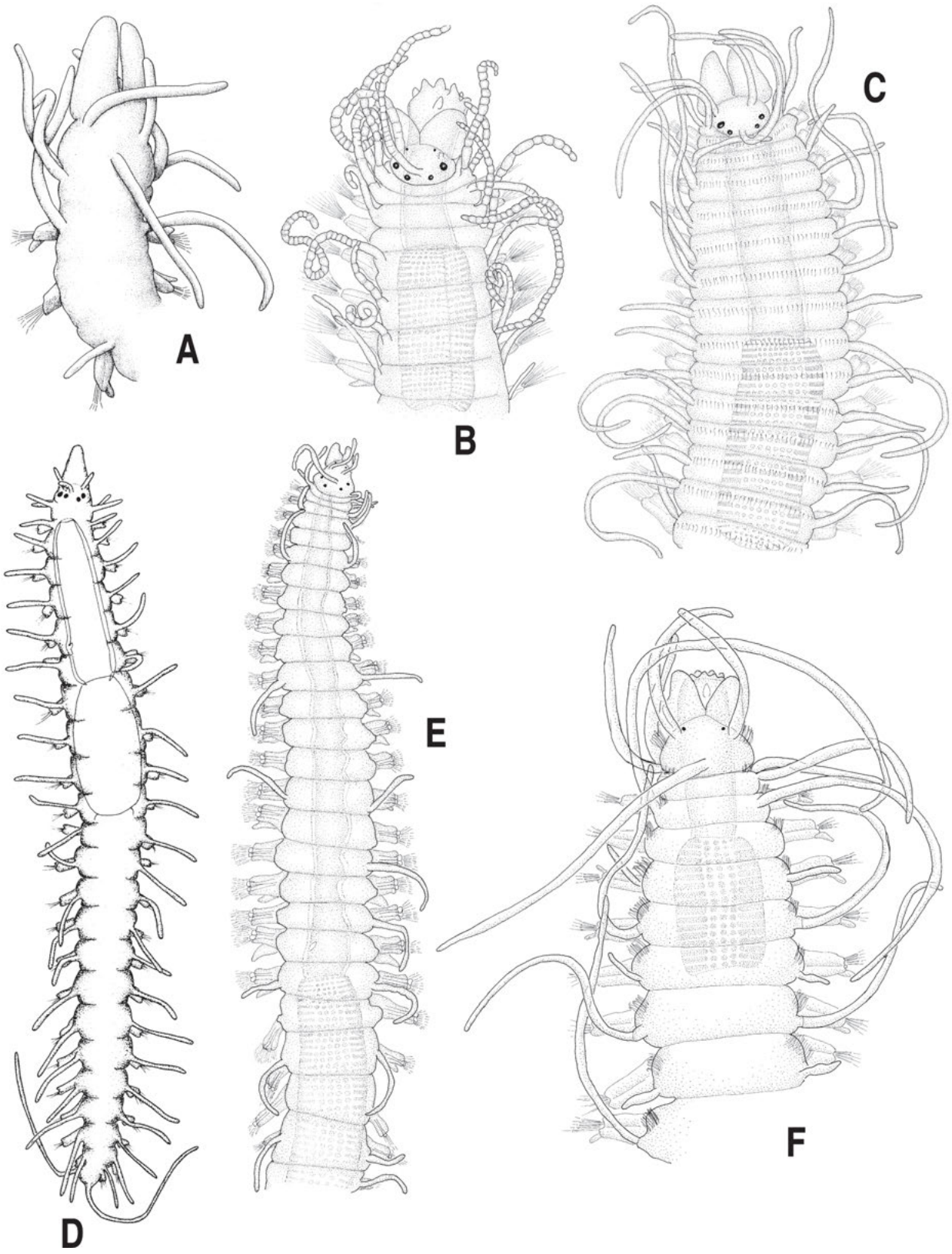


Fig. 7.13.2.40: Anterior ends or whole specimen of species of a further 6 genera considered i*ncertae sedis*. A, *Palposyllis prosostoma* Hartmann-Schröder, 1977. B, *Paraehlersia weissmannioides* (Augener, 1913). C, *Perkinsyllis* serrata (Hartmann-Schröder, 1984). D, *Psammosyllis aliceae* Westheide, 1990. E, *Streptodonta pterochaeta* (Southern, 1914). F, *Westheidesyllis corallicola* (Ding & Westheide, 1997).A, After San Martín (2003); B, C, E, F, after San Martín and Hutchings (2006); D, after Westheide (1990b). A, San Martín's original drawing modified by Jordi Corbera; B, C, E, F, San Martín's original drawings.

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Diagnosis: Prostomium without eyes. Palps elongated, basally fused. Antennae, tentacular cirri, and dorsal cirri smooth, filiform; long anteriorly and posteriorly, shorter in midbody. Ventral cirri digitiform to filiform, elongate. Pharyngeal tooth positioned anteriorly. Compound chaetae falcigerous with short, unidentate blades. Dorsal simple bidentate chaetae on some posterior parapodia. Ventral simple chaeta apparently absent. Reproduction unknown. NE Atlantic and W Mediterranean; only the type species is known. Perhaps, the species *Pionosyllis propeweismanni* Dauvin & Lee, 1983 also belongs to this genus. See San Martín and Aguirrezabalaga (1988) and Dauvin and Lee (1983). Probably it is a Eusyllinae (Fig. 7.13.2.40A).

Paraehlersia San Martín, 2003

Paraehlersia San Martín, 2003: 61.

Type species: *Ehlersia ferrugina* Langerhans, 1881.

Diagnosis: Dorsal ciliary bands on segments. Palps basally fused. Antennae, tentacular cirri, and anterior dorsal cirri annulate or irregularly annulated depending on body size; other dorsal cirri smooth. Parapodia with digitiform, retractile papilla between parapodial lobe and dorsal cirrus. Pharyngeal tooth positioned anteriorly. Compound chaetae include one or more with spiniger-like blades and several with bidentate falcigerous blades. The latter in anterior segments with both teeth similar, posteriorly with proximal tooth longer and more robust than distal tooth (Fig. 7.13.2.8A). Aciculae acuminate. Reproduction by epigamy. Cosmopolitan in tropical and temperate waters; 6 species. Recent papers dealing with this genus are San Martín and Hutchings (2006) and Fukuda et al. (2012). Probably it is a Eusyllinae (Figs. 7.13.2.40B and 7.13.2.41A).

Perkinsyllis San Martín, López & Aguado, 2009

Perkinsyllis San Martín *et al.* (2009): 1479.

Type species: *Pionosyllis longisetosa* Hartmann-Schröder, 1965.

Diagnosis: Anterior segments with a single dorsal row of cilia, double after proventricular segments. Palps basally fused. Antennae, tentacular cirri, and dorsal cirri long to very long. Pharyngeal tooth positioned anteriorly. Compound chaetae elongate falcigers with long, fine, distally directed spines on margin sometimes with slender, spiniger-like forms. Dorsal and ventral simple chaetae on posterior parapodia. Aciculae distally expanded. Reproduction unknown for most species. Ventral brooding reported in 3 species. Cosmopolitan in temperate and tropical waters; 11 species. Recent papers are Fukuda and Nogueira (2013); also in San Martín and Hutchings (2006) several species of this genus are described as *Pionosyllis*. Morphologically, it could belong to the Eusyllinae, but it appears as the sister group of the Syllinae in the molecular analysis (Figs. 7.13.2.40C and 7.13.2.41A).

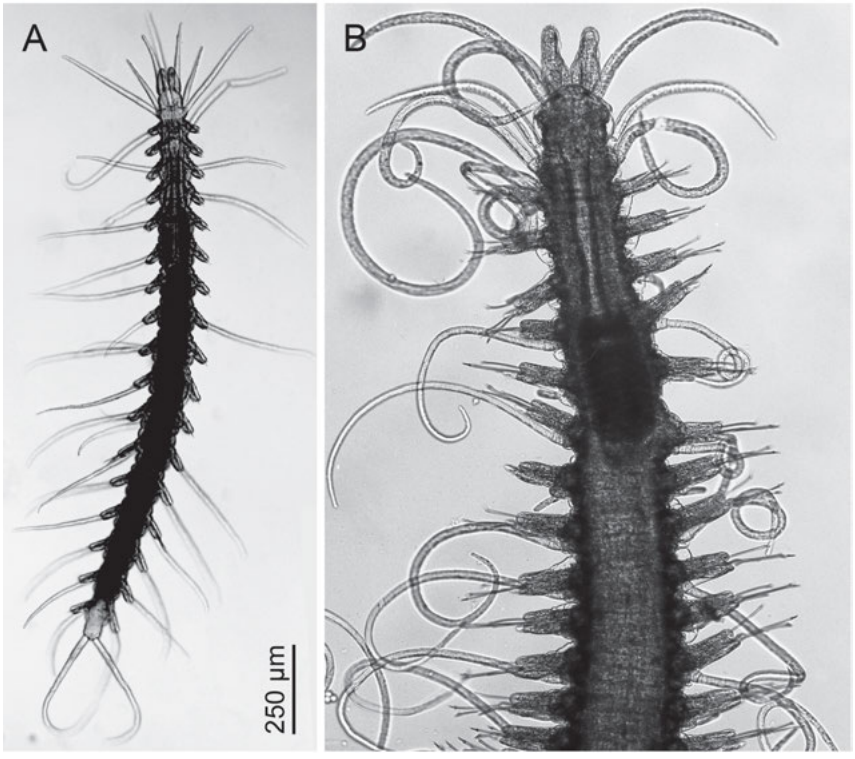


Fig. 7.13.2.41: A, *Perkinsyllis homocirrata* (Hartmann-Schröder, 1958), entire animal. B, *Westheidesyllis corallicola* (Ding & Westheide, 1997), anterior ends. Originals W. Westheide, Osnabrück.

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Psammosyllis Westheide, 1990

Psammosyllis Westheide, 1990b: 165.

Type species: *Psammosyllis aliceae* Westheide, 1990.

Diagnosis: Palps fused, sometimes with a distal notch. Dorsal cirri on all segments smooth, cylindrical, longer than parapodial lobes, shorter than body width. Pharyngeal tooth stout, small, located posteriorly on side of pharynx, which is wide and lacks papillae. Proventricle massive. Compound chaetae heterogomph, with short blades. Dorsal and ventral simple chaetae on some parapodia. Reproduction unknown. Tropical areas of the West Pacific and Indian Ocean; 3 species. See San Martín and Hutchings (2006). Probably, it is a Eusyllinae (Fig. 7.13.2.40D).

Streptodonta San Martín & Hutchings, 2006

Streptodonta San Martín & Hutchings, 2006: 353.

Type species: *Opisthodonta pterochaeta* Southern, 1914.

Diagnosis: Palps basally fused. Antennae, tentacular cirri, and dorsal cirri elongate, smooth, distally tapered. Pharynx and proventricle long, pharyngeal tooth located laterally and distinctly posteriorly, close to proventricle. Compound chaetae with translucent hood, ornamented with several rows of minute spines or with simple row of spines. Dorsal simple chaetae with translucent hood. Ventral simple chaetae present in one species. Aciculae of several anterior parapodia distinctly enlarged. Reproduction by epigamy. Subpolar, temperate Atlantic and Mediterranean, Brazil, Australia; 3 species. See Ramos et al. (2010) and Paresque et al. (2015). Probably, it is a Eusyllinae (Fig. 7.13.2.40E).

Westheidesyllis San Martín, López & Aguado, 2009

Westheidesyllis San Martín, López & Aguado, 2009: 1492.

Type species: *Eusyllis heterocirrata* Hartmann-Schröder, 1959.

Diagnosis: Body with dorsolateral and ventrolateral rows of cilia. Palps basally fused, divergent. Antennae, tentacular cirri, and dorsal cirri long, smooth, cylindrical; short dorsal cirri present on some midbody parapodia. Dorsal cirri absent on chaetiger 2. Ventral cirri distally inserted on parapodial lobes. Pharyngeal tooth anteriorly located. Compound chaetae homogomph, with bifid articulation and short falcigerous blades that are minutely bidentate, with a small proximal tooth; spines of blades short to moderate. Dorsal simple chaetae on posterior parapodia. Tips of aciculae distally rounded or laterally expanded. Reproduction unknown. Tropical areas; 3 species. See Perkins (1981) and San Martín and Hutchings (2006). Probably, it is a Eusyllinae (Figs. 7.13.2.40F and 7.13.2.41B).

Acknowledgments

This study was supported by the project "Caracterización Taxonómica y Sistemática de la familia Syllidae (Polychaeta) basada en datos moleculares y morfológicos. El problema de las especies cosmopolitas y Biodiversidad en el Pacífico," founded by the "Ministerio de Ciencia e Innovación" of the Spanish Government, Project number CGL2009-12292 BOS. The authors thank Drs. José Luis Viejo, Emilio Crespo, and Ma. Paz Molina (UAM) for the help about the origin of the family name. Especial thanks to Tim Worsfold, Unicomarine, Thomson Ecology Ltd. Letchworth, Herts, UK, for his valuable suggestions and help with the English style. Jacinto Pérez Dieste allowed us to use the photograph of Figure 7.13.2.2B. Drs. Günter Purschke and Wilfried Westheide offered us to participate in this handbook and offered valuable advices, information, photos, and suggestions. Alexander Semenov and Nancy Maciolek allowed us to use their photos (Fig. 7.13.2.4) and original drawings (Fig. 7.13.2.34B). Aida Verdes provided us with some interesting literature on Bioluminiscence. Comments and suggestions of two anonymous referees also greatly improved the quality of text and figures.

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7.13.3 Nereidiformia

Charlotte Watson

7.13.3.1 Chrysopetalidae Ehlers, 1864

Introduction

The family Chrysopetalidae Ehlers, 1864 has historically been recognized as a free-living member of the Phyllodocida with complex head appendages, muscular eversible proboscii, lateral jaws, and biramous parapodia bearing simple notochaetae and compound neurochaetae. Evidence for monophyly of the family has included the presence of internally camerated transformative paleael notochaetae (Fauchald and Rouse 1997, Watson Russell 2000a, Rouse and Pleijel 2001, Watson 2020) and a pair of hollow, grooved stylet jaws (Watson and Faulwetter 2017). A recent interesting investigation showed the symbiont families, Nautiliniellidae and Calamyzidae, that putatively lack notochaetae to be derived from chrysopetalids (Aguado et al. 2013), thereby adding 15 taxa to the Chrysopetalidae and extending the chrysopetalid body concept in size and morphological range, including jaw types and feeding behaviors. Chrysopetalidae now comprises three subfamilies: Chrysopetalinae Ehlers, 1864; Dysponetinae Aguado, Nygren & Rouse, 2013; and Calamyzinae Hartmann-Schröder, 1971. At present, Chrysopetalidae encompasses 29 genera, the majority deep-sea dwellers and ~100 species, the majority of which are western Pacific, reefal, cryptic species (Watson personal observation).

Chrysopetalidae are found worldwide, Arctic to Antarctica, across an extraordinary range of habitats and depths. Chrysopetalinae occur in crevices of hard substrates from coral and rocky reefs to within bivalve colonies in deep-sea wood falls and hydrothermal vents; the Dysponetinae from temperate kelp forests to abyssal mud plains. The Calamyzinae have clearly been successful in exploiting deep-sea chemosynthetic ecosystems with free-living taxa inhabiting anoxic basins at the boundary of the hydrogen sulfide zone and bacterial mats associated with whale falls and methane seeps; symbiont taxa variously lead shallow water ectosymbiont or endosymbiont lifestyles within chemosynthetic deep-sea bivalves. A number of species within all three subfamilies (unknown for symbionts) possess planktonic larvae. Metamorphosing larvae and gametous adults display morphological adaptations and strategies that indicate potential for long-distance dispersal (e.g., Meilikovsky 1962, Watson et al. 2014, 2016, Watson 2020).

Chrysopetalinae species are distinguished by short, well-defined segmented bodies and distinctive metallic-colored, internally camerate paleae (flattened notochaetae) held in segmental fans that imbricate down the flattened dorsum (Fig. 7.13.3.1.1A) and a suite of complex sensory characters (summarized in Watson and Faulwetter 2017). Taxa display a specialized buccal structure comprising a well-developed muscular pharynx, proboscis, and a pair of pointed, grooved stylet jaws. The morphology of the jaws and documented association with invertebrates in cryptic habitats led Watson and Faulwetter (2017) to consider this group to be both free-living and facultative symbionts. Chrysopetalinae taxa may possess both morphologically distinguishable and cryptic species, e.g., *Paleanotus* (Watson 2015) or taxa with one basic morphological form that have speciated into many cryptic clades within coral reefs of the Indo-Pacific, e.g., *Arichlidon hanneloreae* Watson Russell, 1998; *Treptopale homalos* Watson, 2010; *Treptopale magdae* Wei, Watson & Gibbs, 2013; and reefs of the Caribbean, e.g., *Arichlidon gathofi* Watson Russell, 2000b.

Free-living, errant taxa of the Dysponetinae are small bodied with less well-defined segments and comprise species distinguished by large fascicles of camerate notochaetal spines that laterally cover the dorsum, a pair of simple stylet jaws and simple sensory characters (Fig. 7.13.3.1.1B; Pleijel and Dahlgren 1998). Morphologically similar species are found in endobenthic shallow sedimentary habitats and considered meiofaunal, e.g., *Dysponetus pseudopapillatus* Dahlgren, 1996. Epibenthic species, e.g., *Dysponetus pygmaeus* Levensen, 1879 and *Dysponetus populonectens* Pleijel et al., 2012, are primarily associated with algal cover; *Dysponetus* cf. *caecus* is a globally occurring species from seamounts to abyssal plains (e.g., Böggemann 2009, Watson et al. 2014, Gunton et al. 2021, Watson personal observation).

Calamyzinae comprises both free-living and symbiont clades (Aguado et al. 2013, Watson et al. 2016). The free-living group includes large to very small-bodied taxa that are bacteriovorus, living and feeding within enriched sediments, e.g., *Vigtorniella zaikai* Kiseleva, 1992, and chemosynthetic whale fall and methane seep habitats, e.g., *Micospina auribohnorum* Watson et al., 2016 (Fig. 7.13.3.1.1C). Some species exhibit modified stylet jaws present in the larvae and lost in the adult, e.g., *Boudemos flokati* Dahlgren et al., 2004 (Dahlgren et al. 2004, Watson et al. 2016); all species possess camerate notochaetal spines. Their comparatively simple morphology has led to minor morphological characters, once barely recognizable

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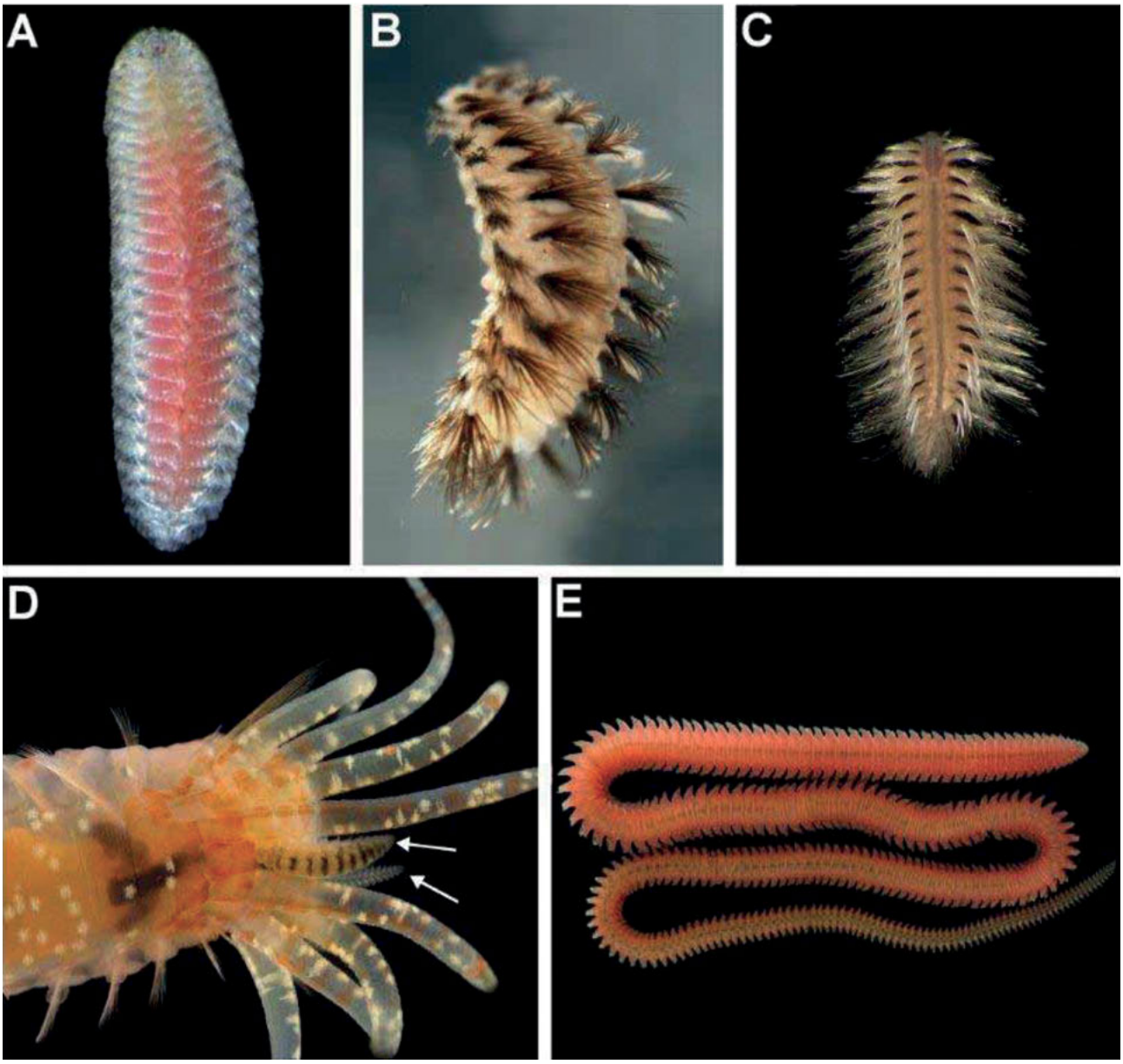


Fig. 7.13.3.1.1: Live photos. A, Chrysopetalinae *Arichlidon gathofi* (~5 mm). B, Dysponetinae *Dysponetus pygmaeus* (~3 mm). C–E, Calamyzinae: free-living *Micospina auribohnorum* (~4 mm) (C); ectoparasite *Calamyzas amphictenicola* (~2.5 mm), arrows indicate two individuals among ampharetid gills (D); symbiont *Shinkai longipedata* (~250 mm) (E). From Watson and Faulwetter (2017). See Acknowledgments for names of photographers.

to separate species (Wiklund et al. 2009), now being used to separate cryptic genera (Watson et al. 2016).

Very large to very small-bodied obligate symbiont taxa live a sedentary lifestyle and display a more radical simplified morphology including undifferentiated lateral antennae and palps and lack of notochaetae, although notoaciculae are often present (Aguado et al. 2013). Former nautiliniellid symbiont taxa reveal stout simple hooked neurochaetae (Figs. 7.13.3.1.1E and 7.13.3.1.8C–E) adaptive to an inquiline lifestyle within mantle cavities of deep-sea host bivalves (e.g., Miura and Hashimoto 1996, Aguado and Rouse 2011). Recently, two new symbiont genera have been described that do possess modified notochaetae: *Spathochaeta octopodis* Jimi et al., 2019 and *Craseoschema thyasiricola* Ravara et al., 2019. The monotypic taxon *Calamyzas amphictenicola* Arwidsson, 1932 possesses a specialized mouth opening and modified stylet jaws adaptive to an ectoparasitic lifestyle on ampharetid polychaetes (Fig. 7.13.3.1.1D; Arwidsson 1932, Aguado et al. 2013, Watson and Faulwetter 2017).

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Morphology

External morphology

Camerate chaetae. Camerate paleal notochaetae are considered a synapomorphy for the family Chrysopetalidae (Rouse and Fauchald 1997, Westheide and Watson Russell 1992, Watson 2000a, Rouse and Pleijel 2001, Pleijel and Gustavsson 2010, Watson and Faulwetter 2017). The definition of *camerate* is "divided into chambers" and *chamber* "an enclosed space, cavity" (Oxford Dictionary Zool.). "Camerate" conveys an *internal* three dimensional sense and is the term preferred by the author; "chambered" was used by Pleijel and Gustavsson (2010) on the basis that the term camerate had been used to describe orbiniid *external* chaetal sculpture by Bleidorn (2005).

Chrysopetalid camerate paleal chaetae are composed of internal longitudinal ribs and thin horizontal septa or diaphragms. Externally, individual palea comprise a slender, basal shaft embedded in the epidermis that broadens distally into a flattened blade and terminates in a sharply pointed or rounded tip. Each palea has a thick cortical coat and thickened, serrate lateral margins and is smooth and slightly convex on the inner ventral side and slightly concave on the outer dorsal side, which may be ornamented with tubercules or raised serrated ribs that commonly gathers detrital scale and bacteria (Figs. 7.13.3.1.2A–C and 7.13.3.1.3A–C; Westheide and Watson Russell 1992, Tilic et al. 2019).

The basal part of the shaft has a more or less oval cross section with small cortical channels; toward the blade, the cortical channels broaden to form broad medullary channels. These channels are separated by thin solid walls stacked with a regular series of horizontal fibrous diaphragms (see in cross section, Fig. 7.13.3.1.4A–C). The medullary part of the palea is completely surrounded by a chaetal cortex with irregular rows of narrow

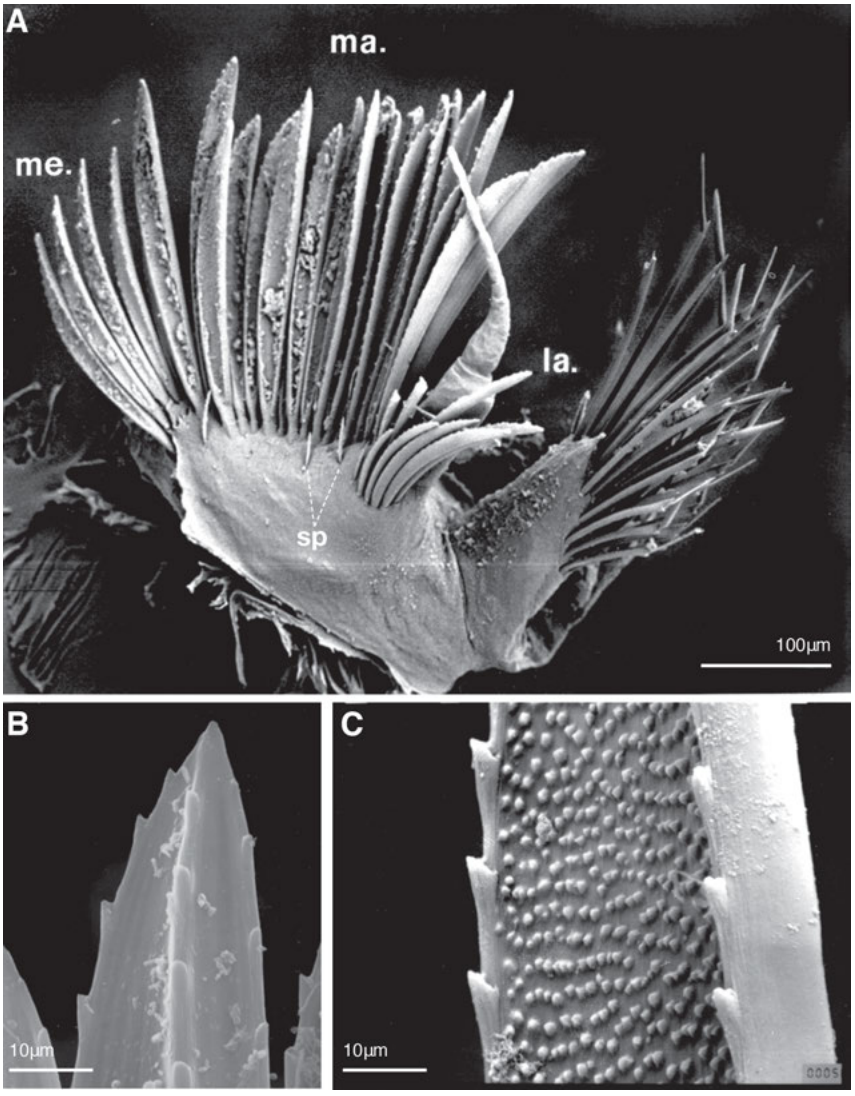


Fig. 7.13.3.1.2: Chrysopetalinae. A–C, *Chrysopetalum* sp. midbody parapodium with paleael notochaetal and compound neurochaetal fascicles. A, Paleal types of notochaetal fan: la, lateral paleae; ma, main paleae; me, median paleae; sp, spine. B, Detail, raised central rib median palea. C, Detail, tubercules on dorsal palea surface, from Westheide and Watson Russell (1992, Fig. 3A, B). SEM images from the author.

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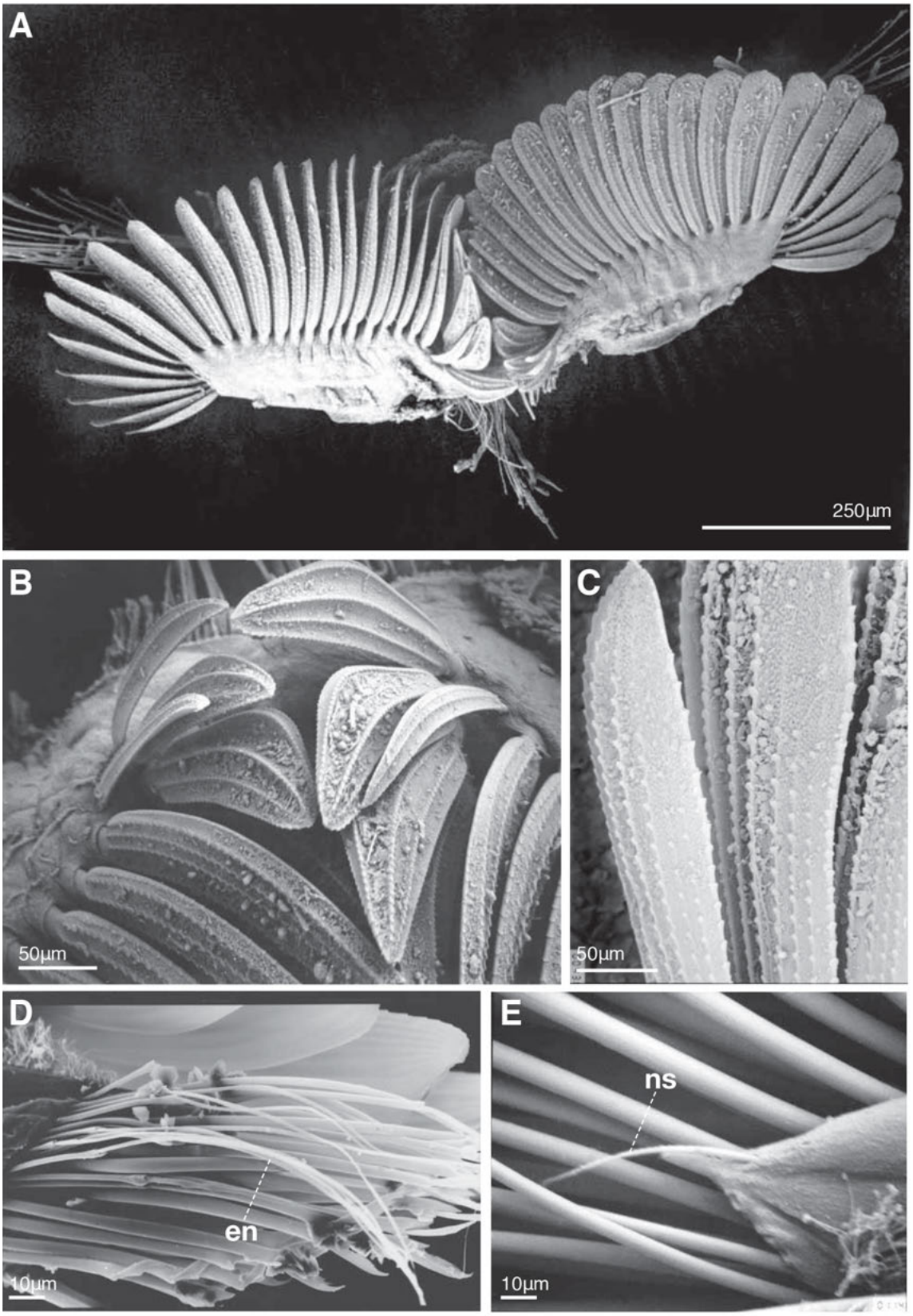


Fig. 7.13.3.1.3: Chrysopetalinae. A–C, *Arichlidon hanneloreae*. A, Midbody notopodia with paleal fans. B, Detail median paleae group. C, Detail main paleae sculpture with raised ribs and tubercules (from Watson Russell 1998). D, E, *Arichlidon gathofi*. Midbody neuropodium. D, en, neurochaetal fascicle with superior epitokous spinigers (from Watson Russell 2000b); E, ns, simple spine overlying neuroacicula. SEM images from the author.

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tubular channels (Fig. 7.13.3.1.4C). Micrographs of sectioned paleae, which have not yet erupted through the surface of the parapodial epidermis, illustrate the continuous process of paleae chaetogenesis, which reveals individual paleae are formed from apex to base (Westheide and Watson Russell 1992, Fig. 2A; Tilic et al. 2019, Fig. 7A–C).

Camerated notochaetae are found in all paleate taxa of the Chrysopetalinae, spinose and paleate taxa of the Dysponetinae, spinose taxa of free-living Calamyzinae, and some ectosymbiont taxa, e.g., *Spathochaeta octopodis* Jimi et al., 2019. Cameration in the shafts of compound neurochaetae is found across taxa of all three subfamilies (e.g., Tilic et al. 2019, Fig. 7E), including the ectosymbiont *Calamyzas* (see Watson and Faulwetter 2017) and *Spathochaeta*. Endosymbiont calamyzins inhabiting deep-sea bivalves possess simple neurochaetae with no apparent cameration, although Aguado et al. (2013) suggested that the presence of longitudinal canals in the chaetae is reflective of a simplification from the camerate condition, e.g., *Shinkai longipedata* Miura & Ohta, 1991 (Fig. 7.13.3.1.5C–E).

Chaetal patterns. Patterns of chaetal morphology within Chrysopetalinae taxa include some noto- and neurochaetal types that are present only at the anterior or posterior end and other chaetal types in the middle body segments that may increase, decrease, or be absent at the anterior and posterior ends. Generally, the largest number and full range of adult chaetal types are found on the middle body segments. Subtle changes in shape, number, and pattern of chaetae occur with growth, so it is ideal to compare a size range of specimens and to then compare the middle body segments from adults of the same size for identification to species (Watson Russell 2000a). Identification to genus of larval chrysopetalids requires entire specimens at the nectochaete or juvenile stages and depends on whether larval notochaetae are very

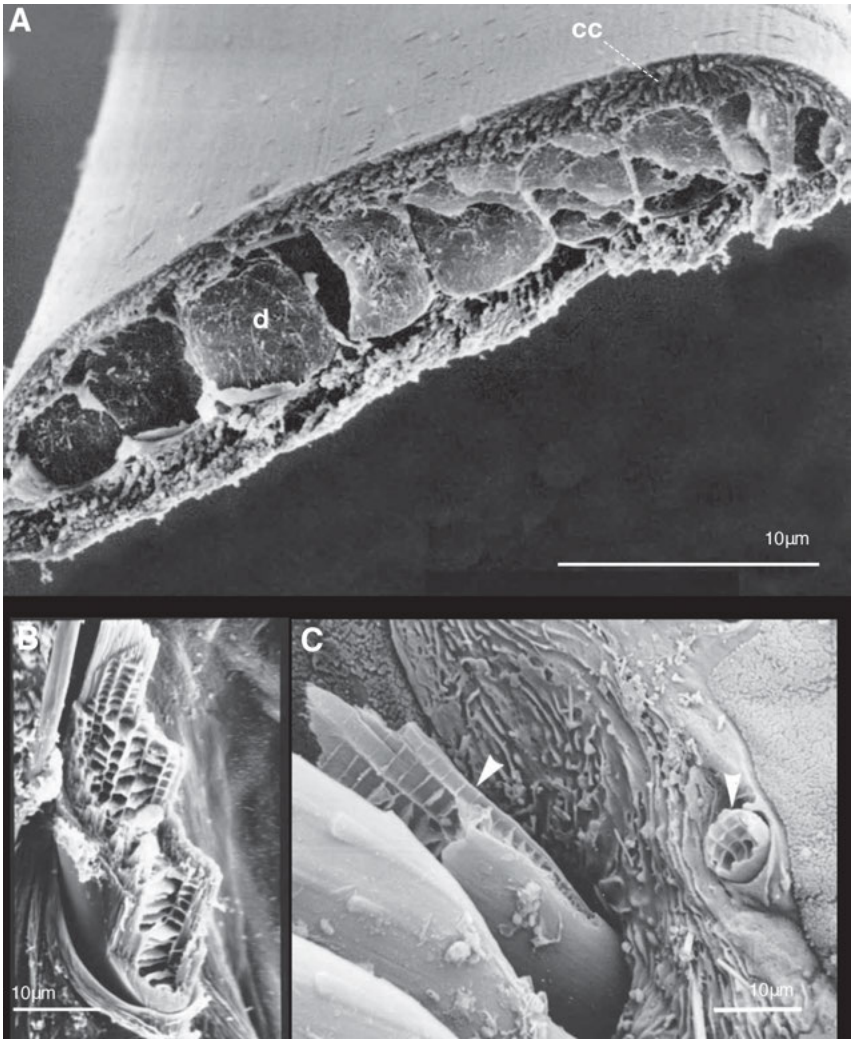


Fig. 7.13.3.1.4: Chrysopetalinae. A, *Bhawania riveti*, cross-sectional view midpalea illustrating diaphragms. cc, chaetal cortex; d, diaphragms. B, C, *Chrysopetalum* sp. internal cameration revealed at broken basal sections of paleae: lateral view (B), basal-lateral view (C); arrows, camerate structure. SEM images from the author.

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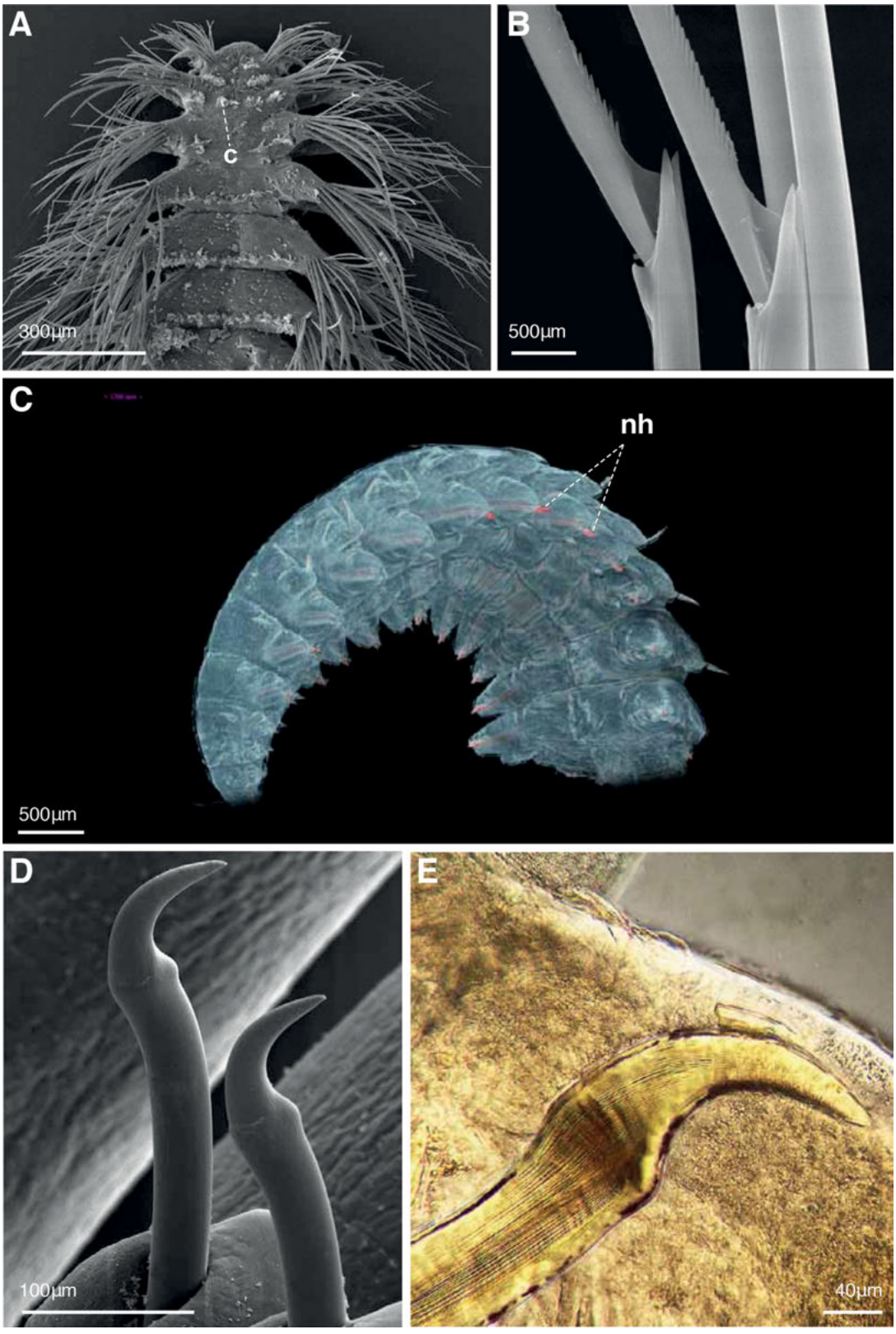


Fig. 7.13.3.1.5: Calamyzinae. A, B, Free-living, *Micospina auribohnorum*. A, Anterior end, dorsal view, *c*, cilia bands. B, Detail bifid shafts of compound neurochaetae, from Watson et al. (2016). C–E, Symbiont, *Shinkai longipedata*. C, Anterior end, laterodorsal/ventral view: nh, neurochaetal hooks, micro-CT scan, color enhanced, Sarah Faulwetter. D, Two neurochaetal hooks midbody, E, Prechaetal view, detail internal structure of single hook, Fig. 7.13.3.1.8D, E. SEM and microphotograph from Aguado and Rouse (2011).

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different to those of adult, e.g., *Strepternos* (see Watson Russell 1997) and *Chrysopetalum* (see Watson 2020), or larval notochaetae bear resemblance to those of adults with identifiable chaetal types initiated in nectochaetes around the fourth to fifth segment, e.g., *Arichlidon reyssi* (Katzmann, Laubier & Ramos, 1974) (see Watson et al. 2014).

Midbody segments support fascicles of foliaceous paleae that originate from shallow dorsal transverse notopodial ridges. Notochaetal types correspond to different positions relative to the dorsal acicula: (1) small fascicle of subacicular, narrow *lateral* paleae; (2) large fascicle of supra-acicular, broad *main* paleae; (3) small fascicle of short *median* paleae that arise at an angle to the main group at the dorsal midline and overlap (Fig. 7.13.3.1.3A, B); (4) subunit paleae, typically situated between different paleael groups; and (5) small serrate spines anterior to these groups, e.g., *Chrysopetalum* sp. (Fig. 7.13.3.1.2A). Recent ultrastructural study further confirms these different notochaetal formative sites (Tilic et al. 2019). Neuropodia of midbody segments have a subacicular fascicle of compound neurosetae that may be divided into three or four groups, depending on the spinigerous or falcigerous article type and their position within the fascicle (Fig. 7.13.3.1.2A; Watson Russell 2000a). Additional chaetal types occur within certain taxa, e.g., all species of *Arichlidon* possesses a simple neurochaetal spine overlaying the neuroacicula and gametous individuals a fascicle of long, slender swimming compound chaetae in a similar position (Fig. 7.13.3.1.3D, E; Watson Russell 1998).

The majority of Dysponetinae species possess a tightly, whorled fascicle of camerate, simple spinose notochaetae that insert in a shallow notopodium and cover the dorsolateral sides of an individual, e.g., *Dysponetus pygmaeus* Levinsen, 1879 (Figs. 7.13.3.1.1B, 7.13.3.1.6A, and 7.13.3.1.7B). Two exceptions are *Dysponetus gracilis* Hartmann, 1965, with paleal notochaetae that insert in loose fans covering the dorsum (Fig. 7.13.3.1.7C, D; Aguirrezabalaga et al. 1999), and *Dysponetus paleophorus* Hartmann-Schröder, 1974, which possesses aberrant paleae-like notochaetae that co-occur with normal spinous notochaetae (Dahlgren 2000). Subacicular compound neurochaetae with mainly falcigerous articles may be divided into three basic groups based on length of article and position; simple, long neurochaetal spines may also be present, e.g., *Dysponetus macroculatus* Dahlgren, 1996 and *D. gracilis* with two paleae-shaped spines (Watson personal observation).

Free-living Calamyzinae species possess very similar camerate notochaetal and neurochaetal fascicles, which are similar in shape, although even more attenuated, when compared to Dysponetinae species. Deep-sea species belonging to both of these subfamilial groups may also possess bifid shafts of compound neurochaetae, e.g., *Micospina auribohnorum* (Fig. 7.13.3.1.5B). Symbiont Calamyzinae taxa display a range of modified chaetal types that appear to maximize the most successful morphological "fit," living either on the surface or within the bodies of their hosts. Ectosymbiont calamyzins display camerate compound neurochaetae and modified notochaetae, e.g., *Spathochaeta,* or lack notochaetae, e.g., *Calamyzas*. Endosymbionts possess subbiramous parapodia and lack notochaetae, although notoacicula are present in many taxa. Simple hooked neurochaetae show differences in numbers and hook shape depending on species; for example, *Iheyomytilidicola lauensis* Aguado & Rouse, 2011 possesses three neurochaetal types: robust simple hooked chaetae, shorter distally bifurcate chaetae, and multiple, slender sigmoid chaetae (Aguado and Rouse 2011, Figs. 13–18) and *Shinkai longipedata* with robust simple hooked chaetae only (Fig. 7.13.3.1.5C–E; Aguado and Rouse 2011).



Fig. 7.13.3.1.6: A, Dysponetinae. *Dysponetus caecus* anterior end with midbody epitokous neurochaetae, microphotograph from Watson et al. (2014).

Body form, prostomia, and pygidia. The inclusion of symbiont taxa within the Chrysopetalidae has greatly extended the chrysopetalid body concept both in size and morphological range (see Fig. 7.13.3.1.1A–E). Chrysopetalinae taxa range in length from *Hyalopale* (<3 mm at ~20 segments) to *Bhawania (*50 mm at ~300 segments). Body length in all taxa is relatively short compared to the number of segments. Segments are short and close together with a flattened to very slight convex dorsum covered in imbricating notochaetal paleal fans and a flat ventrum with a number of taxa possessing segmental ventral pads, e.g., *Thrausmatos* (see Watson 2001). The speciose taxon *Dysponetus* possesses species ranging in length from *Dysponetus pygmaeus*, ~2 mm at 15 segments, to *Dysponetus populonectens*, ~6 mm at 36 segments. Body shape is rectangular, not particularly dorsally convex or with flattened

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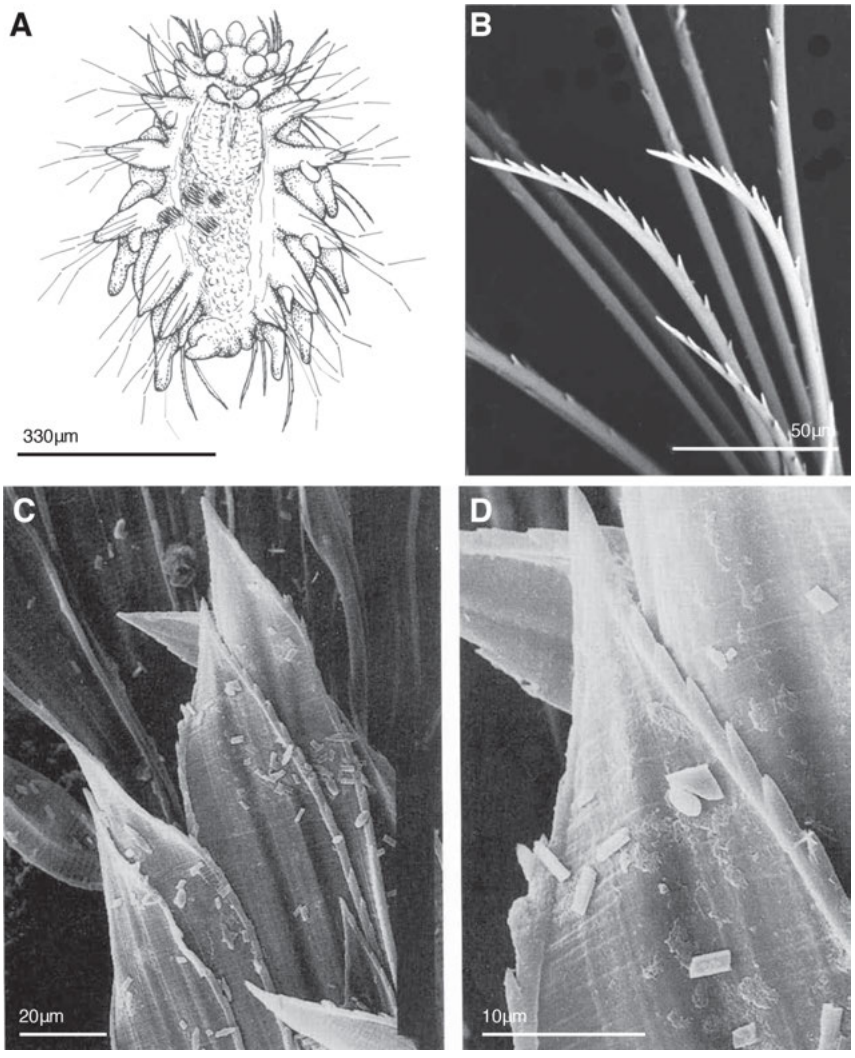


Fig. 7.13.3.1.7: Dysponetinae. A, *Dysponetus pygmaeus* planktonic nectochaete, ventral view (from Watson Russell 1987). B, *Dysponetus bulbosus* detail of spinose notochaetae, SEM image author. C, D, *Dysponetus gracilis* detail of paleael-shaped notochaetae (from Aguirrezabalaga et al. 1999).

ventrum and segmentation not as clearly defined as in Chrysopetalinae. Chrysopetalinae and Dysponetinae taxa possess a well-defined prostomial lobe usually with two pairs of eyes, a median antenna, a pair of lateral antennae, and ventral palps; the latter two appendages differentiated, e.g., *Paleaequor* (Fig. 7.13.3.1.8A, B; Pleijel and Dahlgren 1998, Watson Russell 2000a).

Free-living calamyzin taxa range in length from very small, e.g., *Vigtorniella zaikai* (Kiseleva, 1996) <2 mm length at 14 segments to *Boudemos flokati* (Dahlgren et al., 2004), 40 mm at 91 segments. Symbiont calamyzin taxa exhibit the largest size range within the Chrysopetalidae from very short to very long bodied: the ectoparasitic taxon, *Calamyzas amphictenicola* (Arwidsson, 1932), attains ~2 mm length (12–17 segments), body shape ovate to broadly rectangular (Fig. 7.13.3.1.1D), whereas the inquiline symbiont, *Shinkai longipedata*, is very elongate bodied with deeply incised parapodia and attains 200 mm in length for 300–400 segments (Fig. 7.13.3.1.1E; Aguado et al. 2013). Free-living and symbiont calamyzins lack median antenna and eyes and possess a shallow, curved, lobe-like prostomium fused with anterior segments, e.g., *Micospina auribohnorum* (Fig. 7.13.3.1.5A). Free-living, e.g., *M. auribohnorum*, and some ectosymbiont calamyzins, e.g., *Spathochaeta octopodis*, bear a pair of digitiform, dorsally orientated lateral antennae and a differentiated pair of ventral palps. Some ectosymbionts, e.g., *Calamyzas*, and endosymbionts possess undifferentiated, laterally orientated antennae and palps (Aguado et al. 2013, Watson et al. 2016).

Pygidia in all taxa of the Chrysopetalidae basically comprise a lobe with or without anal cirri. Pygidial shape has two major forms in the Chrysopetalinae: one is consistent between species within a taxon, e.g., quadrate with two anal cirri, e.g., *Treptopale paromolos* (see Watson 2010, Fig. 9A) or conical with two anal cirri, e.g., *Thrausmatos dieteri* Watson, 2001 (see Watson 2001, Fig. 5A, B). A single taxon possesses two forms

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consistent between species within geographical regions: Indo-Pacific *Paleaquor* species display a quadrate pygidium and two anal cirri and Eastern Pacific and Western Atlantic *Paleaquor* species exhibit the same configuration but with an additional anal cone (Watson Russell 1986). Pygidia of free-living calamyzins comprise of a rounded lobe with a pair of anal cirri, e.g., *Micospina auribohnorum* (see Watson et al. 2016) and that of symbiont calamyzins a rounded lobe lacking cirri (Aguado et al. 2013). All *Dysponetus* species possess a pygidial conical lobe without anal cirri (Pleijel and Dahlgren 1998).

Anterior segments. The formulae of the number of the cirri of anteriormost segments vary between and within subfamilial classifications. All taxa of Chrysopetalinae, Dysponetinae (except *Pseudodysponetus*), and free-living Calamyzinae possess an achaetous segment 1 with two pairs of dorsal and ventral tentacular cirri. The formulae of the cirri of segment 2 comprise two patterns: a more commonly occurring pattern 1 comprising two pairs of dorsal tentacular cirri with ventral pair absent seen in chrysopetalid, dysponetid, and free-living calamyzin taxa (Fig. 7.13.3.1.8B), and a less common pattern 2 of two pairs of dorsal and two pairs of ventral tentacular cirri present in a number of chrysopetalid and dysponetid taxa (Watson 2020). Variation is seen in the chaetal formulae and the number of the cirri of segments in segments 2–5 in Dysponetinae taxa and segments 1–3 of Calamyzinae symbiont taxa; clarification in these groups is still ongoing (Watson personal observation).

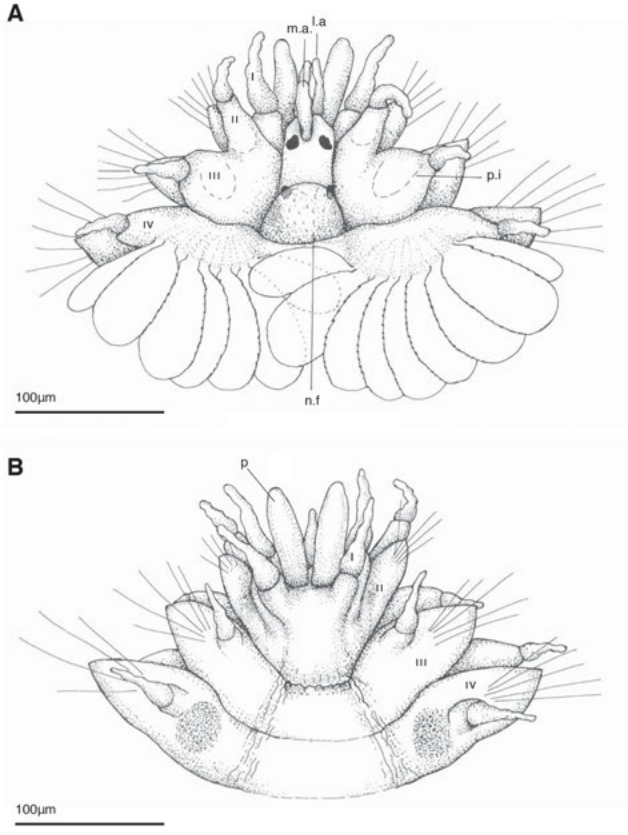


Fig. 7.13.3.1.8: Chrysopetalinae. A, B, *Paleaequor setula* prostomium and anterior four segments: dorsal view (A); ventral view (B): I–IV, segment number; m.a., median antenna; l.a., lateral antennae; n.f., nuchal fold; p, palps; p.i., paleae insertion; from Watson Russell (1986).

Buccal structure, stylet jaws, and feeding. Chrysopetalinae and Dysponetinae are the two subfamilies defined by presence of a mouth appendage: a mouth flap in Chrysopetalinae taxa and buccal cirri in Dysponetinae taxa; characters considered possible synapomorphies for the group by Pleijel and Dahlgren (1998) and Watson Russell (2000a). A proboscis with terminal papillae is also seen in these subfamilies as well as in free-living Calamyzinae taxa. Mouth appendages are absent in all calamyzin taxa and terminal proboscidial papillae are further absent in the symbiont groups (Aguado et al. 2013, Watson and Faulwetter 2017).

Chrysopetalinae taxa possess a distinctive muscular pharynx and cylindrical, eversible proboscis containing two bilateral, calcareous, hollow stylet jaws with a conspicuous longitudinal groove running the entire length, e.g., *Bhawania* spp. (Fig. 7.13.3.1.9A, B). Stylets in all taxa are positioned very close to one another, are distally pointed with tips often dentate, and possess either straight margins or a midway flange according to generic grouping. In conjunction with the muscular pharynx, it is hypothesized that this jaw structure performs a piercing and sucking function with fluids, including possible membrane disruptive enzymes, transported through the hollow cavity (Ehlers 1864, Watson and Faulwetter 2017). Taxa may also possess a partly chitinized pharynx, which in conjunction with the functionality of the stylet jaws, and data on close habitation within sessile invertebrate communities suggest a feeding mode of opportunistic carnivory and facultative symbiosis (Watson and Faulwetter 2017).

All species of Dysponetinae taxa possess a pair of simple, tanned hollow stylet jaws, pointed distally and proximally, with a small swelling midjaw that provides anchoring within the muscular proboscis. The feeding function is posited to be similar to that of Chrysopetalinae taxa, although dysponetids appear free-living with no specific records suggesting facultative symbiosis (Watson and Faulwetter 2017).

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Bacterivorous free-living Calamyzinae taxa inhabit extreme environments. Planktonic larvae and juveniles may possess modified stylet jaws comprising an anterior serrated flat plate and a posterior grooved elongation, e.g., *Vigtorniella zaikai* (Fig. 7.13.3.1.9C, D). Jaws are retained in part in adult *V. zaikai* and completely lost in *Boudemos flokati* adults. It is not known if the presence of jaws facilitates feeding in early life or represents a nonfunctional ontogenetic stage (Watson et al. 2016). Benthic adults inhabit and feed within enriched sediments: *Boudemos flokati* forms a writhing mass hanging off whale bones, which are coated in bacterial mats (Dahlgren et al. 2004) and are associated with bacterial mats on sediment surrounding the whale skeleton; *Boudemos ardabilia* has been filmed close-up in the lab with their extended pharynxes vigorously sucking among dense mats of large filamentous bacteria associated with whale bones (Wiklund et al. 2009, Wiklund personal communication). *Micospina auribohnorum* at methane seeps shows an isotope signature close to that of organisms feeding on sulfide oxide bacteria (Levin et al. 2015, Watson et al. 2016).

Adaptive buccal and chaetal characters in symbiont Calamyzinae taxa are related to a lifestyle that provides a lipid-rich and reliant food source from the host. *Calamyzas amphictenicola* has a modified mouth opening with rings of denticles useful for rasping and gaining entry into host tissue; stylets comprise a small basal angled jaw with a very attenuated, anterior pair of stylets, which can penetrate deep into host tissue (Aguado et al. 2013, Watson

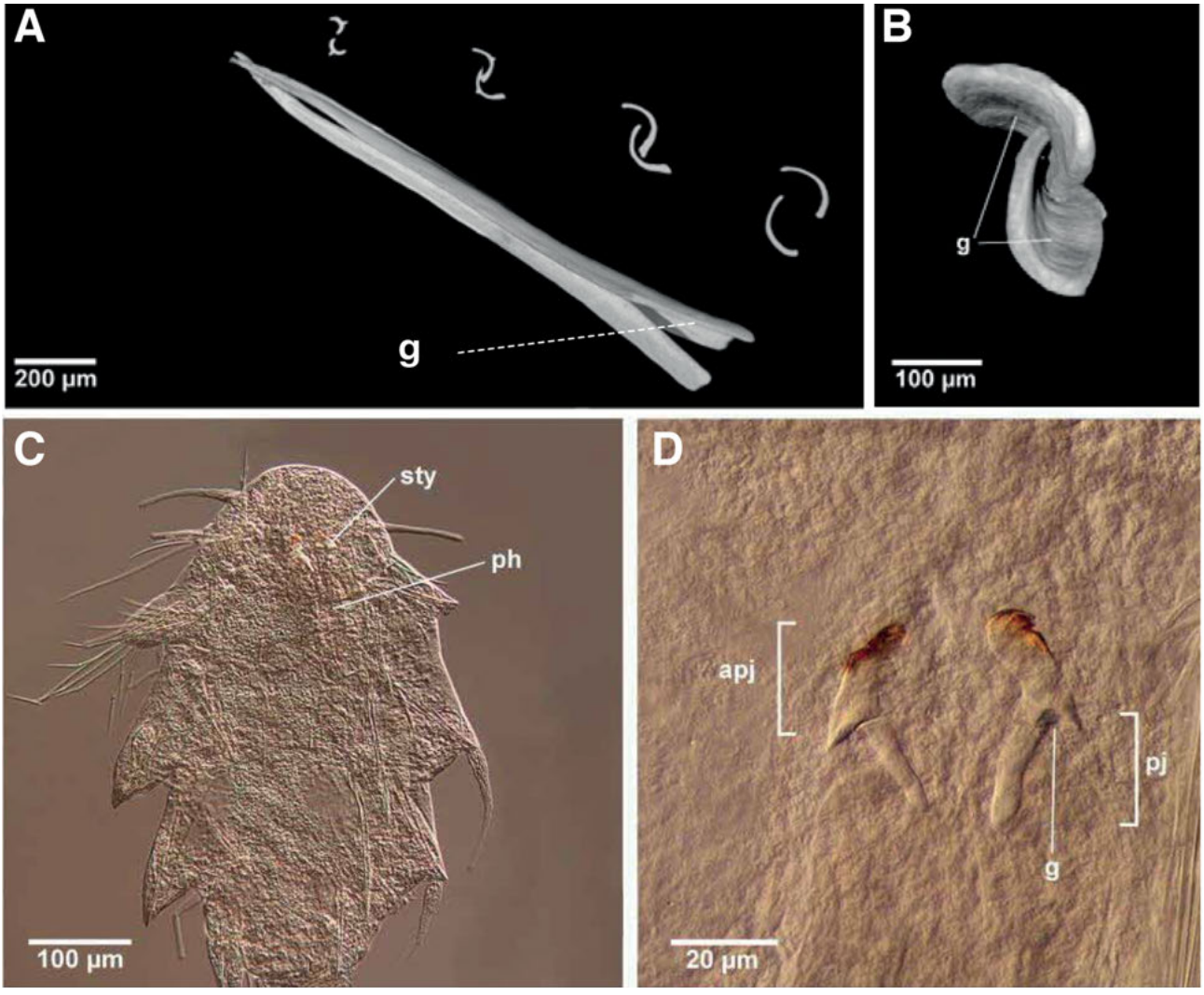


Fig. 7.13.3.1.9: Chrysopetalinae jaws. *Bhawania amboinensis* (A). A, Laterodorsal view and cross sections through jaws along entire length. B, *Bhawania riveti* posterior view; g, groove; micro-CT scan from Watson and Faulwetter (2017); Calamyzinae free-living jaws. C, D, *Vigtorniella zaikai* planktonic larvae. C, Entire body, dorsal view; sty, stylets; ph, pharynx. D. Jaws; apj, anterior platelet jaw; pj, posterior jaw; g, groove; microphotographs from Watson et al. (2016).

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and Faulwetter 2017). *Calamyzas amphictenicola* has been observed attached to different locations over the host body, which indicates a certain mobility aided by camerate compound neurochaetae (Watson and Faulwetter 2017). In comparison, endosymbiont taxa such as *Shinkai longipedata* lead a sedentary existence and have simple hooked neurochaetae useful for purchase while feeding within host bivalve tissue (Fig. 7.13.3.1.5C–E). A pair of small platelet/stylet jaws have recently been found for the first time in adults of the symbiont calamyzin *Shinkai* with the anterior sharp distal structure theoretically functioning well as a scraping tool for partial predation on bivalve tissue (Watson and Faulwetter 2017). Aguado and Rouse (2011) noted that specific calamyzin taxa are associated with certain bivalve taxa, and Neulinger et al. (2006) found that genetic separation of different species of deep-sea bivalves matched the phylogeny of their bacterial symbionts. The specificity of calamyzin symbionts and hosts may also be related to preferential food type.

Anatomy

Nervous system and sensory organs. The ventral nerve cord in *Chrysopetalum debile* (Grube, 1855) appears to be subepidermal, but as epidermal supporting cells are still in contact with nerve cells, it is regarded as basiepithelial. Myoepidermal junctions and additional glial cells divide the ventral nerve cord into several more or less distinct bundles of axons. An entirely intraepidermal position of the nervous system is seen in species of *Dysponetus* (Tzetlin et al. 2002b).

Racovitza's (1896) structural study of the cephalic lobe of *Chrysopetalum debile* (Grube, 1855) included longitudinal and sagittal sections of three enervated regions: first, a sincipital region with a pair of antennal ganglions, four optical ganglions, and a nerve for the median antenna; second, a palp region supporting a pair of palp ganglions; and third, a posterior nuchal region, which possesses a pair of nuchal nerves (Racovitza 1896, Figs. 29–34). A thin transverse ciliated band extends across the middorsal surface of the prostomium, and the slightly visible articulations of the lateral antennae support very small fine hairs (Racovitza 1896, Watson personal observation in *Paleanotus* larvae). Palps are formed from an evagination of the body wall and reinforced along its length by epidermal cells; the tip of the palp is slightly inflated with a slight depression and epidermal cells stretched. It is likely this distal region, supported by thin muscle fibers, is retractile, e.g., *C. debile* in Racovitza 1896 (Figs. 28 and 29) and *Thrausmatos dieteri* (see Fig. 4E of Watson 2001).

Ultrastructural features of nuchal organs are indicative of chemoreceptor function with an olfactory chamber between cuticle and sensory epithelium, a common feature in polychaetes (Storch and Schlötzer-Schrehardt 1988). External nuchal organs are only present in genera of the Chrysopetalinae and take the form of a caruncle or nuchal fold that is located posterior to the prostomium and originating at segment 4 level. Nuchal ciliated patches are found throughout the Dysponetinae, e.g., *Dysponetus* (Dahlgren 1996, p. 576), and in free-living Calamyzinae taxa, e.g., *Micospina* (Fig. 6C of Watson et al. 2016) but appear absent in symbiont taxa (Aguado et al. 2013).

A caruncle is a fixed rounded structure only occurring in taxa with prostomia relatively free of anterior segments, e.g., *Chrysopetalum*, *Acanthopale,* and *Thrausmatos* (see Watson and Faulwetter 2017). Racovitza (1896) described the caruncle of *Chrysopetalum debile* as an evagination of the body wall, which is spherical in shape and attached to the nuchal region by a thin peduncle. Staining of nuchal tissue reveals a cuticle thickened by glandular cells but much thinner on top and possessing very fine, secretive pores in the region of the thickly ciliated transverse ridge (Racovitza 1896, Figs. 33 and 34). Red pigmented chromatic cells are also present in live individuals and are observed in the caruncles of *Chrysopetalum* (see Watson personal observation), *Acanthopale* (see San Martin 1986, Fig. 1), and *Thrausmatos* (see Watson 2001, Fig. 4C).

Highly glandular and unpigmented nuchal folds are present in *Strepternos* (see Watson Russell 1997, Fig. 4B), *Paleaequor* (Fig. 7.13.3.1.8A), *Bhawania* (see Watson Russell 1986), *Arichlidon* (see Watson Russell 1998, Fig. 2B), *Paleanotus* (see Watson 2015, Fig. 8A), and *Treptopale* (see Watson 2010, Fig. 6A) and appear to be very diminished to absent in *Hyalopale* (see Perkins 1985, Watson et al. 2019). Nuchal folds are flexible structures associated with taxa whose prostomia are fused in part to segments 1–3 and appear to be part of the mechanism in contracting the head and anteriormost segments almost completely inwards, e.g., *Paleaequor setula* Watson Russell, 1986 (Watson Russell 1986, Figs. 4–6).

Eyes. Complex eyes are present in polychaetes and may comprise a primary and secondary retina, containing many sensory and pigmented supportive cells, and a lens (Eakin and Hermans 1988). All shallow water species of Chrysopetalinae have complex eyes, although, interestingly, adults of a species complex of *Arichlidon reyssi* (Katzmann, Laubier & Ramos, 1974) possess eyes (Katzmann et al. 1974) regardless of a 1 to 5000m range of depth (Watson Russell 1998). Simple eyes consisting of sensory and pigmented supportive cells are seen in metamorphosing larvae and juveniles of the deep-sea

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taxon *Strepternos didymopyton* Watson Russell, 1991 that are lost in adults (Watson Russell 1997), and eyes are absent in *Thrausmatos dieteri* adults, which dwell at deep-sea vents (Watson 2001). Complex, simple or the complete absence of eyes is reported across taxa of the Dysponetinae from both shallow and deep-sea depths (e.g., Pleijel and Dahlgren 1998, Böggemann 2009) and eyes appear always absent in free-living and symbiont species of Calamyzinae (Aguado et al. 2013, Watson et al. 2016).

Cuticle, ciliation, glands. The cuticle is made up of a grid of collagen fibers in *Chrysopetalum debile* with the underlying epidermis thicker ventrally than dorsally, 30 µm versus 5 µm (Fig. 7.13.3.1.11A; Tzetlin et al. 2002a). There are two dorsal and one ventral transverse ciliary bands on each trunk segment, for example seen in *Arichlidon* (Fig. 7.13.3.1.10A; Watson Russell 1998). Tzetlin et al. (2002a) suggested that these cilia are important in paleate species as they would generate a continuous flow of water underneath the dorsal cover of paleal notochaetae, allowing a continuous gas exchange. External segmental grooves run across the trunk and parapodia between the comparatively short segments; in *Aphrodite*, such grooves direct water currents during respiration (Van Dam 1940). The function of the ciliated epidermis as a gill-like structure is supported by what is known of the preference of settling on well-oxygenated reefs by larval paleate species of Chrysopetalinae taxa; Australian and overseas studies have shown greater chrysopetalid recruitment to windward sites with high current, surge, and clear water (references in Watson 2010).

Interramal rows of cilia, defined by Purschke et al. (2005) as lateral sensory organs, also occur in a number of Chrysopetalinae. Cilia rows are present below the dorsal cirrophore and continue along the notopodial posterior edge and along the neuropodial superior edge; they are seen clearly in microscope view in all species of *Paleanotus* (Watson 2015, Figs. 6D and 8K). Close-up of lateral organs belonging to *Chrysopetalum* sp. reveals disc-shaped distal

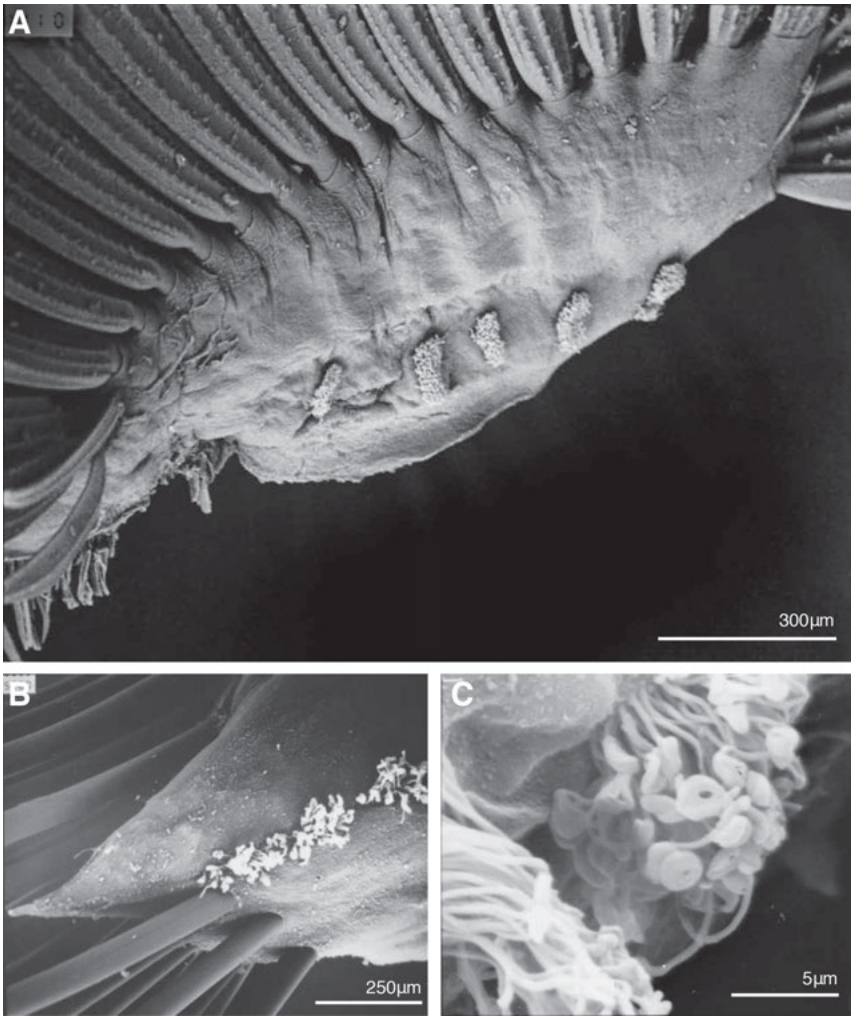


Fig. 7.13.3.1.10: A–C, Chrysopetalinae ciliation patterns. A, *Arichlidon hanneloreae* cilia clumps at base of paleal fan; from Watson Russell (1998). B–C. *Chrysopetalum* sp. B, Neuropodial interramal cilia; C, detail, distal "disc" tips of cilia. SEM images from the author.

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tips (Fig. 7.13.3.1.10B, C); it is not known if this disc structure is naturally occurring or an artifact.

Complex glandular structures are particularly conspicuous within the dorsal cirrophore in mature *Chrysopetalum* species (Perkins 1985, Watson 2020) and in a similar position but directly posterior to the dorsal cirrophore in all *Paleanotus* species (Watson 2015). Gland cells are further concentrated in glandular fields situated medioventrally, lateroventrally, in interramal zones, and on the parapodia. Each glandular field is made up of two types of gland cells: ellipsoid electron dense granules and spherical granules (Tzetlin et al. 2002a).

In *Dysponetus*, the thin cuticle measures 2–3 µm; orthogonally arranged layers of collagen fibers are absent in the cuticle. The epidermis is made up of supporting cells characterized by electron-lucent vacuoles; these appear to be empty and arranged in a monolayer and are particularly evident in the tentacular and parapodial cirri where the cells are densely packed with these vacuoles (Fig. 7.13.3.1.11C; Tzetlin et al. 2002a). This lack of collagen fibers in the cuticle and epidermal supporting cells with vacuoles is typical of meiobenthic interstitial polychaetes (Westheide 1982). External segmental grooves and ciliary bands/patches are absent in the trunk region except for cilia of sensory cells; clusters of gland cells, like those observed in *Chrysopetalum*, have not been observed (Tzetlin et al. 2002a).

Ciliate bands are also found in bands across the dorsum and ventrum and interamally in some free-living Calamyzinae taxa, e.g., *Micospina auribohnorum* (Fig. 7.13.3.1.5A; Watson et al. 2016), but do not appear to be present in symbiont calamyzins (Aguado et al. 2013).

Coelom, blood vascular system. Tzetlin et al. (2002a) found the chrysopetalid body cavity to be truly coelomate, as is typical of most polychaetes (Bartolomaeus 1994), in their ultrastructural study of *Chrysopetalum debile* and *Dysponetus pygmaeus*. In both species, the coelomic cavity is small due to the extensive development of the gut and the longitudinal, oblique, and parapodial muscles, with the remaining space filled with developing and mature gametes.

The larger-bodied *Chrysopetalum* species has an almost complete coelomic lining of the dorsal longitudinal muscle, although it only covers the ventral longitudinal muscle in part. The cells of the somatic lining result in a two- or three-layered myoepthelium in *Chrysopetalum*, but the smaller-bodied *Dysponetus* species, in contrast, represents a more simple construction in which the somatic lining is formed by a single myoepithelium (Tzetlin et al. 2002a).

In both species groups, the blood vascular system comprises conspicuous dorsal and ventral longitudinal blood vessels. Blood vessels are situated within the extracellular matrix, including the presence of an intestinal blood sinus. In *Chrysopetalum debile*, these major vessels give rise to numerous segmental vessels supplying the epidermis, parapodia, and nephridia with a well-developed system of blood capillaries immediately below the epidermis and most abundant in the interramal zone (Fig. 7.13.3.1.11A). The blood vascular system is well developed despite the small size of *Dysponetus pygmaeus*. Major blood vessels give rise to the intestinal vascular plexus, which consists of a system of wide vascular lacunae in the lamina surrounding the gut and nephridia; epidermal vessels were not observed (Fig. 7.13.3.1.11C; Tzetlin et al. 2002a).

Muscles. The absence of circular muscles in the body wall musculature in Chrysopetalidae was confirmed by a confocal laser scanning microscopy study of *Dysponetus pygmaeus* (see Tzetlin et al. 2002b) and histological sections of *Shinkai* sp. (see Aguado et al. 2013). Musculature of the Chrysopetalidae is most similar to that of the Aphroditidae; both families possess a complex and highly developed muscular system (Storch 1968, Mettam 1971). Dorsal expansion of the chrysopetalid notopodium allows various parapodial muscles to occupy a large part of the body cavity; prominent are acicular muscle complexes and longitudinal muscle fibers (Fig. 7.13.3.1.11A; Tzetlin et al. 2000a).

Longitudinal muscles of the trunk are arranged in three bands of dorsal, lateral, and ventral fibers in *Chrysopetalum debile*. The ventral longitudinal muscle is represented by two prominent bundles of fibers on both sides of the ventral nerve cord; a strong contraction of this muscle causes the animal to curl up, presenting a battery of protective/defensive chaetae to an aggressor (Watson personal observation). The dorsal longitudinal muscle consists of three layers: transverse muscle fibers running from the midline toward the parapodial base separate the two inner layers from the outer layer of the dorsal longitudinal muscle. Tzetlin et al. (2002a) considered that the presence of double layer of dorsal longitudinal muscles, in part separated by transverse muscle fibers, may be a specific feature of Chrysopetalinae taxa.

Dorsal musculature of the trunk has a lattice-like appearance with a highly developed system of transverse, oblique, dorsoventral, and parapodial muscles. Dorsoventral muscles form a network arrangement and surround the gut forming prominent attachment zones with

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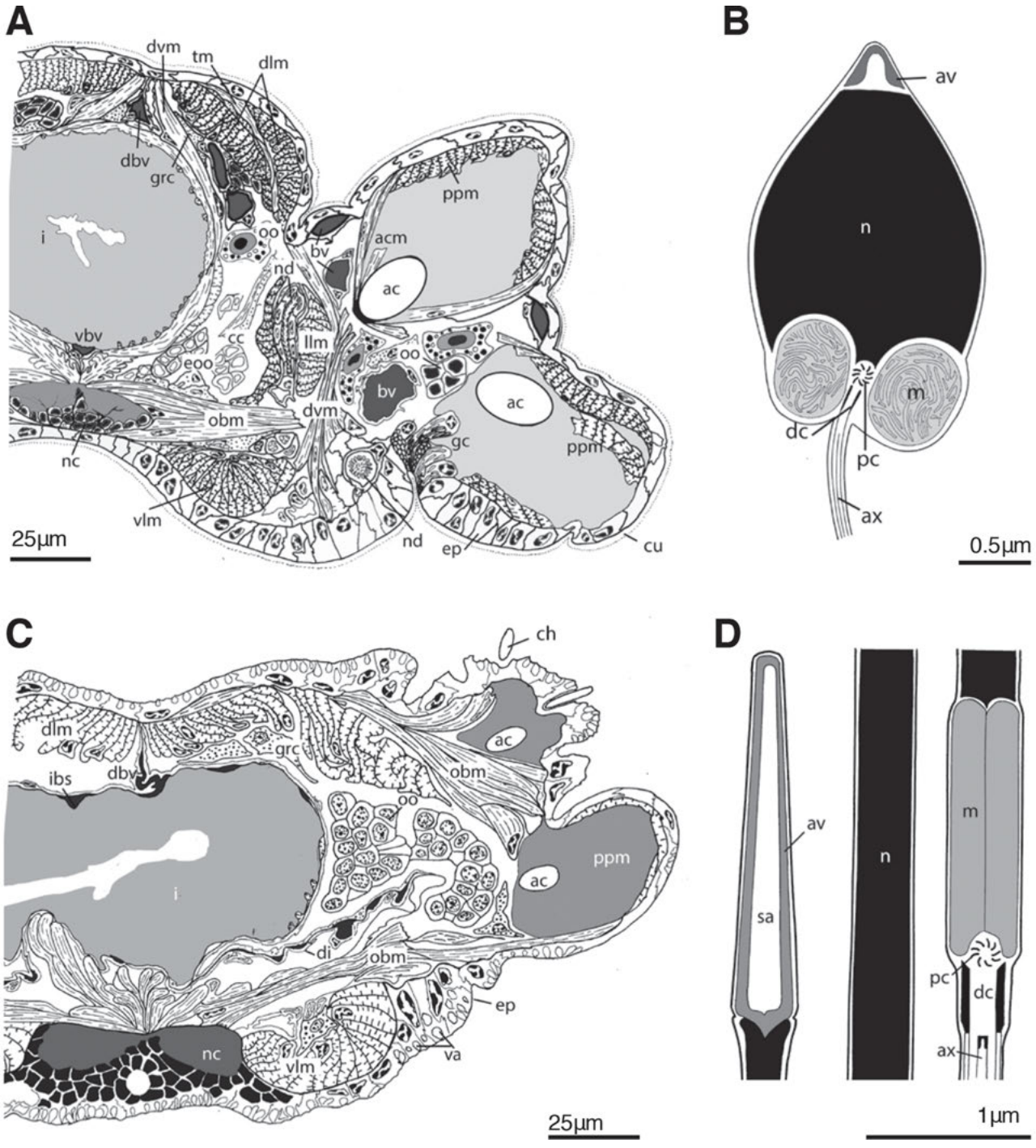


Fig. 7.13.3.1.11: A, Cross section drawings of midbody segments showing arrangement of musculature and blood vessels, note absence of circular muscles in body wall. A, *Chrysopetalum* sp.; B, *Chrysopetalum debile*; C–D, *Dysponetus pygmaeus*. ac, acicula; acm, acicular protractor muscle;bv, blood vessel; cc, ciliated coelomocyte; ch, chaetae; cu, cuticle; dbv, dorsal blood vessel; di, dissepiment; dlm, dorsal longitudinal muscle; dvm, dorsoventral muscle; eoo, early oocyte; ep, epidermis; fc, follicle cell; gc, gland cells; grc, granulocyte; i, intestine; ibs, intestinal blood sinus; llm, lateral longitudinal muscle; nc, ventral nerve cord; nd, nephridioduct; obm, oblique muscle; oo, oocyte; ppm, parapodial muscle complex; tm, transverse muscle; va, vacuole; vbv, ventral blood vessel; vlm, ventral longitudinal muscle. B, D, Spermatozoa: av, acrosomal vesicle; ax, axoneme; dc, distal centriole; m, mitochondrion; n, nucleus; pc, proximal centriole; sa, subacrosomal material (from Tzetlin et al. 2002a).

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each other and the intrinsic musculature of the intestine. The coelomic cavity is traversed by a prominent oblique muscle band, which originates at the ventral nerve cord and runs into the base of the parapodia. The muscle system of the parapodia is divided into an acicular muscle complex and the intrinsic parapodial muscles. Muscle fibers attached to the base of the acicula in notopodium and neuropodium run transversely and penetrate the longitudinal muscle bands, while being in direct contact with the extracellular matrix of the epidermis (Tzetlin et al. 2002a).

The muscle system in *Dysponetus* species represents a more simple type of muscle construction. Longitudinal muscle fibers cover the entire width of the animal and are arranged in a pair of dorsal and ventral bundles. Each bundle occurs in a single layer and is not dorsally or ventrally covered by coelothelial cells. The dorsal longitudinal muscle is arranged in a monolayer, and the lateral longitudinal and dorsoventral muscles are lacking. In the noto- and neuropodium, the oblique muscles are attached either to epidermal supporting cells or to follicle cells making up the chaetal follicules; these fibers form a nearly complete transverse layer (Fig. 7.13.3.1.11C; Tzetlin et al. 2002a). As in *Chrysopetalum*, the dorsoventral muscles surrounding the gut are present, but in *Dysponetus*, they are not developed in the midsegmental zone where the intestine forms lateral extensions. Muscle systems of free-living and symbiont Calamyzinae taxa have not been described.

Nephridia. The nephridial system in Chrysopetalinae and Dysponetinae taxa is represented by typical metanephridia confirming the observations of Fage (1906). Segmentally arranged metanephridia are present in all segments of the trunk in *Chrysopetalum debile* and in all segments, except for segment 5/6 in *Dysponetus pygmaeus*. In *C. debile*, the funnels are situated dorsolaterally in proximity to the lateral longitudinal muscle and lead to the nephrioduct, whose distal part is close to a zone of gland cells that are situated at the point where the posterior edge of the neuropodium meets the ventrum. Nephridial openings are situated in a similar neuropodial position in *Dysponetus* species, although areas of dense gland cells are absent. The entire nephridium including the funnel is surrounded by an extracellular matrix and a thin coelomic lining; the funnel cells are densely ciliated. A distinct nephridial blood vessel is present only in *C. debile*, whereas small spaces surrounding the nephridia of *D. pygmaeus* are interpreted as small blood spaces (Fig. 7.13.3.1.11A, C; Tzetlin et al. 2002a).

Reproduction and development

A number of Chrysopetalinae, Dysponetinae, and free-living Calamyzinae taxa possess planktonic larvae with a morphology indicating a potential for long-range dispersal within the water column (Meilokovsky 1962, Cazaux 1968, Blake 1975, Bhaud 1986, Watson et al. 2014, 2016, Watson 2020). Provisional long spines and primary spinose or paleal chaetal types are linked to an ability to delay metamorphosis while seeking a suitable benthic site with retardation of segment growth and retention of larval chaetal types and larval tentacular segment 1. Final benthic settlement leads to loss of larval morphology and generation of adult segment 1 and chaetae and cirri of adult segments 2 and 3 (Watson Russell 1987, 1997, Watson et al. 2014, Watson 2020). An ability to travel in the plankton is also seen in adults of some Chrysopetalinae and Dysponetinae taxa, which exhibit long-shafted epitokous neurochaetae assisting gametous adults to travel midwater (Aguirrezabalaga et al. 1999, Watson Russell 1998, 2000a, Watson et al. 2014). Mature adults of some Chrysopetalinae taxa are also found in the plankton, which do not display specialized neurochaetae (Meilokovsky 1961, Watson Russell 2000b).

Chrysopetalinae. Gonochorism is indicated for the majority of Chrysopetalinae taxa (summarized in Watson and Faulwetter 2017). Extraovarian vitellogenesis, where the gametes are produced from the peritoneal linings surrounding the blood vessels and gut, is observed in the Chrysopetalidae, e.g., *Chrysopetalum debile* (see Tzetlin et al. 2002a, Watson personal observation), and appears to be the common type in what is known of oogenesis in species of the Phyllodocida (Eckelbarger 1992). Spermatozoa in Chrysopetalinae taxa is of the "primitive" type (Franzen 1977) with a small acrosome and small spherical nucleus followed by four cristae-rich mitochondria, e.g., *C. debile* (Fig. 7.13.3.1.11B; Tzetlin et al. 2002a), *Strepternos didymopyton* (see Watson Russell 1997: Fig. 1E), and *Treptopale paromolos* (see Watson 2010, Fig. 8C). Tzetlin et al. (2002a) suggested that this type of sperm ultrastructure is indicative of external fertilization and a planktonic larval stage.

Complex glandular patterns are observed in parapodia of developing gametous male and female adults and especially prominent in the swollen glands of the dorsal cirriphore, e.g., *Chrysopetalum debile* (see Tzetlin et al. 2002a, Watson 2020) and *Strepternos didymopyton* (see Watson Russell 1977) or posterior to the dorsal cirrophore in *Treptopale* (Watson 2010) and *Paleanotus* species (see

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Watson 2015). The function of these glands linked to gametogenesis is still being investigated (Watson personal observation).

Oocyte sizes differ within and between chrysopetalid genera, and this is hypothesized to relate to the time larvae spent in the plankton and their different larval metamorphosing strategies. Ovigerous females with eggs at the smaller size range have been observed in larger-bodied species, e.g., *Chrysopetalum debile* with a body length of ~12 mm has eggs ~30–50 μm (Ehlers 1864) and 80 μm in diameter (Tzetlin et al. 2002a). *Strepternos didymopyton* with a similar length of 12 mm possesses eggs of ~30–80 μm (Watson Russell 1997).

Interestingly, both *Chrysopetalum* and *Strepternos* exhibit the longest extended developmental patterns during the period from late nectochaete larvae to adult as measured by rate of chaetal change to segment formation. This is possible to document where planktonic larvae exhibit a very different form of primary notochaetae to benthic adult paleael types, which are initiated from the posterior segments of an individual and in the lateral main paleae position of the notochaetal fascicle. This process is clearly seen in *Chrysopetalum* sp. where a 6-segment nectochaete displays notochaetal primary spines in all notopodia down the body. Notochaetal paleae are initiated at the 7- to 8-segment stage, but primary spines persist in anterior segments until the 17-segment stage. Short larval spines are retained at the base of the mature notochaetal fan, which illustrates the transformative stages of rounded serrate spines to broad spines with internal longitudinal ribs and serrated margins (Fig. 7.13.3.1.3A; Watson 2020, Figs. 2–5). *Strepternos didymopyton* possess larvae with expanded, primary paleae that change over time to adults with elongate, pointed paleae fans, e.g., 11 segmented late nectochaete (Fig. 7.13.3.1.12A,B), 27 segmented juvenile (Fig. 7.13.3.1.12C), and 54 segmented adult (Fig. 7.13.3.1.13; Watson Russell 1991, 1997).

The rate of change appears related to environmental factors within a critical developmental period. Benthic postlarvae may also keep provisional spines and primary chaetae and retard adult chaetal types; individuals also retain the larval episphere and larval segment 1 with two pairs of tentacular cirri, while at the same time body segments are developed. When metamorphosis occurs with final settlement, it appears to initiate loss of larval segment 1, transitory chaetal types, and subsequent genesis of achaetous segment 1, which carries the adult two pairs of tentacular cirri. The episphere shrinks to the size of the adult prostomium with full generation of appendages, which appears to further coincide with the initiation of chaetal and cirri change and forming the final pattern of adult segments 11–111 (Watson Russell 1987, 1997, Watson 2020). It is hypothesized that the retardation of anterior segmental and chaetal development is indicative of a larval strategy with a competitive advantage of delaying full metamorphosis and final settlement at a critical life cycle stage (Watson personal observation).

A sequence of loss and initiation of cirri and podia in segments 1–3 is illustrated in larvae and juveniles of *Chrysopetalum* spp. (Watson 2020). Pattern 1, observed in the majority of Chrysopetalinae taxa, is observed in a recently settled 6-segment nectochaete, which then changes during metamorphosis to pattern 2 by the 17-segment late juvenile stage (patterns explained in "Anterior segments" this paper; Watson 2020, Figs. 3, 4, and 6).

Arichlidon species are small bodied, length ~5 mm, and possess oocytes that are small but relatively large to the size of the body, e.g., 30–60 μm in *Arichlidon gathofi* and 50–60 μm in *Arichlidon reyssi* (see Watson Russell 2000b). Intestinal oil globules are seen in trochophore, metatrochophore, and nectochaete larvae of *A. reyssi* (see Cazauz 1968, Watson et al. 2014), which Cazaux (1968) estimated would enable larvae to live off their reserves and remain at the six-segment stage for up to three weeks in the plankton.

Early planktonic larval stages possess chaetal types clearly designed for life in the water column with the long provisional spines of anterior chaetigers retained by the larvae to 6/7 segment stage and creating a larger surface area to float and travel further (Fig. 7.13.3.1.14A–D; Meilokovsky 1962, Cazaux 1968, Watson et al. 2014). Before impending metamorphosis, planktonic nectochaete larvae of *A. reyssi* exhibit primary paleal notochaetal fans that are just starting to unfold and cover the dorsum (Fig. 7.13.3.1.14C, D). The planktonic nectochaete paleal types are similarly shaped but more rounded than those of adult paleae that are beginning to appear at posterior segments 4–6 (Watson et al. 2014). A single larval neurochaetal spine overlying the aciculum is also retained in adults (Fig. 7.13.3.1.3E; Watson Russell 1997).

Arichlidon reyssi planktonic larvae have been mostly recorded from coastal embayments (Cazaux 1968, Bhaud personal communication), but adults of a *A. reyssi* sp. complex have been recorded from abyssal depths of the East Mediterranean (Watson Russell 1998) and deepwater seamounts of East Atlantic (Watson et al. 2014). Unidentified chrysopetalid early and middle nectochaete larvae, collected from plankton samples in the Gulf Stream within the 100- to 0-m layer in 3000–3500 m depth (Mileikovsky 1962), may belong to the deep-sea taxon *Strepternos*

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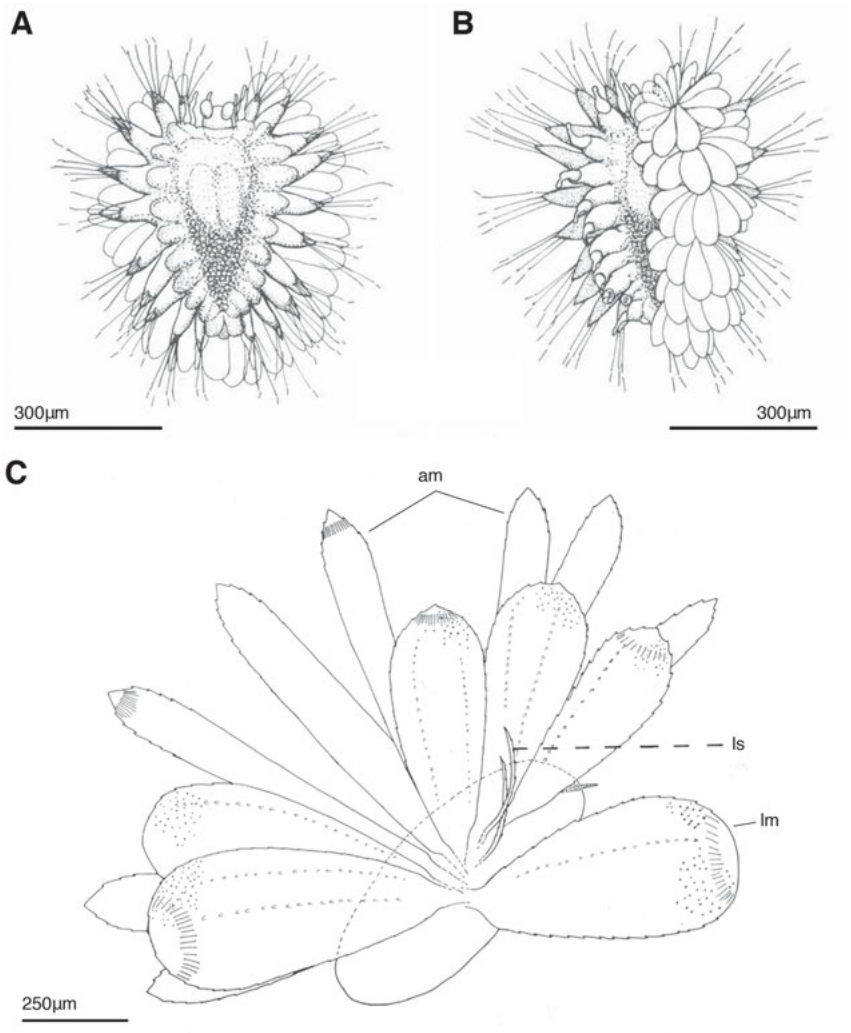


Fig. 7.13.3.1.12: Chrysopetalinae. Larval/adult notochaetal paleael patterns in *Strepternos didymopyton*. A, Nectochaete 10 segments, ventral view. B, Dorsal view. C, Primary larval notochaetae, larval spines, and developing adult notochaetae of segment 3 in juvenile 27 segments. am, adult main paleae; lm, larval main paleae; ls, larval spine (from Watson Russell 1997).

but most likely belong to *Arichlidon* species, based on Mileikovsky's figures (Watson Russell 1997).

Transitory compound swimming neurochaetae insert superior to the neuropodial aciculae and have been reported in mature planktonic and benthic specimens of all nominal species of *Arichlidon*, e.g., *Arichlidon gathofi* (Fig. 7.13.3.1.2D; Watson Russell 2000b). Swimming adults and long-lived larvae of *Arichlidon reyssi* are potential factors pointing to long-distance travel via stepping stones of individuals belonging to ancestral populations between mainland NE Atlantic and the isolated Senghor Seamount, NE Atlantic. *A. reyssi* is one of three chrysopetalid species recorded from Senghor Seamount that all possess evidence of neurochaetal supra-acicular swimming fascicles (Watson et al. 2014). The numbers and frequency of collections of *Arichlidon* species worldwide give some indication of the success of the planktonic larvae of this taxon in original colonizing events throughout the oceans and subsequent formation of cryptic species complexes, e.g., *Arichlidon hanneloreae* common throughout the Indo-Pacific (Watson Russell 1998).

Ovigerous females of smaller-bodied taxa often have oocytes at a comparatively larger size range, e.g., *Paleanotus chrysos*, ~250 µm (Watson 2015), and *Treptopale paromolos*, ~150 µm (Watson 2010). Laboratory-raised trochophore larvae of *Paleanotus bellis* Johnson, 1897 were seen feeding with algae in the stomach but failed to develop (Blake 1975). Plankton collected metatrophore and nectochaete *P. bellis* larvae were observed with golden-brown intestinal contents of oil or yolk globules with stylet jaws present at the seven-segment nectochaete stage (Blake 1975, Watson personal observation). Once settlement is made, metamorphosis appears to establish quickly with loss of larval segment 1, provisional chaetae,

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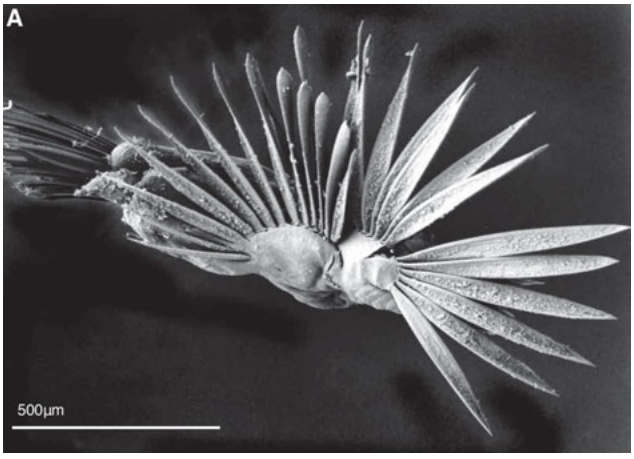


Fig. 7.13.3.1.13: Chrysopetalinae. A, *Strepternos didymopyton* midbody notopodium, double main paleae fan, adult 54 segments (from Watson Russell 1987).

and primary paleae. Subsequent generation of adult segment 1 takes place, co-occurring with shrinkage of the larval episphere and rapid development of median, lateral antennae, and ventral palps and replacement adult notochaetal types (Blake 1975, Watson personal observation).

Gamete-bearing adults of *Treptopale* and *Paleanotus* species have been collected from the plankton in lagoons of tropical reefs but do not bear accessory epitokous neurochaetae (Watson Russell 2000a). Mature individuals of both taxa share very similar parapodial pigments and oil globules associated with developing oocytes and spermatozoa (Watson 2010, 2015). Mileikovsky (1962) described the species *Paleanotus schmardai* (type material now lost, Watson personal observation) found swimming at 310 m depth in an area within the Arctic Circle. Mileikovsky's (1962) figures indicate that the notochaetal fan of this species does not belong to *Paleanotus* sensu stricto (Watson personal observation) and there is no record of swimming neurochaetae.

Dysponetinae. Gonochorism is more evident in slightly larger, more epibenthic *Dysponetus* species (~6 mm length), e.g., *Dysponetus populonectens* (see Pleijel et al. 2012, Fig. 1A, B). Very small species (2 mm length or less), often associated with sediments, are considered endobenthic with three species exhibiting copulatory organs indicating likely hermaphroditism — a specific adaptive feature of meiobenthic polychaetes capable of only producing a limited number of eggs and a limited ability to find mating partners (Westheide 1984).

Females with mature oocytes of diameter ~100 µm have been recorded for three species: *Dysponetus paleophorus* Hartmann-Schröder, 1974 (in Dahlgren 2000), *Dysponetus caecus* Langerhans, 1880 (*sensu* Pleijel and Dahlgren 1995), and *Dysponetus macroculatus* Dahlgren, 1996. Penial papillae have been observed in three meiofaunal species: *Dysponetus pygmaeus* possess one pair on segment six (Tzetlin et al. 2002a), and *Dysponetus pseudopapillatus* (see Dahlgren 1996) and *Dysponetus ovalisetosus* (see Darbyshire and Brewin 2015) each have one pair on segment eight. Male and female gametes were found in the same individual of *D. pygmaeus*, which Tzetlin et al. (2002a) labeled as a most likely protandric hermaphrodite. The structure of *D. pygmaeus* sperm is modified to a long filiform shape (Fig. 7.13.3.1.11D) and is characteristic of annelids with internal fertilization (Franzen 1977).

There is a single larval reference of one planktonic specimen of seven segments belonging to *Dysponetus pygmaeus* (Watson Russell 1987). Morphology at this late nectochaete stage is similar to that of the adult: an adult prostomium with fully formed appendages, including a pair of buccal cirri, is present as well as adult notochaetal and neurochaetal types and an adult pygidium (Fig. 7.13.3.1.7A; Watson Russell 1987). Epitokous, very long-shafted and bladed, swimming neurochaete have been described in *Dysponetus caecus*, a gametous male at Senghor Seamount in ~3000 m exhibiting also a marked increase in spinose notochaetal length of segments 9–13, the same segments that possess epitokous neurochaetae (Fig. 7.13.3.1.6A; Watson et al. 2014). *Dysponetus gracilis* Hartmann, 1965 from deep waters of the NW and NE Atlantic also possess epitokous neurochaetae (Aguirrezabalaga et al. 1999, Watson personal observation). This species is exceptional among species of the Dysponetinae in the possession of fans of broad paleate notochaetae, which lack internal ribs but are individually flattened with serrate margins (Fig. 7.13.3.1.7C, D; Aguirrezabalaga et al. 1999, Watson personal observation).

Calamyzinae, free-living. Planktonic *Vigtorniella zaikai* nectochaete larvae, 3- to 5-segment stage, inhabit the narrow transition layer between upper oxygenated waters and lower anoxic waters at the boundary of the hydrogen sulfide zone in the Black Sea, often living for long periods in cyclonic gyres (bottom depths of 1000–1286 m). Settled nectochaetes have been recorded (Fig. 7.13.3.1.9C) in settling densities of 6550–9150 individuals per square meter (Zaika et al. 1999); a high percentage of mature adults have never been observed (Sergeeva et al. 2011). Planktonic larvae raised in the laboratory grew very slowly, and by 8 months some benthic adults were present in the culture

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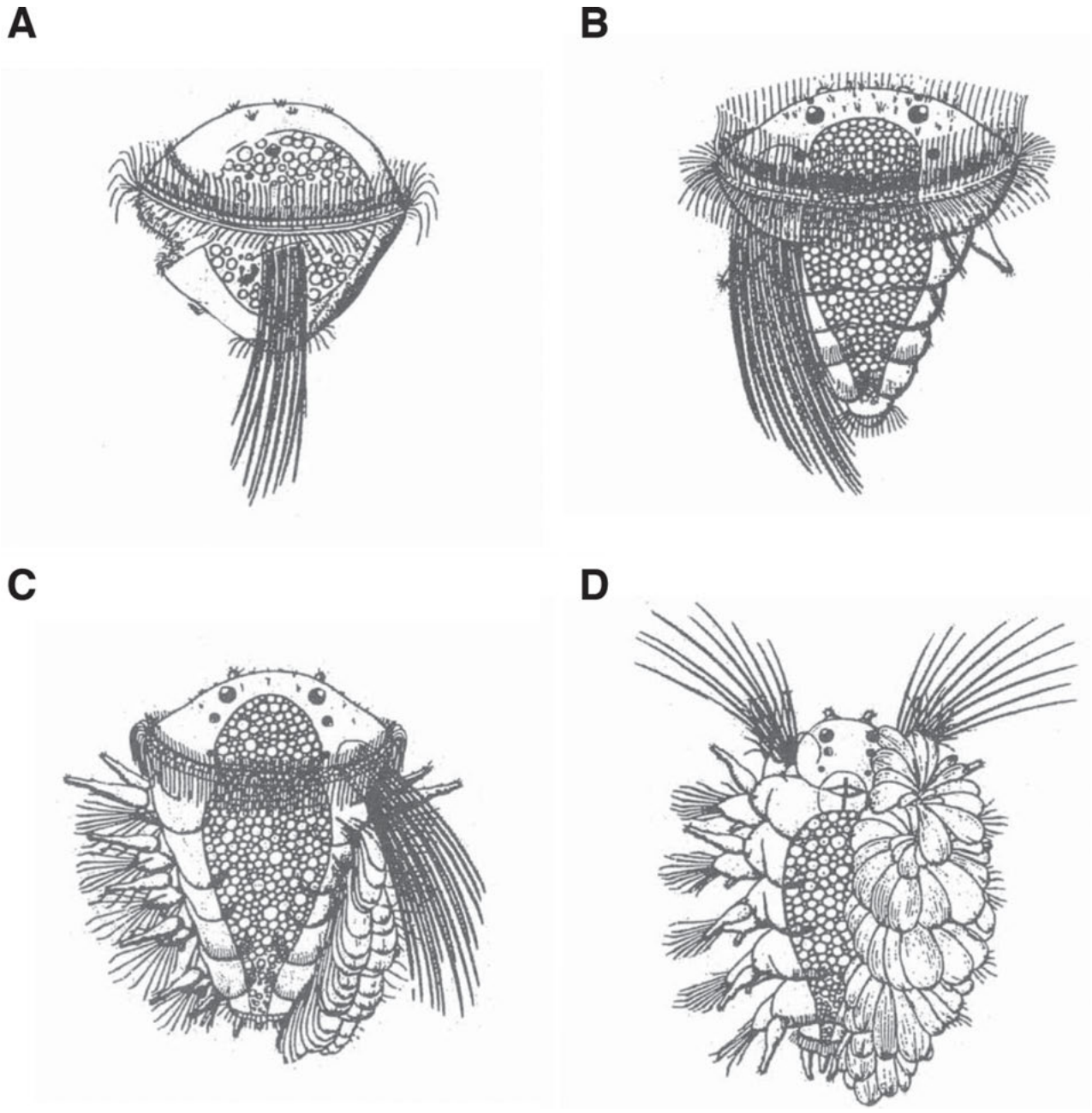


Fig. 7.13.3.1.14: Chrysopetalinae. Planktonic larval stages of *Arichlidon reyssi* with primary spines and primary paleae. A, Trochophore (250 µm). B, Metatrochophore 1 (340 µm). C, Metatrochophore 11(450 µm). D, Nectochaete 1 (550 µm) (from Cazaux 1968).

(Zaikai et al. 1999). Murina (1997) stated the long larval life results from the yolk reserves, but as oocytes reach 40 µm, a size considered uniquely small for lecithotrophy (Rouse 2000), it is likely some sort of larval feeding must occur (Watson et al. 2016).

Oocyte size reaches 100 µm in larger-bodied *Boudemos flokati*, which underwater cameras have recorded en masse on whale bones and surrounding benthos, as well as in individuals swimming off the benthos throughout the cadaverous colony (Dahlgren et al. 2004). Molecular analyses indicate that free-living calamyzin larvae may travel long distances, e.g., *Micospina auribohnorum*, recorded from whale falls off California and methane seeps off Costa Rica, present nearly identical *CO1* sequences, indicating individuals most probably use stepping zones over a ~5500-km distance (Watson et al. 2016).

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Symbionts. A number of former nautiliniellid genera exhibit sexual and color dimorphism. Mature females of *Shinkai longipedata* had deep purplish-brown parapodia with elongated notopodia and differed from whitish colored males with short notopodia (Miura and Hashimoto, 1996); the males of *Shinkai fontefridae* Aguado & Rouse, 2011 were pink colored and the females longer and wider with large midbody notopodia full of yellow oocytes, and *Vesicomyicola trifurcatus* Dreyer et al., 2004 included gravid females with green parapodia and pink colored males. A single reference to gamete size is from a figure of *Natsushima graciliceps* Miura & Hashimoto, 1996 with oocytes measuring 50–60 μm. No larvae have been described. Arwidsson (1932) described gametous males with sperm and females with large eggs, 140–170 μm, in the tiny ectosymbiont *Calamyzas amphictenicola*.

Biology, ecology, and behavior

Chrysopetalinae species are now among the most common polychaete taxa associated with habitat complexity in tropical embayments and fringing mainland and offshore coral reefs worldwide (Watson Russell 2000a, Watson 2010). Hutchings and Murray's (1982) study of recruitment of polychaetes onto dead coral blocks at Lizard Island, Great Barrier Reef, South West Pacific, revealed Chrysopetalidae fourth among the seven most numerically dominant families; a similar quantitative example was found by Chivers et al. (2013) for Chrysopetalidae collected by cores at Senghor Seamount, Northeast Atlantic.

Species of Dysponetinae on the other hand are usually collected in numbers of no more than a few individuals except in rare cases where a preferred biotope is located, e.g., 22 specimens from epifaunal scrapings of *Dysponetus ovalisetosus* Darbyshire & Brewin, 2015. Free-living, opportunistic bacteriovore calamyzins can occur in exponential numbers when food sources are abundant, e.g., *Vigtorniella zaikai* settling densities of ~9000 individuals per square meter (Zaika et al. 1999) and *Boudemos flokati* ~8000 individuals per square meter (Dahlgren et al. 2004). Calamyzinae symbionts may comprise a male and female pair living on the body of the host, e.g., *Calamyzas amphictenicola* (Arwidsson 1932, Aguado et al. 2013, Watson and Faulwetter 2017) or within the host, e.g., *Shinkai longipedata* Miura & Ohta, 1991(Aguado and Rouse 2011, Fig. 83).

Chrysopetalids are small bodied, with a few exceptions. It was revealed that out of 14 taxa studied, representing three subfamilies, just over a third were 5 mm in length or less, approximately a third were 20 mm or less, and of the remaining three taxa, two were 50 mm or less with a lone deep-sea symbiont taxon measuring ~200 mm in length (summarized in Watson and Faulwetter 2017). Individuals, especially belonging to taxa of Chrysopetalinae and Dysponetinae, possess a relatively fragile body with species of some taxa automatically fragmenting during collection, e.g., *Treptopale* (Watson, 2010) and *Paleanotus* (Watson, 2015); species are also capable of posterior regeneration, e.g., *Thrausmatos dieteri*.

Direct evidence has been scarce regarding the behavior and general ecology of Chrysopetalidae. All 10 taxa of Chrysopetalinae possess metallic, reflective notochaetal paleate fans that camouflage and protect the entire body; adults dwell deep down among flora and fauna in crevices of coral and rocky reefs or among aggregations of sedentary polychaetes, e.g., *Paleaequor* Watson Russell, 1986 or deep-sea bivalve colonies, e.g., *Strepternos* Watson Russell, 1991. Observations of live individuals that have been removed from refuges indicate that they flatten and "stick" themselves to the curve of the Petri dish and stay very still but move slowly when disturbed by bright light, eventually curling up in a ball (Watson personal observation). The very small, light-bodied species of *Dysponetus* are primarily meiobenthic and remain well hidden. One live observation described a *Dysponetus* individual inhabiting the upper layer of liquid bottom mud and using its thin notochaetae for soaring and floating in the mud (Tzetlin et al. 2002a).

Remote filming in the deep-sea and direct observations of species kept in acquaria have enabled study of free-living calamyzin taxa that are capable of achieving very high biomass, e.g., larger-bodied *Boudemos flokati* forming a writhing mass while feeding on bacterial mats hanging off whale bones (Dahlgren et al. 2004) and very small-bodied *Vigtorniella zaikai* planktonic larvae raised in the lab and developing very slowly over many months with adults living within particles of flocculent bacterial mats (Zaikai et al. 1999). Observations of live calamyzin obligate symbionts include *in situ* male and female pair of *Calamyzas amphictenicola* tucked in the branchial groove of an ampharetid polychaete with coloring mimicking that of its host's gills (Fig. 7.13.3.1.1D; Watson and Faulwetter 2017). Male and female pairs of nautiliniellid symbiont taxa, e.g., *Shinkai longipedata*, were often found to inhabit a single clam between gill lamellae and foot and revealed sexual and color dimorphism (Miura and Hashimoto 1996, Aguado and Rouse 2011).

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Taxonomy and phylogeny

Systematics and cryptic speciation

The first chrysopetalid described — *Palmyra debilis* Grube, 1855 from the Mediterranean — was placed within the family Palmyridae. Ehlers (1864) established the family Chrysopetalidae to include *Chrysopetalum fragilis* Ehlers, 1864 from the Adriatic Sea and questioned Grube's species *debilis*. Subsequent common usage has favored *debilis* when referring to the Mediterranean *Chrysopetalum* species, and recent redescription of the taxon established *debilis* as the type species (Watson 2020). *Palmyra sensu stricto* has been referred to the Aphroditidae (Watson Russell 1989; see Phylogeny section).

Ehlers (1864) also incorporated the paleate genera *Paleanotus* Schmarda, 1861 and *Bhawania* Schmarda, 1861 within the Chrysopetalidae, and later Levinsen (1879) included his spinose genus *Dysponetus*. In the past 40 years, an additional seven new paleate genera have been described, five primarily from coral reefs: *Treptopale* Perkins, 1985; *Hyalopale* Perkins, 1985; *Acanthopale* San Martin, 1986; *Paleaequor* Watson Russell, 1986; *Arichlidon* Watson Russell, 1998; and three deep-sea genera: *Strepternos* Watson Russell, 1987; *Thrausmatos* Watson, 2001; and *Pseudodysponetus* Böggemann, 2009 (latter a spinose taxon). Two older paleate taxa were synonymized by Perkins (1985): *Palmyra (Palmyropsis*) Claparède, 1864 with *Chrysopetalum* and *Psectra* Grube, 1868 with *Bhawania*.

Two subfamilies Chrysopetalinae Ehlers, 1864, including paleate taxa, and Dysponetinae Aguado, Nygren & Rouse, 2013, erected for spinose taxa, were nominated within the Chrysopetalidae (Aguado et al. 2013). Earlier cladistic studies ascertained *Chrysopetalum caecum* Langerhans, 1880 belongs within *Dysponetus* (see Dahlgren and Pleijel 1995), and current molecular studies are underway to determine whether the speciose *Dysponetus* constitutes a single or paraphyletic genus (Watson et al. in preparation).

The families Nautiliniellidae Miura & Laubier, 1989 (endosymbionts in deep-sea bivalves) and Calamyzidae (*Calamyzas amphictenicola* Arwidsson, 1932 ectosymbiont on tube dwelling ampharetids) are now ascertained to be derived chrysopetalids that both belong within the subfamily Calamyzinae Hartmann-Schröder, 1971 (Aguado et al. 2013). A new ectosymbiont taxon living on an octopus, *Spathochaeta octopodis* Jimi et al., 2019, has been recently described. *Vigtorniella* Kiseleva, 1992 was established for a very small-bodied, free-living taxon and is now also included within the chrysopetalid subfamily Calamyzinae (Aguado et al. 2013); two new taxa, *Boudemos* Watson et al., 2016 and *Micospina* Watson et al., 2016, have also been added to the free-living calamyzins (Watson et al. 2016).

Former nautiliniellid obligate endosymbionts are composed of mostly monotypic taxa and would benefit from additional morphological study, especially the composition of chaetae and cirri of segments 1–3 in light of the revision by Aguado et al. (2013), as well as further molecular analyses to clarify relationships (Aguado and Rouse 2011, Watson personal observation). A new endosymbiont taxon found within a bivalve, *Craseoschema thyasiricola* Ravera & Aguado, 2019, was also recently described. *Santelma* Blake, 1993 was erected as a nautiliniellid genus by Blake (1993), but it displays a number of aberrant characters and was subsequently referred to the Pilargidae by Miura and Hashimoto (1996).

Systematic studies over the past 40 years have included worldwide (e.g., *Paleaequor* (see Watson Russell 1986), *Treptopale* (see Watson 2010), and *Arichlidon* (see Watson Russell 2000b)) and Indo-Pacific revisions of genera (e.g., *Arichlidon* (see Watson Russell 1998) and *Paleanotus* (see Watson 2015)) that reveal a high degree of cryptic speciation (Watson personal observation). A taxon may comprise clearly identifiable species based on morphology as well as wide-spread cryptic species, e.g., *Paleanotus* (see Watson 2015), or be composed of exclusively cryptic species that are more difficult to tell apart morphologically and may be based on difference in a single chaetal type, e.g., *Arichlidon* (see Watson Russell 1998, 2000b). A single phylogeographic molecular study found that the two nominal *Treptopale* species erected by Watson (2010) from northern Australian coral reefs actually comprised nine clades (Wei Nu et al. 2013).

Cryptic speciation in two deep-sea *Vigtorniella* species (=*Boudemos*, Calamyzinae) was investigated in a study by Wiklund et al. (2009), who found that genetically well-delineated species found in separate ocean basins at different depths can be morphologically similar. Further morphological and molecular research into taxa of the free-living Calamyzinae revealed "cryptic" genera, i.e., separation of genera based on morphological characters usually used at a level to separate species (Watson et al. 2016).

Phylogeny

The phylogenetic position of the Chrysopetalidae within Annelida has a long, varied history and is still under scientific debate. Chrysopetalidae display a unique notochaetal morphology but also has characters found within the Aphroditiformia and Nereidiformia classificatory groups, as

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defined by Fauchald (1977). Day (1967) included the Chrysopetalidae in the Palmyridae; Fauchald (1977) placed both families separately within the order Phyllodocida. The rosettes of notochaetal paleal fans are a distinct character shared by chrysopetalids and palmyrids, but palmyrids possess an aphroditid head, alternating cirrose segments and simple, noncamerate notochaetae and neurochaetae. Subsequently, *Palmyra* was included within the family Aphroditidae (Watson Russell 1989); its position further corroborated in a molecular study of the Aphroditiformia (Wiklund et al. 2005).

Notochaetal cameration, a major character considered monophyletic for the family Chrysopetalidae, has been recently re-defined. The uniqueness/singularity of this character now embraces the phylogenetic/developemental concept of the capacity of a camerate notochaetal spine to develop into a camerate notochaetal palea (Watson 2020). However chaetal cameration per se is controversial as to whether it constitutes a pleisiomorphic or homoplasic state (Westheide and Watson Russell 1992, Watson 2000a, Rouse and Pleijel 2001, Pleijel and Gustavsson 2010). Annelid chaetae, including polychaete families possessing species with broad, "paleate" chaetae, are constructed of a series of longitudinal tubes with undivided narrow channels (Specht 1988). Chrysopetalid paleal chaetae are characterized by a system of very large camerate channels that are composed of internal longitudinal ribs and thin horizontal septa or diaphragms (Westheide and Watson Russell 1992). This ultrastructure could potentially reveal plesiomorphic features of annelid chaetae because these paleae show high similarity to chaetal structures of early polychaetous fossils such as *Canadia spinosa* Walcott, 1911 from the Burgess Shale. *C. spinosa* and recent Chrysopetalinae taxa are active, motile animals with complex nervous systems and share a very similar covering of protective/defensive paleal notochaetae: see reconstruction of comparative parapodia by Conway Morris (1979) and discussion of specific comparative notochaetal and spinous neurochaetal types by Watson Russell (1997); Watson (International Polychete Conference 2019, oral). Westheide and Watson Russell (1992) hypothesized that *C. spinosa* and paleate chrysopetalids possess this type of chaetal construction to reduce weight without losing strength and rigidity, necessary for counterbalance between the demands for protection and locomotion. Butterfield (1990) established that longitudinally arranged internal channels, with the existence of horizontal diaphragms not excluded, were integral to *C. spinosa* paleal chaetae and placed the taxon within the order Phyllodocida. Eibye-Jacobsen (2004) proposed *C. spinosa* has no supporting characters placing it within the Phyllodocida and that furthermore *Canadia* "can not be referred to any extant subgroup in Polychaeta … and used to polarize character evolution within the annelid crown group." The position of *Canadia* has, at present, been resolved within the annelid stem group by Butterfield (2006) and by Parry et al. (2016) in an interesting paper that considers the impact of fossil data on annelid phylogeny inferred from discrete morphological characters. The morphological characters of *Canadia* are of considerable and continuing interest, e.g., *C. spinosa* and the early evolution of the annelid nervous system (Parry and Caron 2019), in the search for definition of ancestral states in crown group annelid candidates.

Depending on characters considered in various morphological analyses, hypotheses place the Chrysopetalidae either in a more basal position as the sister group to all Phyllodocida taxa except the Aphroditoidea (Rouse and Fauchald 1997) or in a more derived position within the Nereidoidea, being regarded as either closely related to or nested within the Hesionidae (Glasby 1993, Dahlgren and Pleijel 1995). Molecular analyses indicated chrysopetalid and hesionid clades were individually supported with no evidence that these taxa are nested (Pleijel and Dahlgren 1998) and nereidids subsequently posited as the sister group to the chrysopetalids (Dahlgren et al. 2000). This latter sister group relationship of taxa has not been recovered by most recent comprehensive molecular studies (e.g., Rousset et al. 2006, Struck et al. 2007, Weigert et al. 2014); indeed, as yet no taxa of the family Chrysopetalidae have been included in any large-scale phylogenomic analyses.

The molecular studies of Dahlgren et al. (2004) and Wiklund et al. (2009) were the first to look at relationships within the Chrysopetalidae by comparing paleate and spinose chrysopetalid taxa. Analyses, based on a hesionid out-group, placed *Vigtorniella* species (=*Boudemos)* as sister to *Dysponetus*, suggesting a close evolutionary link to sediment-dwelling fauna (Wiklund et al. 2009). The molecular study by Aguado et al. (2013) used a syllid out-group which placed Dysponetinae basal to the Chrysopetalinae and Calamyzinae. A study on free-living calamyzins found that the relationships between subfamilies differed with different out-groups: for example, a phyllodocid out-group positioned Chrysopetalinae as basal indicating a closer relationship of Dysponetinae and Calamyzinae (Watson et al. 2016).

The grooved jaw form is considered a non-homoplasious synapomorphy that supports the monophyly of the family Chrysopetalidae (Watson and Faulwetter 2017). Morphological data indicate that this jaw form in association with sensory characters observed in each subfamily (summarized in Watson and Faulwetter 2017) is best explained as apomorphy, for example, Chrysopetalinae

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displays a range of stylet jaw types and complex developed sensory morphologies (Tzetlin et al. 2002a, Watson and Faulwetter 2017); Dysponetinae has a single type of simple jaw and less developed sensory morphologies (Dahlgren and Pleijel 1995, Tzetlin et al. 2002); Calamyzinae exhibits specialized jaw types and the least developed sensory morphologies (Aguado et al. 2013, Watson et al. 2016). However, the direction of evolution of these characters is not yet clear. Understanding the transitional states of these morphologies and matching them with sequence data with selective out-groups is still a work in progress and crucial for eliciting the direction of evolution within the Chrysopetalidae (Watson and Rouse in preparation).

Classification and taxonomy

Classification is based on a first detailed diagnosis of the family Chrysopetalidae plus extended diagnoses of Chrysopetalinae (Watson and Faulwetter 2017, Watson 2020), Dysponetinae (Aguado et al. 2015), and Calamyzinae (Aguado et al. 2013, Watson et al. 2016).

Chrysopetalidae Ehlers, 1864

Diagnosis: Body length very short to very long; flattened or arched dorsum, flattened ventrum. Prostomium well developed with median antenna (lacking in Calamyzinae taxa), two *lateral antennae* and differentiated ventral *palps* or simple lobe-shaped prostomium with undifferentiated two lateral antennae and palps; eyes present or absent. Nuchal organs present in all taxa except symbiont taxa. First or tentacular segment, achaetous, with pair of tentacular cirri in majority of taxa; exceptions in dysponetid and calamyzin symbiont taxa. Midbody chaetal segments with *dorsal and ventral cirri. Muscular pharynx with eversible proboscis and pair of grooved stylet jaws;* terminal proboscidial papillae present except in symbiont taxa; mouth appendages present in chrysopetalids and dysponetids. Notochaetae paleate, spinose or absent; neurochaete compound and/or simple; *chaetal types fully or partly camerate. Pygidial lobe* with or without pair of anal cirri. *Italics*: present in all taxa of Chrysopetalidae.

Chrysopetalinae Ehlers, 1864

Diagnosis: Large to small elongate body covered dorsally in overlapping notochaetal fans comprising lateral, main, and medial paleal fascicles; camerate paleae with internal longitudinal ribs, horizontal septa. Prostomium with median antennae, pair of lateral antennae, ventral palps. Segment 1 achaetous with pair of tentacular cirri; chaetous segment 2 with one or two pairs of tentacular cirri. Strongly muscularized pharynx with well-developed proboscis, terminal proboscidial papillae; pair of slender pointed stylet jaws, diverse-shaped according to taxon; mouth cover present. Compound falcigerous and spinigerous neurochaetae with camerate shafts. Well-developed muscular and sensory systems: complex eyes; nuchal caruncle or nuchal fold, interramal lateral organs, ciliary bands on body present in most taxa, complex parapodial glands. Taxa may exhibit various retractile structures of anterior end and dorsal cirri. Pygidium rounded or conical with two anal cirri (Watson 2020).

Chrysopetalum Ehlers, 1864

Type species: *Chrysopetalum debile* (Grube, 1855)

Diagnosis: Morphologically distinguishable and cryptic species; large to smaller-bodied range. Notochaetal main paleae saber shaped or symmetric shaped originating from multiple centers, forming "prickly" or flattened, bright golden, silver, or pearly transparent fans covering dorsum; raised tubercule pattern on main paleae dorsal surface. Well-developed lateral and median paleal fascicles, latter with central raised rib in most species. Prominent prostomium not fused with anterior segments; two pairs of tentacular cirri on segments 1 and 2 (8 cirri total). Neurochaetae predominantly falcigerous, simple spines may be present. Lateral organs present. Live specimens with red pigmented spots on rounded caruncle, tips of large cylindrical palps with distal tip depressions and glandular ventral pads.

Acanthopale San Martin, 1986

Type species: *Acanthopale perkinsi* San Martin, 1986

Diagnosis: Endemic genus and monotypic. Unique notochaetal morphology comprises fascicles of golden-colored, curved, heavily serrated spines, and slender main paleae originating from two major centers: anterior group paleae broad and relatively shorter, posterior group paleae longer, more slender. Lateral subacicular serrate spines present; short, flattened median paleae group interlock midline from midbody down. Paleae lack tubercules, raised ribs. Dorsal and ventral cirri long and attenuated. Prominent prostomium not fused with anterior segments; segment 1 achaetous with two pairs tentacular cirri; segment 2 with two pairs tentacular cirri, notochaetae (8 cirri total in segments 1 and 2). Neurochaetae falcigerous with bifid tips. Lateral organs present. Live specimens with ovoid ciliated caruncle with posterior notch; red pigmented spots on caruncle, tips of large cylindrical palps with distal tip depressions; glandular ventral pads present.

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***Thrausmatos* Watson Russell, 2001**

Type species: *Thrausmatos dieteri* Watson, 2001

Diagnosis: Cryptic species. Multilayered, symmetrical main paleae originate from multiple centers; main paleae with shallow raised ribs, tubercules absent. Lateral paleae present, discreet median fascicle absent. Dorsal and ventral cirri long and attenuated. Small prostomium not fused with anterior segments with ciliated ovoid caruncle with posterior notch and red pigment spots, palps basally ovoid shaped with cirriform, distally retractile tips; eyes absent in adults. Two pairs of tentacular cirri on segments 1 and 2 (8 cirri total). Neurochaetae comprise falcigers with long, slender bifid-tipped blades and additional small fascicle of short spinigers in supra-acicular position. Thickened epidermis covered in bacteria, appears to lack ciliation and lateral organs; glandular ventral pads prominent. Individuals rarely collected entire, fragment easily.

***Bhawania* Schmarda, 1861**

Type species: *Bhawania myrialepis* Schmarda, 1861

Diagnosis: Cryptic species. Broad and long bodied with dorsum completely covered by flattened, golden-brown to deep copper colored, main paleael notochaetal fans that originate from single center; main paleae with large raised ribs and tubercules. Large fascicle of "eroded" lateral paleae present, median fascicle minimal; retractile styles of dorsal cirri. Small prostomium fused with anterior segments, retractile in conjunction with large nuchal ridge, with large cylindrical palps. Two pairs of tentacular cirri on segments 1, one pair on segment 2; ventral cirri absent (cirri 6 total). Neurochaetae falcigerous with superior fascicle of spinigers; some species with inferior short spinigers. Lateral organs, pigmented ventral pads present.

***Paleaequor* Watson Russell, 1986**

Type species: *Paleaequor setula* Watson Russell, 1986

Diagnosis: Cryptic species. Slender bodied, dorsum completely covered by flattened, golden-brown, notochaetal paleal fans; main paleae with hyaline tips, slender raised ribs, and tubercules. Small fascicle of well-developed lateral paleae present, median fascicle minimal; retractile styles of dorsal cirri. Small prostomium, fused with anterior segments, retractile in association with small nuchal fold, cylindrical palps. Two pairs of tentacular cirri on segments 1, one pair on segment 2; ventral cirri absent (6 cirri total). Neurochaetae falcigerous with superior fascicle of spinigers; some species with inferior short spinigers. Lateral organs, ventral pads present.

***Arichlidon* Watson Russell, 1998**

Type species: *Arichlidon hanneloreae* Watson Russell, 1998

Diagnosis: Cryptic species. Small, broad bodied, with dorsum completely covered by silver to gold colored, often brown-pigment flecked, paleael fans forming a carapace; middorsal convex ridge formed by interlocking large median paleael fascicles. Main paleae originate from single center; main with heavily ornamented raised ribs and tubercules. Well-developed lateral and median paleal fascicles present. Prostomium fused with anterior segments, two large pairs of complex eyes often fused into a rectangular, dark-colored block, large cylindrical palps, and glandular nuchal fold. Two pairs of tentacular cirri on segments 1 and one pair on segment 2; ventral cirri absent (6 cirri total). Neurochaetae falcigerous with superior spinigers and uniquely shaped short inferior falcigers; simple spine overlies neuroacicula. Lateral organs, ventral pads present.

***Strepternos* Watson Russell, 1991**

Type species: *Strepternos didymopyton* Watson Russell, 1991

Diagnosis: Cryptic species. Large bodied, distinctive broad anterior end. Pale golden-colored notochaetal paleal fans, originating from two centers: slender, narrow, symmetrical main paleae with slightly raised ribs, tubercules absent. Slender lateral paleae present, median fascicle absent. Dorsal styles partly retractile within large cirrophores. Very small prostomium fused with anterior segments, capable of being completely retracted in conjunction with anterior segments; broad, elongate-ovate palps and very small nuchal fold present. Simple eyes present in larvae, absent in adults. Two pairs of tentacular cirri on segment 1 and one pair segment 2; ventral cirri absent (6 cirri total). Neurochaetae falcigerous. Lateral organs, ventral pads present.

***Paleanotus* Schmarda, 1861**

Type species: *Paleanotus chrysolepis* Schmarda, 1861

Diagnosis: Morphologically distinguishable and cryptic species: large to smaller-bodied range. Slender to moderately broad bodied, dorsum completely covered by fans of flattened bright golden to silvery colored, asymmetric-shaped main paleae. Main paleae originate from single center, smooth or with raised ribs, tubercules absent. Well-developed lateral and median fascicles. Prostomium, fused with anterior segments, with oval palps, glandular nuchal fold. Two pairs of tentacular cirri on segment 1, one pair on segment 2, ventral cirri absent (6 cirri total).

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Neurochaetae falcigerous. Well-developed lateral organs; ventral pads absent.

***Treptopale* Perkins, 1985**

Type species: *Treptopale rudolphi* Perkins, 1985

Diagnosis: Cryptic species. Elongate, slender bodied narrowing at anterior end. Flattened pale golden to silvery colored, symmetric-shaped main paleae originate from single center, paleal fans cover dorsum; main paleae smooth or with raised ribs, tubercules absent. Well-developed lateral and median fascicles. Prostomium fused with anterior segments, with moderate sized oval palps, glandular nuchal fold. Two pairs of tentacular cirri on segment 1, one pair on segment 2; ventral cirri absent (6 cirri total). Neurochaetae falcigerous. Well-developed lateral organs; ventral pads absent.

***Hyalopale* Perkins, 1985**

Type species: *Hyalopale bispinosa* Perkins, 1985

Diagnosis: Cryptic species. Very small, rectangular bodied. Hyaline, asymmetric-shaped main paleae originate from single center, with multiple fine longitudinal ribs, tubercules absent. Lateral and median paleael types absent: simple lateral spines present, medial spines may be present. Prostomium fused with anterior segments, with moderate sized oval palps; very small glandular fold appears diminished to absent. Two pairs of tentacular cirri on segment 1, one pair on segment 2; ventral cirri absent (6 cirri total). Neurochaete falcigerous. Lateral organs present, ventral pads absent.

Dysponetinae Aguado, Nygren & Rouse, 2015

Diagnosis: Very small to small bodied. Prostomium well to less well developed with two lateral antennae, median antenna, ventral palps; antennae and palps uni- or biarticulated, eyes present or absent. Nuchal structure comprise ciliated dorsolateral patches. Strongly muscularized pharynx with little proboscidial development, terminal proboscidial papillae, pair of simple, tanned, stylet jaws; mouth cover absent, buccal cirri may be present. Segments 1–6 with variable chaetal and cirri formulae. Slender, spinous, or broader paleae-like notochaetae, smooth or with spinulations, originate in single whorl or fan. Dorsal and ventral cirri globular to cirrose in shape. Compound neurochaetae predominantly falcigerous, some spinigerous, bifid chaetal tips and shafts present or absent; neurochaetal simple spines present or absent. Camerate notochaete and neurochaetal shafts. Simple body wall musculature. Body ciliation, lateral organs, and complex glands absent. Pygidium rounded with conical projection, anal cirri absent.

***Dysponetus* Levinsen, 1879**

Type species: *Dysponetus pygmaeus* Levinsen, 1879

Diagnosis: Species with small morphological differences and cryptic species. Small bodied, often fragile. Prostomium well-developed free of anterior segments or simple lobe fused with anterior segments, with median and two lateral antennae, globular or cirriform ventral palps; eyes present or absent; nuchal structure ciliated dorsolateral patches. Buccal cirri present or absent. First segment achaetous with two pairs of cirri; segments 2 and 3 with various chaetal and cirri formulae according to species. Midbody notopodial chaetigers commonly with fascicle of spines with two alternating rows of spinelets; broader paleal-like notochaetae rarely present. Neurochaetae compound falcigers and/or spinigers, neurochaetal simple spines may be present. Pygidium rounded with conical projection.

***Pseudodysponetus* Böggemann, 2009**

Type species: *Pseudodysponetus fragmentosus* Böggemann, 2009

Diagnosis: Cryptic species. Very small bodied with tapering anterior and posterior ends. Prostomium not fused with anterior segments, with biarticulated median, lateral antennae and globular ventral palps; eyes absent. Nuchal organs present; buccal cirri absent. Segment 1 with collar-like structure posterior to prostomium; segments 1 and 2 uniramous, achaetous, each with pair of dorsal cirri; segments 3–6 with neuropodia only, ventral cirri start segment 4. Notopodia reduced, with few notochaetae starting from segment 7 (chaetiger V). Midbody notopodial chaetigers with smooth, acicular-like notochaetal spines, dorsal cirri globular to cirriform; neuropodia with falcigerous compound neurochaetae. Pygidium with conical projection.

Calamyzinae Hartmann-Schröder, 1971

Diagnosis: Very small to very large bodied. Prostomial shallow lobe fused to anterior segments, with two digitiform lateral antennae; oval palps ventral (free-living) or digitiform palps ventrolateral (symbionts); median antenna absent, eyes absent. Muscular pharynx, terminal papillae present (free-living) or absent (symbionts); stylet jaws present (often absent in free-living adults). Segment 1 achaetous with two pairs of tentacular cirri; segment 2 with pair dorsal cirri, notochaetae, neurochaetae, ventral cirri absent (free-living). Segments 1–3 with variable chaetal and cirri formulae (symbionts). Spinous notochaetae present (free-living; *Spathochaeta* and *Craseoschema* symbionts) or absent (notoacicula present in majority of ectosymbiont genera); neurochaetae compound falcigers (free-living and endosymbionts)

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or simple hooks (ectosymbionts). Camerated chaetae present or absent (endosymbionts). Pygidium rounded, with two filiform anal cirri present (free-living taxa) or absent (symbionts).

Free-living taxa

***Vigtorniella* Kiseleva, 1996**

Type species: *Vigtorniella zaikai* (Kiseleva, 1992)

Diagnosis: Cryptic species. Very small bodied. Short, filiform lateral antennae same length as palps; small oval palps ventral. Two part stylet jaw present in larvae: anterior platelet jaw and posterior elongate grooved jaw; posterior jaw lost in adults. Anterior two segments fused with prostomium; segment 2 with whip-like, spinigerous neurochaetae, ventral cirri absent. Spinose needle-like notochaetae with one row of fine serrations. Prechaetal neuropodial lobe absent; neurochaetae very slender-bladed falcigers with slender joints.

***Micospina* Watson, Carvajal, Sergeeva, Pleijel & Rouse, 2016**

Type species: *Micospina auribohnorum* Watson, Carvajal, Sergeeva, Pleijel & Rouse, 2016

Diagnosis: Cryptic species. Very small bodied. Short, filiform lateral antennae little longer than palps; small oval palps ventral. Jaws absent in adults. Notochaetae slender spines with two rows of serrations; only distal third serrate. Prechaetal neuropodial lobe present. Neurochaetae slender-bladed falcigers with slender, bifid joints.

***Boudemos* Watson, Carvajal, Sergeeva, Pleijel & Rouse, 2016**

Type species: *Boudemos flokati* (Dahlgren, Glover, Baco & Smith, 2004)

Diagnosis: Cryptic species. Small to moderately large bodied. Filiform lateral antennae length varies; small oval palps ventral. Jaws present in larvae, absent in adults (*B. flokati*). Notochaetae range from slender serrate spines to thicker, rounded "frayed" spines (*B. flokati*). Prechaetal neuropodial lobe present. Dorsal cirri vary from slender, attenuated (*B. ardabilia*) to thicker, robust (*B. flokati*). Neurochaetae slender-bladed falcigers with enlarged, bifid joints; larger falcigers with basal groove on article.

Ectosymbiont taxa

***Spathochaeta* Jimi, Moritaki & Kajihra, 2019**

Type species: *Spathochaeta octopodis* Jimi, Moritaki & Kajihra, 2019

Diagnosis: Small, slender body with segments well delineated and distinctive, thin "winglike" dorsal lobes, overlying dorsal cirrophores and cirri in part, down body. Prostomium shallow lobe fused to anterior segments, two digitiform lateral antennae, small, rounded ventral palps. Segment 1 achaetous with pair of long dorsal and ventral tentacular cirri. Segment 2 biramous with long dorsal cirri, notochaetae, and neuropodia with neurochaetae; neuropodia positioned behind the long ventral cirri of segment 2 originating from body. Buccal structure comprises muscular pharynx with lateral lobes; jaws not observed. Midbody notopodium with dorsal cirri, dense fascicles of simple notochaetae comprise slender, camerated shaft and expanded, spatulate tips. Midbody neuropodium with ventral cirri, dense fascicles of long-bladed compound falcigers with camerate shafts; cilia on superior edge of neuropodia. Shallow pygidial lobe with no appendages. (Diagnosis based largely on Jimi et al. (2019) and examination of specimen by Watson 2019.)

***Calamyzas* Arwidsson, 1932**

Type species: *Calamyzas amphictenicola* Arwidsson, 1932

Diagnosis: Cryptic species. Very small, broad, rectangular body, segments well delineated with prominent neuropodia. Prostomium shallow lobe fused to anterior segments, two digitiform lateral antennae, digitiform palps ventrolateral. Segment 1 with neuropodia, neurochaetae, and pair of ventral cirri; segment 2 with pair of dorsal cirri, neuropodia, chaetae, pair of ventral cirri. Buccal structure comprises: muscular pharynx, large sucker-type ventral mouth opening surrounded by ring of denticles and very attenuated pair of stylets with posterior small basal angled jaw structure. Midbody notopodium with dorsal cirri, chaetae absent; neuropodium with short-bladed compound falcigers with camerate shafts, ventral cirri. Shallow pygidial lobe with no appendages.

Obligate endosymbiont taxa

*Author's note: It is not clear that *Craseoschema*, with camerate notochaetae and compound neurochaetae signifying mobility, belongs within the obligate endosymbiont group, but the author Ravera (personal communication) asserted that the specimen was found inside a bivalve.

Former nautiliniellid genera, below, need revision of the chaetal and cirral formulae for anterior segments 1–3, in light of revision by Aguado and Rouse (2011) and Aguado et al. (2013). Former nautiliniellid genera number eleven. Only four have been analyzed for DNA, and the majority of taxa are monotypic. It is likely future revision will reduce the number of genera and reveal cryptic species (Watson personal observation).

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***Craseoschema* Ravera & Aguado, 2019**
Type species: *Craseoschema thyasiricola* Ravera & Aguado, 2019
Diagnosis: Elongate body, arched dorsally. Prostomium shallow lobe fused to anterior segments, two dorsolateral inserted, cirriform cirri, basally swollen (lateral antennae), small, pad-like ventral palps. Segments 1–3 with pair of digitiform dorsal and ventral cirri, neuropodia with compound neurochaetae. Notopodia evident at segment 4. Muscular pharynx; jaws not observed. Midbody notopodium a small, rounded lobe with dorsal cirri, fascicles of simple notochaetae comprise slender, camerated shafts, slightly curved with some spinelets subdistally; rounded distal tips possess dense area of small spines. Midbody neuropodium a large lobe with ventral cirri inserted at base, fascicles of falcigerous falcigers with camerate shafts, short, finely serrate blades with distal-most longer spines in two rows. Pygidium a conical lobe.

***Nautiliniella* Miura & Laubier, 1990**
Type species: *Nautiliniella calyptogenicola* Miura & Laubier, 1989
Diagnosis: Body long, arched dorsally. Parapodia subbiramous: short notopodia form globular pads, with acicula, dorsal cirri; neuropodia form globular pads supported by stout neuroacicula, with short ventral cirri and one projecting stout hook and several embedded hooks.

***Natsushima* Miura & Laubier, 1990**
Type species: *Natushima bifurcata* Miura & Laubier, 1990
Diagnosis: Body long, arched dorsally. Parapodia subbiramous: notopodia short or elongated, notoacicula present or absent, dorsal cirri; neuropodia short with stout neuroacicula, short ventral cirri, three neuropodial hooks and numerous shorter bifurcate chaetae with curved distal teeth.

***Shinkai* Miura & Laubier, 1990**
Type species: *Shinkai sagamiensis* Miura & Laubier, 1990
Diagnosis: Body arched dorsally with numerous segments. Parapodia subbiramous: notopodia short or elongated with dorsal cirri, notoacicula slender; neuropodia short with ventral cirri, stout neuroacicula, with up to 15 neuropodial hooks varying from stout to slender (one species with subdistal spines on posterior hooks).

***Petrecca* Blake, 1990**
Type species: *Petrecca thyasira* Blake, 1990
Diagnosis: Body oval in cross section. Parapodia subbiramous: long, slender notopodia with long, slender acicula, short, digitiform dorsal cirri; short neuropodia with slender neuroacicula, short, digitiform ventral cirri and one to two large neuropodial hooks.

***Miura* Blake, 1993**
Type species: *Miura spinosa* Blake, 1993
Diagnosis: Small bodied, oval in cross section. Prostomium broad, lateral antennae lacking. Parapodia subbiramous: thickened notopodial lobe lacking aciculae and dorsal cirri; neuropodia with slender neuroacicula, short, lobe-like ventral cirri and four to six simple neuropodial hooks sharply pointed with subapical notch.

***Mytilidiphilia* Miura & Hashimoto, 1993**
Type species: *Mytilidiphilia enseiensis* Miura & Hashimoto, 1993
Diagnosis: Body long, arched dorsally. Parapodia subbiramous: notopodia short, inflated, stout notoacicula, short, conical dorsal cirri; neuropodia short supported by stout neuroacicula, with very short, conical ventral cirri, up to 35 slender neuropodial hooks with simple or inflated subdistal ends.

***Laubierus* Blake, 1993**
Type species: *Laubierus mucronatus* Blake, 1993
Diagnosis: Body dorsolaterally flattened, ribbon-like. Parapodia subbiramous: notopodia with notoacicula, relatively long, conical dorsal cirri; neuropodia supported by stout neuroacicula, with ventral cirri and two to three thick hooks and additional mucronate chaetae.

***Flascarpia* Blake, 1993**
Type species: *Flascarpia alvinae* Blake, 1993
Diagnosis: Body long, arched dorsally. Parapodia subbiramous: notopodia a soft lobe with blood loop, dorsal cirri, lacking aciculae; neuropodia triangular shape with stout neuroacicula, short, cirriform ventral cirri and seven to eight stout neuropodial hooks with two subterminal protruberances.

***Thyasiridicola* Miura & Hashimoto, 1996**
Type species: *Thyasiridicola branchiatus* Miura & Hashimoto, 1996
Diagnosis: Body long, arched dorsally. Parapodia subbiramous: long, slender notopodia with long, slender acicula,

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short dorsal cirri; neuropodia supported by stout neuroacicula, with ventral cirri and about 5 neuropodial hooks.

***Iheyomytilidicola* Miura & Hashimoto, 1996**

Type species: *Iheyomytilidicola tridentatus* Miura & Hashimoto, 1996

Diagnosis: Body long, arched dorsally with numerous segments. Parapodia subbiramous: broad notopodia with notoacicula and conical dorsal cirri; neuropodia supported by stout neuroacicula, with ventral cirri, tridentate neuropodial hooks with small distal fang and additional mucronate chaetae.

***Vesicomyicola* Dreyer, Miura & van Dover, 2004**

Type species: *Vesicomyicola trifurcatus* Dreyer, Miura & van Dover, 2004

Diagnosis: Body long, arched dorsally. Parapodia subbiramous: notopodia with acicula, dorsal cirri with inflated base, tapering tip; neuropodia with neuroacicula, ventral cirri, four to seven simple hooks midbody, up to seven trifurcate hooks in posterior segments.

Acknowledgments

I appreciate being able to use the fine photos of live chrysopetalids taken by Greg Rouse (Fig. 7.13.3.1.1A, C, E), Fredrik Pleijel (Fig. 7.13.3.1.1D), and Monika Kedra/Slawomira Gromisz (Fig. 7.13.3.1.1B) (http://www.iopan.gda.pl/projects/Polychaeta/list/DysPyg.html) (from Watson and Faulwetter 2017). I also thank Alexander Tzetlin and Günter Purschke for their permission to reproduce Figure 7.13.3.1.11, Florencio Aguirrezabalaga for Figure 7.13.3.1.7 C, D, Maite Aguado for Figure 7.13.3.1.5D, E, and Sarah Faulwetter for the micro-CT scans, Figure 7.13.3.1.5C, 9A, B (from Watson and Faulwetter 2017). Ongoing support from the Museums & Art Galleries of the Northern Territory, Darwin, N.T. is gratefully acknowledged as are reviews of this chapter by Maite Aguado and Thomas Dahlgren.

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Torkild Bakken, Christopher J. Glasby, Cinthya S.G. Santos, and Robin S. Wilson

7.13.3.3 Nereididae Blainville, 1818

Introduction

The family Nereididae is one of the most diverse polychaete families with more than 50 genera described (43 considered valid) with approximately 705 valid species (Read and Fauchald 2019). Many species are abundant in easily accessible intertidal habitats and are known to anglers and harvesters as bait, to aquaculturists as a valuable feed supplement, and to physiologists and other biologists as ideal subjects for laboratory study. For example, *Platynereis dumerilii* has been established as a model organism in a range of biological disciplines. It has been successfully kept in cultures for decades, where *P. dumerilii* is well suited because it breeds well in laboratory conditions and is easy to maintain in culture (reviewed in Fisher et al. 2010). It has given the opportunity to detailed studies of embryonic and developmental biology in annelids, nerve and muscle development, and mechanisms of metamorphosis (Fisher et al. 2010) to gene regulatory expression in spiralin development (Vopalensky et al. 2019). The biochemistry, physiology, and reproductive biology of common species is thus well studied (e.g., Schroeder and Hermans 1975, Zeeck et al. 1988, Hardege 1999). By contrast, the few studies of nereidid phylogeny are limited in taxonomic coverage and leave many taxa unresolved; thus, the current generic classification represents an artificial convenience rather than natural relationships. The family's position within Phyllodocida is unclear, with recent authors having proposed that the Nereididae may be most closely related to either Hesionidae or Syllidae (see *Phylogenetic relationships with other annelids*, below). Previous classifications of the family have been based on character distribution and similarities among taxa without using specific analytical methods.

Nereidids are diverse and range in size from a few millimeters in *Micronereis* Claparède, 1863 (Paxton 1983) to 2 m in *Paraleonnates uschakovi* Khlebovich & Wu, 1962 (Hong et al. 2012). Although nereidids are most common and species rich in shallow marine habitats, they occur in a wide range of environments, from the deep sea to estuaries, freshwater streams, and even temporary rainwater puddles in moist terrestrial environments (Wilson 2000). A diverse range of feeding strategies are represented, as well as a wide variety of reproductive strategies (Pagliosa 2005, Wilson 1991, Jumars et al. 2015).

Morphology

External morphology

The nereidid body is elongated and "wormlike," comprising many similar segments and with well-developed parapodia in all segments except the first achaetous tentacular segment. Anterior chaetigers are usually somewhat wider than in rest of the body, which is often tapering toward the posterior end with a terminal anus and one pair of anal (or pygidial) cirri. The body is usually round in cross section or slightly flattened dorsoventrally (Fig. 7.13.3.3.1).

Prostomium. The prostomium is triangular to trapezoidal (also referred to as inverted T-shaped, pyriform, or pear-shaped) being widest at its posterior part, sometimes with an anterior cleft. It has one pair of biarticulated ventral palps (excepting *Micronereis* in which palps comprise a single article) and one pair of cirriform (usually) antennae, rarely one antenna or none. Palps and antennae are sensory organs with homologues across polychaete groups (Orrhage 1993). Usually, two pairs of eyes are present, but eyes may be absent.

Peristomium. The origin and development of the peristomium has been debated. Some studies have argued that the peristomium is of presegmental origin (reviewed by Schroeder and Hermans 1975), whereas Pleijel (2001) considered the peristomium to be limited to lips as no documentation could be found for the presegmental theory (Pleijel 2001). Current understanding of the development of the four pairs of tentacular cirri supports Pleijel (2001): the anterior tentacular cirri are developed in connection to the prostomium as prostomial appendages (Schroeder and Hermans 1975), whereas the posterior tentacular cirri were found to be developed from the parapodial notopodial lobe in the six-chaetiger larva in *Neanthes fucata* (Savigny, 1822) (Gilpin-Brown 1959). Cephalic metamorphosis and transformation of first pair of parapodia into posterior tentacular cirri in six-chaetiger larvae is corroborated in studies of *Platynereis dumerilii* (Audouin & Milne Edwards, 1833) (Fischer et al. 2010).

Parapodia. Parapodial morphology varies widely across nereidids and provides many characters important for identification. Parapodia in namanereidines are strongly reduced, lacking notopodial ligules (Glasby 1999), whereas in the other nereidids, at least one notopodial ligule is present. Genera such as *Ceratocephale* Malmgren, 1867; *Dendronereis* Peters, 1854; and *Gymnonereis* Horst, 1919 have complex parapodial structures (Hylleberg and

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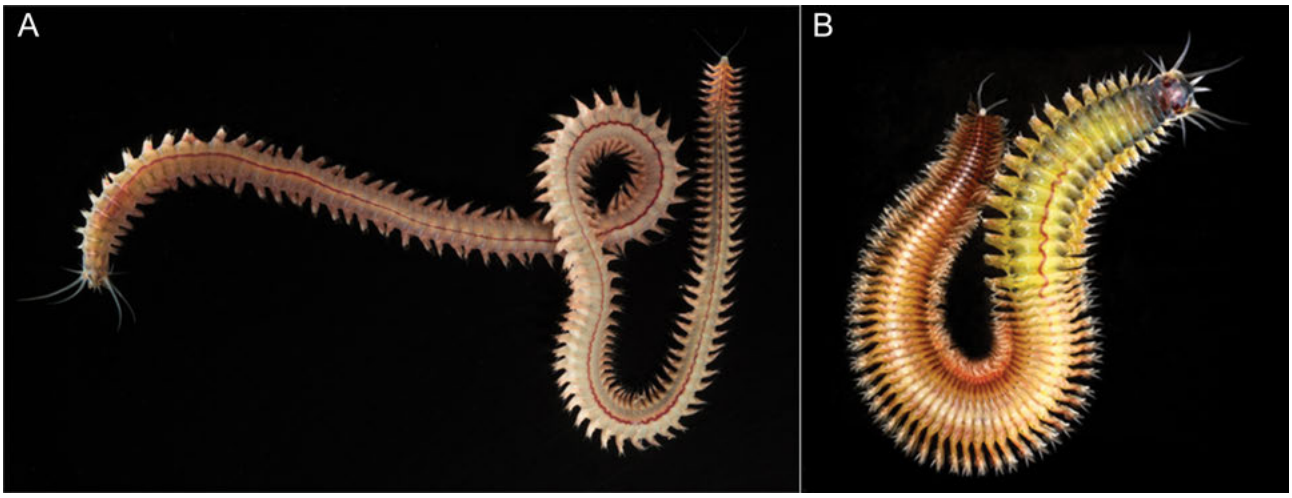


Fig. 7.13.3.3.1: General outline of Nereididae. A, an atoke with regenerating tail end, *Neanthes vaalii* Kinberg, 1865. B, a partially metamorphosed epitoke, *Pseudonereis anomala* Gravier, 1899. Photos from Leon Altoff, Marine Research Group of the Field Naturalists Club of Victoria (A), D. Riek (B).

Nateewathana 1988). The great variation in parapodial characters has been useful in harvesting data for phylogenetic analyses, although homology of structures has been problematic across the family (Bakken and Wilson 2005).

Parapodial characters also vary throughout the body, typically observed as reduction, loss, elongation, or foliaceous enlargement of the dorsal notopodial or ventral neuropodial ligules, as well as pre- and postchaetal lobes being restricted to a number of anterior chaetigers (Bakken and Wilson 2005). Careful examination of parapodial characteristics is therefore necessary in identifications, as well as careful outline in species descriptions. Presenting end-view illustrations of parapodia (introduced by Southern 1921) has proved to be useful in species descriptions to encompass complete diversity of characters in a parapodium, including position of chaetal fascicles. End-view drawings were included as part of a review of parapodial morphology (Hylleberg et al. 1986, Hylleberg and Nateewathana 1988) (Fig. 7.13.3.3.2). Following these important reviews, some additions and modifications have been reported later: characteristics of notopodial lobes and ligules (Bakken 2002) and distinctions and review of a neuropodial prechaetal lobe rather than the widely reported and misinterpreted prechaetal ligule in different groups (Bakken and Wilson 2005, Santos et al. 2005, Darbyshire 2014).

For detailed and adequate descriptions of species and to contribute to comparisons between species and species groups, careful descriptions of parapodial characters are necessary. Therefore, it is strongly recommended to follow the terminology and illustrations suggested by Hylleberg and Nateewathana (1988), with later adjustments. A detailed description of each character in the original review (Hylleberg et al. 1986, Hylleberg and Nateewathana 1988) was presented by Bakken and Wilson (2005) and Santos et al. (2005) and further updated by Villalobos-Guerrero and Bakken (2018).

Chaetae. Chaetae are attached to muscles in the parapodium in epidermal innervations and are highly movable and can be extended and withdrawn. Different types of chaetae are arranged in fascicles in different positions in the parapodia. Traditionally, six different types of chaetae have been recognized in nereidids (Fauvel 1923, Chambers and Garwood 1992): simple (unarticulated), homogomph and heterogomph falcigers, homogomph and heterogomph spinigers, and paddle or swimming chaetae (Figs. 7.13.3.3.3 and 7.13.3.3.4). Delineation of species has led to careful studies of a greater variability in chaetae morphology, and the sesquigomph (alternatively hemigomph) chaeta has been added to the six general types (Perkins 1980). Homogomph, heterogomph, and sesquigomph are descriptions of the angle of the articulation between the shaft and the blade (Fig. 7.13.3.3.3). The blade itself takes different forms, and several types have been described, representing important characteristics for identification and in delineations between species (Figs. 7.13.3.3.3 and 7.13.3.3.4) (Bakken and Wilson 2005). Chaetae characteristics tend to be homoplasious in phylogenetic analyses and

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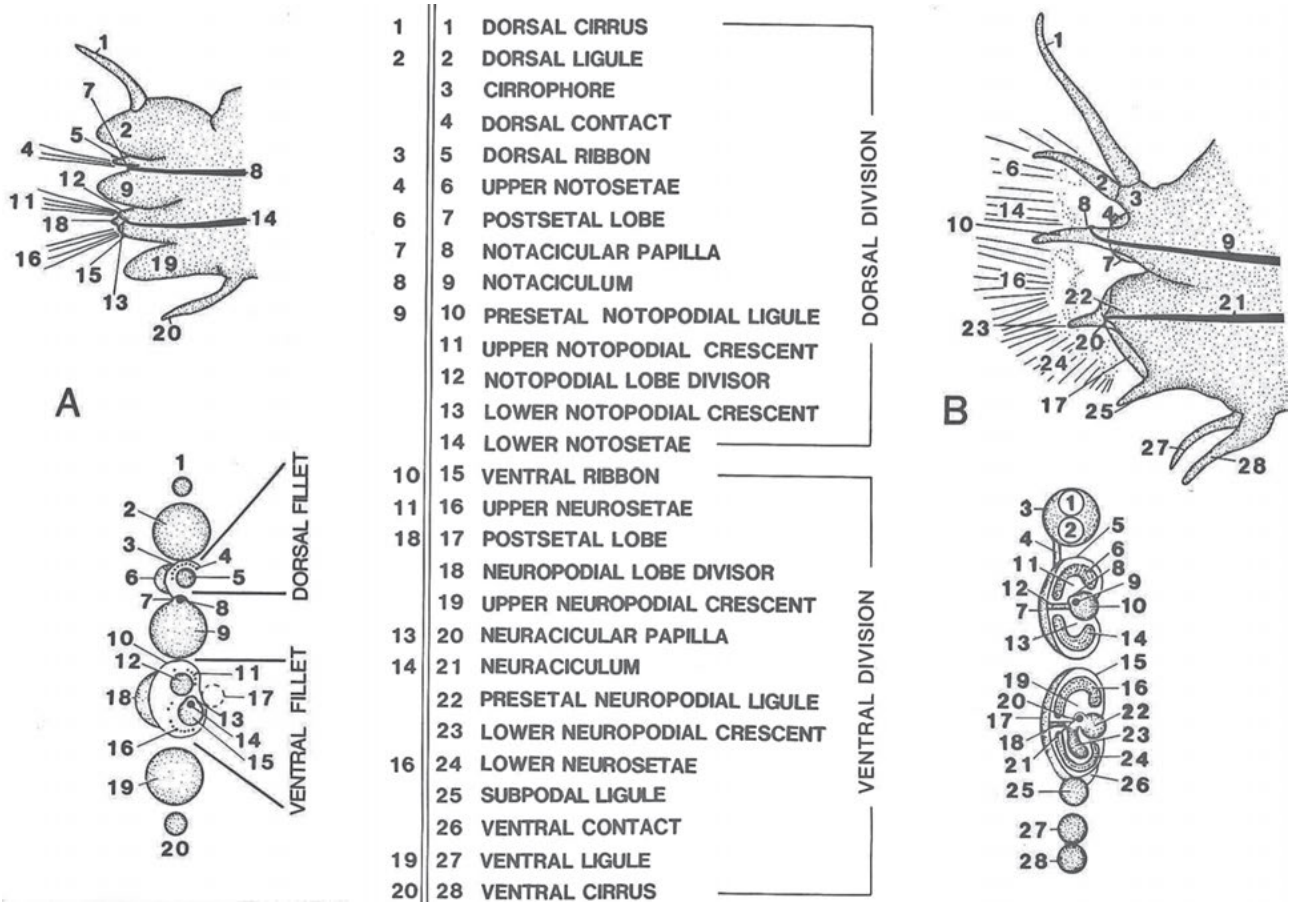


Fig. 7.13.3.3.2: Diagram of characteristics and terminology of parapodia in Nereididae with an anterior view (top) and end-view (below) to present all necessary details of parapodial characters. A, schematic nereidid parapodium. B, parapodium from a *Gymnonereis* species. From Hylleberg and Nateewathana (1988).

should be given more attention in descriptions to better encompass morphological variation and for homology testing in studies of evolutionary relationships (Bakken and Wilson 2005, Santos et al. 2005). Different types are found across taxa, and further information will be provided when this character is studied in more detail.

The basis for classification of chaetae is the angle between the blade and the end of the shaft (Claparède 1870), which is parallel in homogomph (Fig. 7.13.3.3.3A), slanted in heterogomph (Figs. 7.13.3.3.3B and 7.13.3.3.4A) and an intermediate condition (literally "one and a half") in sesquigomph (Figs. 7.13.3.3.3C and 7.13.3.3.4C) chaetae. The length of the blade is also taxonomically informative (Fig. 7.13.3.3.3D–F) (Bakken and Wilson 2005) and should be described as a ratio between the width at the base and length of the blade (Fig. 7.13.3.3.3D–F, a/b). Chaetal blade type and length may vary both within a parapodium, from dorsal to ventral, and from the anterior to posterior ends of the specimen. The third component in chaetae characteristics is shape of the blade. The shape and form of blades encompasses large variations, including the presence and size of serrations, terminal teeth, and tendons (Fig. 7.13.3.3.3). Chaetae occur in bundles, termed fascicles, in the parapodium as is easily observed in end-view (Fig. 7.13.3.3.2). There is usually one fascicle in the notopodium and two in the neuropodium (Fig. 7.13.3.3.2), but variation occurs, and even more fascicles have been recognized (Glasby 1999, Santos et al. 2005). A single type of chaeta may be present in all fascicles, or more commonly several types are found across fascicles; types of chaetae in respective fascicles are important taxonomic characteristics.

Aciculae are supporting chaetae inside parapodia (Fig. 7.13.3.3.2) and are present in all neuropodia and all notopodia but may be absent from notopodia the first one or two chaetigers in some taxa. The position of aciculae has been important for assessing the phylogenetic position of the namanereidines (Glasby 1999).

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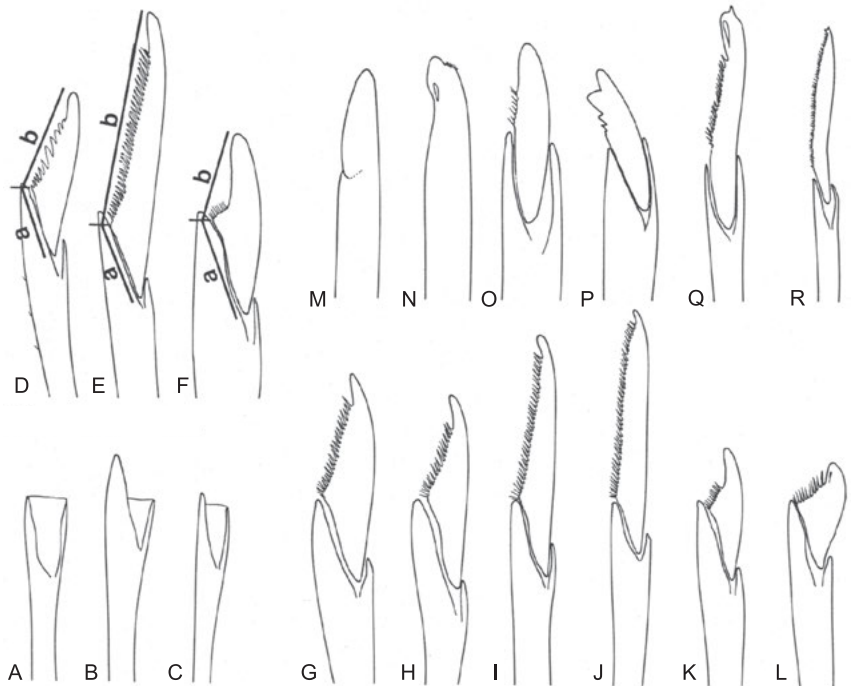


Fig. 7.13.3.3.3: Characteristics of chaetae in Nereididae. A, Homogomph articulation. B, Heterogomph articulation. C, Sesquigomph articulation. D–L, Heterogomph falcigers. M, N, Simple chaetae. O–R, Homogomph falcigers. Letters a and b in D–F denote ratio between width at the base (a) and length (b) of the blade. Illustration by R.S. Wilson.

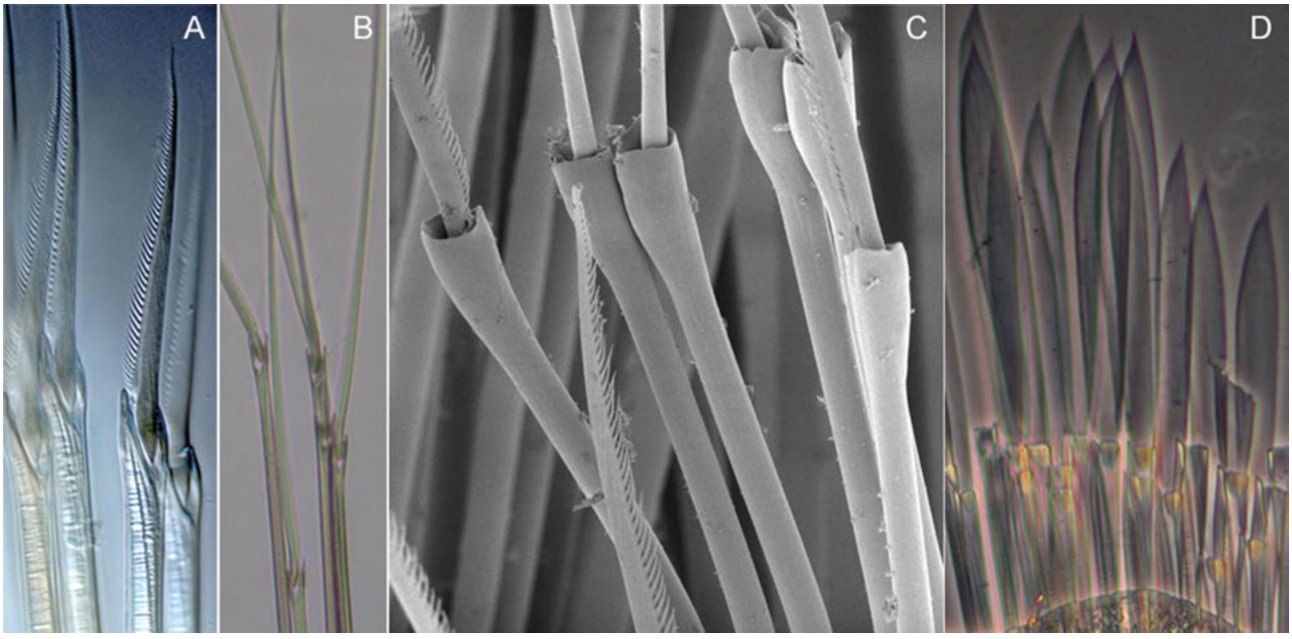


Fig. 7.13.3.3.4: Spinigerous chaetae in Nereididae. A, Heterogomph spinigers with short blades in *Leonnates decipiens* Fauvel, 1929. B, Homogomph spinigers with long blades in *Hediste diversicolor* (O.F. Müller, 1776). C, SEM of sesquigomph spinigers from *Ceratocephale abyssorum* (Hartman & Fauchald, 1971). D, Modified paddle chaetae in an epitokous specimen of *Eunereis elitoralis* (Eliason, 1962). Photo from C.J. Glasby, T. Bakken, and R. Wilson.

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Internal morphology

Muscles. The organization of the muscular system in polychaetes and their methods of study have been reviewed by Gardiner (1992) and Tzetlin and Filippova (2005), whereas muscle ultrastructure has been reviewed by Lanzavecchia et al. (1988). Here we summarize the characteristics of the muscular system common to all polychaetes then proceed to consider studies and muscular structures particular to Nereididae. The anatomy and nomenclature of individual muscle groups is described in detail by Mettam (1967) for *Hediste diversicolor* (O. F. Müller, 1776) (as *Nereis diversicolor*).

The principal elements of polychaete muscle anatomy are circular and longitudinal muscle fibers found in the body wall, together with oblique and transverse muscle elements and others associated with parapodia, chaetae and aciculae, and septa which divide the coelom (Fig. 7.13.3.3.5).

The arrangement of longitudinal muscles differs across polychaete families; in Nereididae, they provide the main propulsive force during rapid crawling (Gray 1939). Longitudinal muscles are located dorsally and ventrally and are larger than the other muscle elements (Fig. 7.13.3.3.5); their insertion into the epidermis is responsible for the appearance of segmentation (Mettam 1967).

The segmental musculature (oblique muscles, bracing muscles, and muscles of the parapodial complex) is shown schematically in Fig. 7.13.3.3.5 (from Tzetlin and Filippova 2005) and in more detail for *Hediste diversicolor* in Fig. 7.13.3.3.7 (from Mettam 1967). Elements of the segmental musculature are attached to chaetae, aciculae, and parapodia and are responsible for movements of those structures during crawling.

Mettam (1967) notes that the arrangement of oblique muscles differs among nereidid taxa. However, there has been no systematic research into musculature across the Nereididae, and anatomical studies have been published for only a handful of species. It is likely that significant differences in muscle arrangement will be found when studies have been undertaken of additional Nereididae taxa. The most extensive comparative study is that of Defretin (1949), who noted differences in musculature between five nereidid species: *Nereis pelagica* Linnaeus, 1758; *Neanthes irrorata* (Malmgren, 1867) (accepted as *Neanthes nubila* (Savigny, 1822)); *Eunereis longissima* (Johnston, 1840) (as *Nereis longissima*); and *Websterinereis glauca* (Claparède, 1870) (as *Leptonereis glauca*) (Grube 1840). However, Defretin's (1949) study focused on histological changes associated with epitoky, and muscle anatomy was described incompletely. Other relevant studies are Snodgrass (1938) on *Alitta virens* (Sars, 1835) as (*Neanthes virens*), Gray (1939) on locomotion in *Hediste diversicolor* (as *Nereis diversicolor*), and Mettam (1967) in *Hediste diversicolor* (as *Nereis diversicolor*), *Alitta virens* (as *Neanthes virens*), *Neanthes fucata* (Savigny, 1822) (as *Nereis fucata*), and *Neanthes irrorata* (as *Nereis irrorata*). Many subsequent textbook treatments are based on these original sources.

The buccal tube of nereidids (pharynx) is the anterior portion of digestive tract, which is modified as a thick, muscular region called the pharyngeal bulb, which has been described in detail by Pilato (1968a, b) based on a study of *Perinereis cultrifera* (Grube, 1840). The pharynx bulb is slightly flattened dorsoventrally, and the muscles of the bulb attach to the base of the jaws and are evidently responsible for movement of the jaws. The retractor muscles of the pharyngeal bulb act in opposition to the protractor muscles of the bulb, enabling evagination (extension) and invagination (retraction) of the pharynx (Pilato 1968a, b).

Circular muscles were shown only dorsally in the schematic diagram of Tzetlin and Filippova (2005) (see our Fig. 7.13.3.3.6), but Mettam (1967, p. 248) noted that they are present dorsally and ventrally, located immediately under

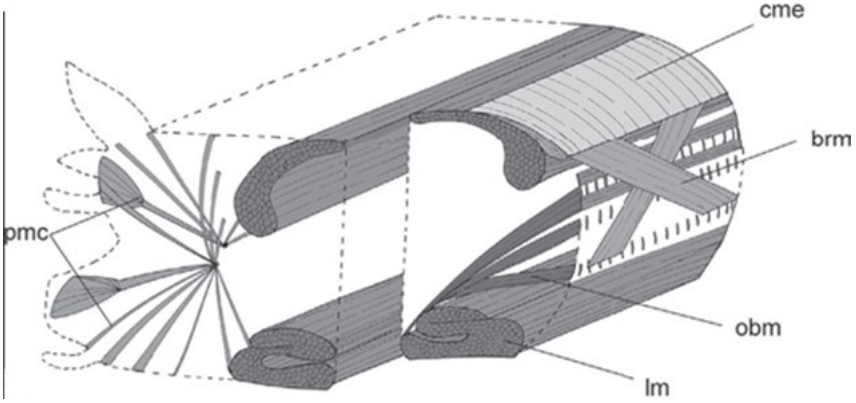


Fig. 7.13.3.3.5: *Nereis* sp. muscle anatomy. brm, bracing muscle; cme, circular muscle element; lm, longitudinal muscle; obm, oblique muscle; pmc, parapodial muscle complex. From Tzetlin and Filippova (2005, fig. 4b).

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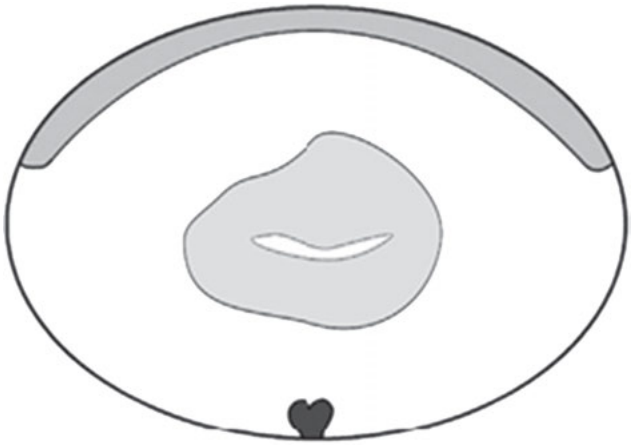


Fig. 7.13.3.3.6: Schematic diagram showing the position of circular muscles in Nereididae. From Tzetlin and Filippova (2005, fig. 2k).

the integument but are only well developed in the posterior two-thirds of each segment. Circular muscles forming a cylinder are typically poorly developed compared with longitudinal muscles (Tzetlin and Filippova 2005). In Nereididae, the circular muscle layer is most strongly developed as dorsoventral elements located between parapodia (Mettam 1967) (Figs. 7.13.3.3.7 and 7.13.3.3.8). Ventral parapodial muscles are well-developed muscles ventrally located in the neuropodium and are apparently derived from the circular muscle layer (Mettam 1967).

The absence of circular muscles occurs in many families and may be associated with alternate locomotion behaviors (for example, in taxa such as *Aphrodita* Linnaeus, 1758, which move by slow motion of large parapodia). Thus, Tzetlin and Filippova (2005) argue that the absence of circular muscles represents the plesiomorphic state with various reductions in parapodial and pharyngeal structures occurring as derived states in members of Scolecida and other taxa. However, the question remains open, and for a discussion of alternative views, see Rouse and Pleijel (2001).

Irrespective of which is the plesiomorphic condition, the relationship between anatomy of musculature in Nereididae and mode of locomotion is well demonstrated. Nereididae, and other polychaetes in which the volume of coelomic fluid is constrained for each segment by septa, rely on muscular contractions and parapodial movements of segments of fixed volume to crawl across benthic substrates (Gray 1939, Tzetlin and Filippova 2005). Mettam (1967) proposed that crawling used coordinated parapodial movements (not body undulations) caused by contractions of muscles attached to aciculae and the parapodial walls. Clark (1962) described septal reduction in Nereididae and corresponding further development of the parapodial muscle (using *Perinereis cultrifera* as an example), but this was corrected by Mettam (1967), who claimed that Clark's description applies to neither *Hediste diversicolor* (as *Nereis diversicolor*) nor *Alitta virens* (as *Neanthes virens*); in both septa "are probably efficient bulkheads to fluid pressure and cannot be called reduced" (Mettam 1967, p. 272).

Different muscles are used in swimming, in which contractions of longitudinal muscles cause lateral undulations to pass along the body while oblique muscles "row" the parapodia back and forth (in *Hediste diversicolor*, as *Nereis diversicolor*; Mettam 1967).

The ultrastructure of polychaete muscle has been reviewed by Lanzavecchia et al. (1988); however, at that time only about 25 polychaete species had been studied and those authors were unwilling to generalize across other polychaetes, in which muscle fibers are mainly helical or double-obliquely striated, although single obliquely striated fibers and cross-striated fiber types have also been observed, as have those with irregular organization (Lanzavecchia et al. 1988). In Nereididae, muscle fibers of only four species have been studied: *Neanthes irrorata*, *Nereis pelagica*, *Hediste japonica*, and *Perinereis* sp. (Iwamoto and Takahashi 1983, Kawaguti and Ikemoto 1958, Wissocq 1977, 1978).

Muscle ultrastructure is modified during sexual metamorphosis (epitoky) in nereidids, in which changes favor fast swimming: atokal fibers with few mitochondria are replaced by fibers with large numbers of mitochondria arranged in a continuous layer (Wissocq 1977, 1978).

Digestive system. The digestive tract in polychaetes comprises foregut, midgut, and hindgut (Tzetlin and Purschke 2005). In the Nereididae, these elements are present as a buccal cavity, axial muscular eversible pharynx, and esophagus (together comprising the foregut), whereas the remainder of the digestive tract is an undifferentiated tube (constituting the midgut and hindgut) terminating in a terminal anus (Rouse and Pleijel 2001). In Nereididae, and in all Phyllodocida, a separate stomach cannot be distinguished (Saulnier-Michel 1992). The anterior extremity of the eversible pharynx constitutes the mouth and carries a pair of laterally oriented jaws (Fig. 7.13.3.3.9) and is divided into a terminal (maxillary) ring and basal (oral) ring (Fig. 7.13.3.3.10). The pharynx may be bare or may have paragnaths (hard processes of various shapes) or soft papillae, or both. The jaws and paragnaths are both composed of scleroprotein (Voss-Foucart et al. 1973, Bakken et al. 2009).

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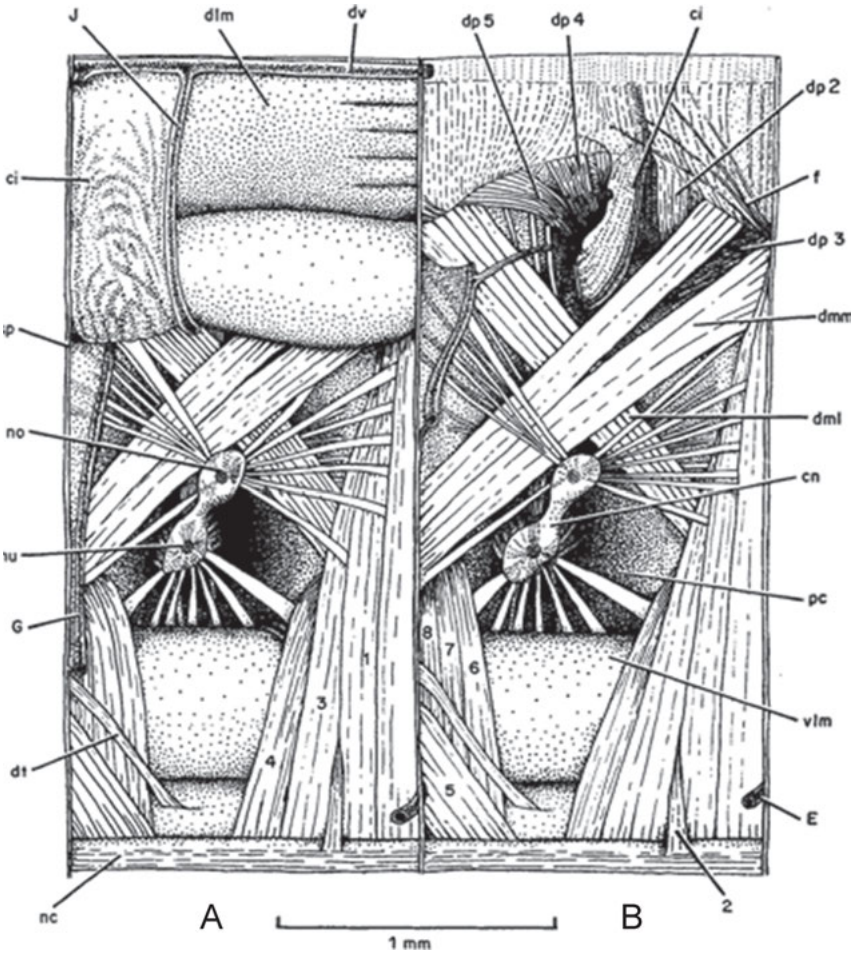


Fig. 7.13.3.3.7: Body musculature in nereidids, from *Hediste diversicolor* (as *Nereis diversicolor*), showing the arrangement of well-developed circular muscles as dorsoventral elements (dlm, dml, dmm, dp) between parapodia in two consecutive segments looking into the parapodial coelom (A); in the anterior segment (B), the dorsal longitudinal muscle is removed. From Mettam (1967, fig. 5).

The pharyngeal papillae and paragnaths are regularly arranged and are of great taxonomic utility (Kinberg 1865, Bakken and Wilson 2005). The regular arrangement divides the pharynx into numbered areas, a system established by Kinberg (1865), where the areas were instated to facilitate description of number and distribution of paragnaths and papillae. Kinberg must have invented the system when studying the rich diversity of the worldwide nereidid material he collected during the Swedish Eugenie Expedition 1851–1853, where he participated as a zoologist (Kinberg 1910). This system has been used ever since, and it is convention to assign these areas with Roman numerals from I to VIII. Kinberg (1865) originally used Arabic numerals (Fig. 7.13.3.3.11) but used Roman numerals in a chart used for delineation of nereidid genera (Fig. 7.13.3.3.12).

As number and distribution of paragnaths are important characters in species descriptions, so are different types of paragnaths. Bakken et al. (2009) reviewed the known types of paragnaths with updates provided by subsequent authors (Fig. 7.13.3.3.13) (Glasby et al. 2011, Villalobos-Guerrero and Carrera-Parra 2015). Conde-Vela (2018) suggested a revised and updated pharyngeal scheme from the one originally described by Kinberg (1865), as an aid in describing pharynx and paragnaths characteristics in more detail. This new suggestion has been tested along elaborations on previous knowledge of paragnaths types and characteristics (Villalobos-Guerrero 2019). Further, Tosuji et al. (2019) demonstrated that species in the *Perinereis nuntia* group add paragnaths in area VI as long bars break into shorter bars during ontogeny, emphasizing the need for a revision of how we apply the pharyngeal scheme to identification. These works show that information on paragnath types and characteristics will increase when these important characters are given more attention in species discrimination in future studies.

Soft papillae may occur in place of paragnaths (or, in a few taxa, as well as paragnaths), especially in genera sometimes referred to subfamily Gymnonereidinae. As with paragnaths, different forms of papillae have been described (Fig. 7.13.3.3.13). Partly sclerotized papillae have

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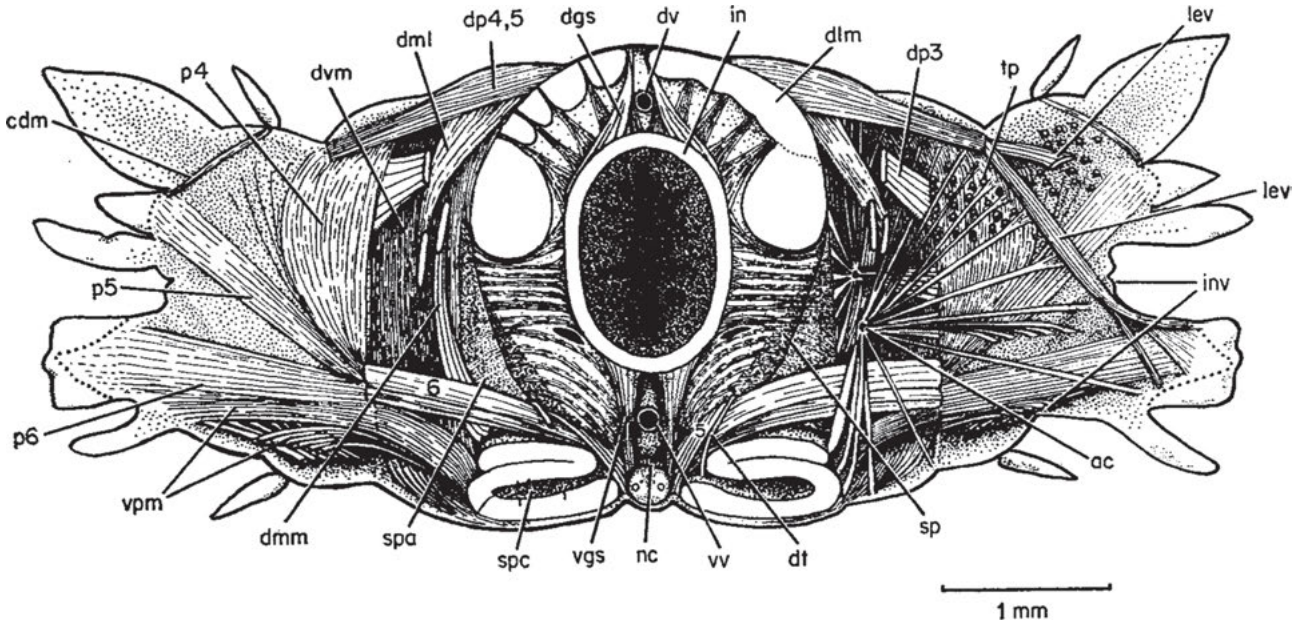


Fig. 7.13.3.3.8: Details of anatomical features in nereidids, from *Hediste diversicolor* (as *Nereis diversicolor*). ac, acicular muscles; cdm, dorsal cirrus muscle; dgs, dorsal gut suspensor; dlm, dorsal longitudinal muscle; dml, lateral diagonal muscle; dmm, median diagonal muscle; dp 3–5, dorsal parapodial muscles; dvm, dorsoventral muscle of body wall; dt, transseptal diagonal muscle; dv, dorsal vessel; in, intestine; inv, invagination line of parapodium; nc, nerve cord and supraneural muscle; p 4–6, parapodial intrinsic muscles; sp, septum; spa, anterior fold of septum; spc, septal connectivity tissue; tp, transparapodial muscles; vgs, ventral gut suspensor; vlm, ventral longitudinal muscle; vpm, ventral parapodial muscles; vv, ventral vessel. From Mettam (1967, fig. 6a).

been reported in *Leonnates* spp. (Qui and Qian 2000), *Paraleonnates* spp. (Hutchings and Reid 1991), and in *Neanthes glandicincta* (Southern, 1921) [Southern 1921 (as "paragnaths seated on rounded papillae"); Lee and Glasby 2015a]. Bakken et al. (2009) proposed that paragnaths and papillae are homologous and that the "presence of papillae" is the plesiomorphic state; however, these hypotheses remain to be tested.

In some Nereididae taxa, a pair of cecal (esophageal) glands are located posterior to the pharynx (Fig. 7.13.3.3.14). The presence/absence of cecal glands was used by Khlebovich (2001) to designate two tribes within the subfamily Nereidinae: Nereidini (presence) and Leonnatini (absence). The cecal glands of Khlebovich (2001) are evidently those structures referred to as esophageal pouches by Kay (1974), who showed that they are the main site of the production of proteolytic enzymes in *Alitta virens*.

The esophagus secretes mucus that assists in lubricating the intestine, whereas the anterior part of the intestine is responsible for the production of lipolytic and carbohydrate-digesting enzymes. The esophageal wall of *Alitta virens* contains both deep serous cells (thought to be responsible for the production of tryptic enzymes) and mucous-secreting gland cells (Michel and De Villez 1979, 1980). The posterior part of the gut has no role in enzyme production and is probably mainly responsible for absorption (Kay 1974). The intestine may also harbor gregarines, which are the most common intestinal parasites (Schrevel 1963). The microbial community may also play a beneficial role in alleviating pollution stress through using polyaromatic hydrocarbons as carbon sources (in *Neanthes chilkaensis* (Southern, 1921)) (Markande et al. 2014).

Coelom. The coelom in adult Nereididae is the body cavity surrounding the digestive tract and develops from pseudoceolomate larvae, perhaps suggesting a pseudocoelomate origin for bilaterians (including Annelida), although many authors have assumed the reverse, that is, the presence of a coelom was the plesiomorphic condition in bilaterians (Rieger and Purschke 2005). The role of the coelom in understanding the evolution of the Bilateria is reviewed by Rieger and Purschke (2005). In addition to its role in locomotion, the fluid-filled coelom is also significant in being the space where gametes are stored before release (see Reproduction), in osmoregulation, and as a space for endoparasites.

In estuarine Nereididae, the coelomic fluid plays a role in osmoregulation: in *Alitta succinea* (Leuckart, 1847)

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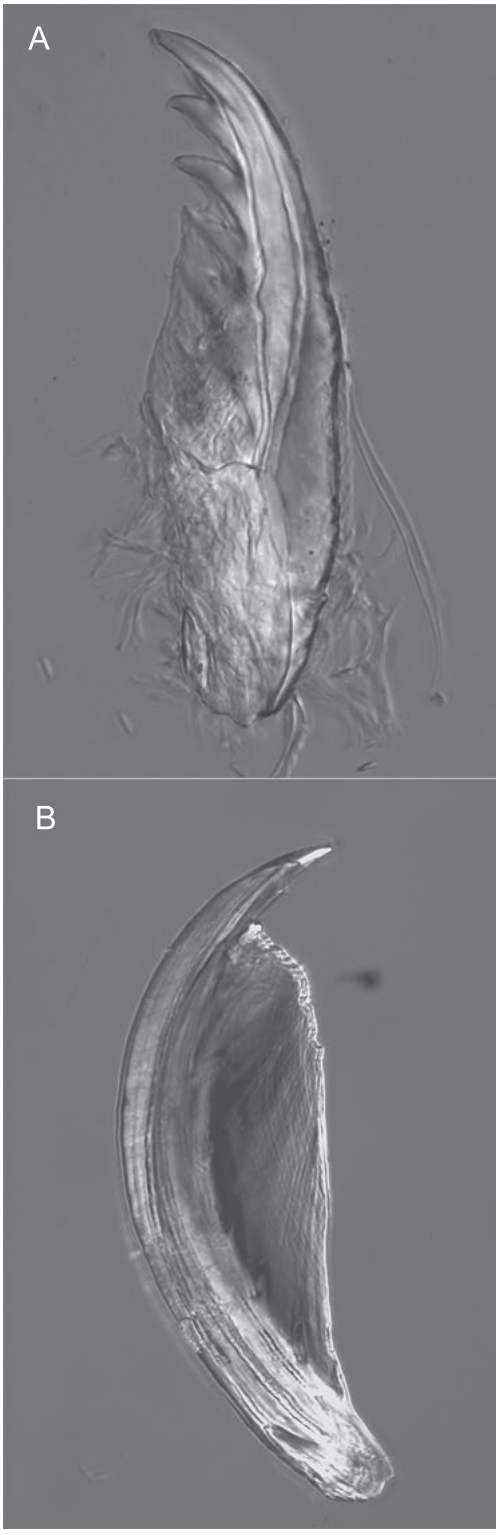


Fig. 7.13.3.3.9: Major jaw morphology types in Nereididae. A, Typical sickle-shaped and serrated (sometimes these can be smooth) found in many genera, including *Namanereis*. B, Wing-shaped bifid jaws found only in some *Namanereis* species. Modified after Glasby et al. (2014, fig. 3g (*Namanereis pilbarensis* Glasby, Fiege & Van Damme, 2014) and fig. 6f (*Namanereis socotrensis* Glasby, Fiege & Van Damme, 2014)).

and *Hediste diversicolor*, the coelomic fluid is isotonic with the environment at normal and hypersaline conditions, but below salinity of 35 ppt is regulated by the retention of sodium chloride. Different populations vary in this capability, suggesting genetic variability (Oglesby 1970, Freel et al. 1973). There are apparently no such studies of the freshwater and terrestrial Namanereidinae.

The coelom of Nereididae is host to a variety of endoparasites, including multicellular parasites (cf. Orthonectida), yeasts, and coccidians. Host reactions to these coelomic parasites include phagocytosis by coelomocytes, paralysis, and encapsulation in nodules (Porchet-Hennere and M'Berni 1987). The mode of infection of the coelom for yeasts is apparently via cuticular pores or glands but is unknown for larger microorganisms (Porchet-Hennere and M'Berni 1987).

Blood system. The circulatory system of Nereididae consists of a single connected system of longitudinal dorsal and ventral blood vessels from which branches reach into the coelom, tissues, and organs (Wilson 2000). Internally, the digestive tract is richly vascularized (Fig. 7.13.3.3.15A). The blood vessels lack a lining, and it is thus inferred that they are not endothelial and instead are derived from the interstitial space (Nakao 1974). The walls of the dorsal longitudinal blood vessel have well-developed internal muscular layer and are evidently an effective pump of blood (Nakao 1974).

The respiratory pigments of Nereididae are hemoglobins (Weber 1978, Rouse and Pleijel 2001) and in *Alitta virens* have a high oxygen affinity (Economides and Wells 1975). However, a study including *Alitta succinea* and 43 other annelid taxa found a large diversity of hemerythrin (Hr) genes, which led the authors to an explanation for the need to carry oxygen, as hemerythrin has 25% higher affinity for oxygen than hemoglobin (Costa-Paiva et al. 2017). The expression of Hr genes among annelids is much more common than previously reported, revealing unrecognized diversity of these genes in this phylum. Burrow ventilation and oxygen uptake in nereidid species are strongly correlated with habitat and are highest in species from anaerobic habitats with high levels of organic matter and lowest in species from clean, well-irrigated sediments (Kristensen 1983).

Branchiae, present as vascularized parapodia structures, appear to have evolved independently in several lineages of Nereididae (Banse 1977b) (these are not homologous with structures also termed "branchiae" in other polychaete families). The branchiae of *Tambalagamia* Pillai, 1961 are expanded notopodial ligules, and those

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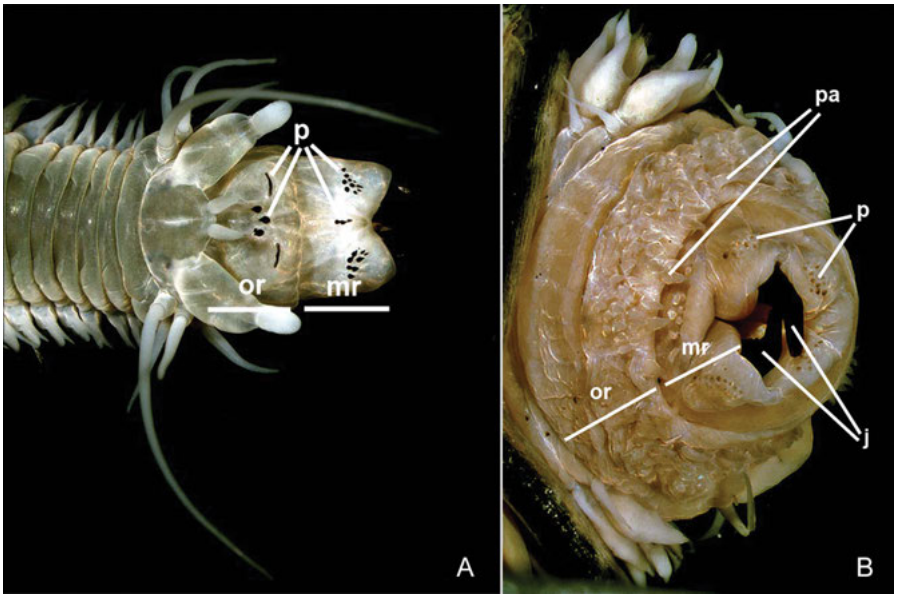


Fig. 7.13.3.3.10: The pharynx in Nereididae is divided into a terminal (maxillary) ring with the mouth and a pair of jaws, and a basal (oral ring), that may carry hard paragnaths or soft papillae. A, Dorsal view from *Perinereis helleri* (Grube, 1878). B, Anteroventral view from *Leonnates* sp. j, jaws; p, paragnaths; pa, soft papillae; mr, maxillary ring; or, oral ring. Photo from C.J. Glasby.

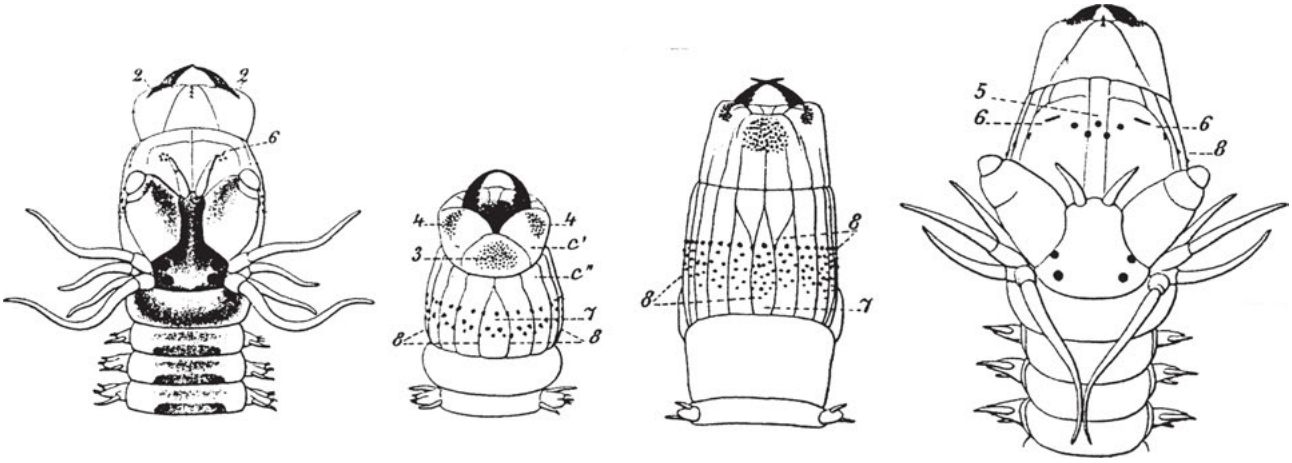


Fig. 7.13.3.3.11: The original illustrations Kinberg (1865) used to delineate areas to describe pharyngeal armature in nereidids. Area I–IV is placed on the maxillary ring and area V–VIII on the oral ring. It has been convention to refer to the areas with Roman numerals. Following the most common distribution pattern of paragnaths, areas VII and VIII are usually referred to as one, as areas VII–VIII in descriptions. Modified from Kinberg (1910).

of *Gymnonereis* are represented by greatly elongated and highly vascularized dorsal cirrophores in median segments. Even the branchiae of *Dendronereis* and *Dendronereides* Southern, 1921, which were once thought to be closely related genera, are quite different and represent dorsal cirri and notopodial ligulae, respectively, rather than homologous structures (Southern 1921, Santos et al. 2005). The detailed investigation of *Hediste diversicolor* by Kaufmant (1965) shows that the parapodial lobes are highly vascularized (Fig. 7.13.3.3.15B). No doubt this example is indicative of most or all Nereididae, which, despite most taxa lacking "branchiae," evidently use parapodia as the principal structures for oxygen exchange.

Excretory system. The excretory system of Nereididae, and of all polychaetes, is termed a metanephridial system

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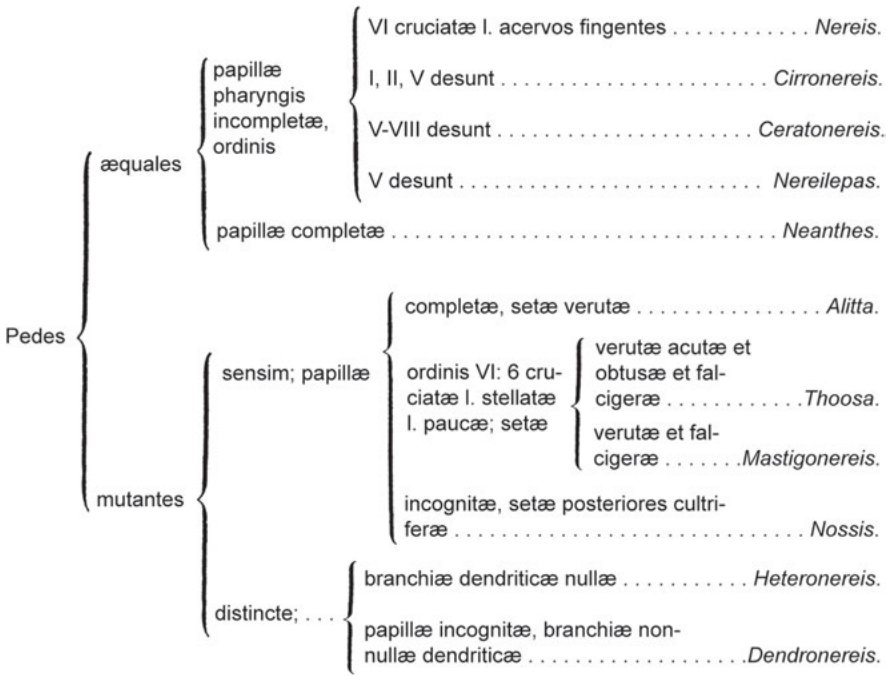


Fig. 7.13.3.3.12: Kinberg (1865) described each area on the pharynx using Roman numerals, which has later been established as a convention, in this key of nereidid genera. Modified from Kinberg (1865).

defined as "any nephridial system with muscle-mediated filtration of vascular fluid into a coelomic cavity and reabsorption by an open duct" (Ruppert and Smith 1988, p. 235). The ultrastructure, function, and homology of nephridial systems of polychaetes have been reviewed by many authors (Goodrich 1945, Smith 1992, Rouse and Fauchald 1997, Ruppert and Smith 1988, Rouse 2000, Rouse and Pleijel 2001, Bartolomaeus and Quast 2005). It must be noted that Rouse and Fauchald (1997) presented evidence contradicting the tight correlation between taxa with blood vessels and metanephridia versus taxa without blood vessels and having protonephridia proposed by Ruppert and Smith (1988). However, further discussion of this topic is beyond the scope of this family treatment, and instead, we focus on comparative studies relevant to the Nereididae.

In Nereididae, nephridia were first described by Goodrich (1893). The bulk of each nephridium is located ventrally within the parapodia where a nephridiopore allows secretion of excretory products. Nephridia occur in most segments except the anteriormost and posteriormost and comprise a nephridiostome, which is a funnel projecting anteriorly in the coelom and posteriorly through the septum into the following segment (Goodrich 1945, Bartolomaeus and Quast 2005). Podocyte cells, which perform the excretory function in Nereididae, allow filtration of fluid transferred from the blood into the coelom (Ruppert and Smith 1988) (Fig. 7.13.3.3.16). Nakao (1974) first reported podocytes from Nereididae.

A higher degree of vascular development of nephridia in Nereididae species, which inhabit low or fluctuating salinity environments, has been demonstrated in several studies (Krishnan 1952, Krishnamoorthi 1963, Jones 1967, Smith 1984).

Hasse et al. (2010) described the ontology of nephridial development in *Platynereis dumerilii* in which nephridia pass through three distinct morphological stages. The accumulation of environmental mercury in nephridia (and other organs) was demonstrated by Jensen and Baatrup (1988) for *Alitta virens* (as *Nereis virens*).

Sensory organs. Polychaetes possess a wide range of sensory structures, isolated or forming sense organs of several kinds, including (1) the appendages of the head region, namely, palps, antennae, and tentacular cirri; (2) the appendages of the trunk region and pygidium, parapodial cirri, and anal cirri; (3) the nuchal organs; (4) the dorsal organs; (5) the lateral organs; (6) the eyes; (7) the photoreceptor-like sense organs; (8) the statocysts; (9) various kinds of pharyngeal papillae; and (10) the apical organs present in trochophore larvae (Fig. 7.13.3.3.17) (Orrhage and Müller 2005). Some, like nuchal organs and eyes, are present in most polychaete species, whereas other sensory structures are restricted to certain higher taxa, or groups of closely related species or, more rarely,

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Fig. 7.13.3.3.13: Scleroprotein paragnaths and soft papillae are important characters in Nereididae. A, Soft papillae in *Dendronereis heteropoda* Southern, 1921. B, Paragnaths in *Micronereis halei* Hartman, 1954. C, Partly sclerotized papillae in *Leonnates* cf. *indicus* Kinberg, 1865. D, Pyramidal paragnaths in *Perinereis rhombodonta* Wu, Sun & Yang, 1981. E, Conical paragnaths in *Perinereis akuna* Wilson & Glasby, 1993. F, Smooth bars in *Perinereis vancaurica* (Ehlers, 1868). G, Shield-shaped bars in *Pseudonereis trimaculata* (Horst, 1924). H, Rod-like paragnaths in rows in *Platynereis polyscalma* Chamberlin, 1919. I, Short and long rows with rod-like paragnaths in *Platynereis antipoda* Hartman, 1954. J, Melted paragnaths as observed in the syntype of *Nereis* (*Ceratonereis*) *ramosae* (Horst, 1919) (= *Neanthes pachychaeta*) (Fauvel, 1918). K, Rodlike paragnaths in *Solomononereis maurauensis* Gibbs, 1971. L, P-bars in *Pseudonereis anomala* Gravier, 1899. Photos from A. Rose and C.J. Glasby.

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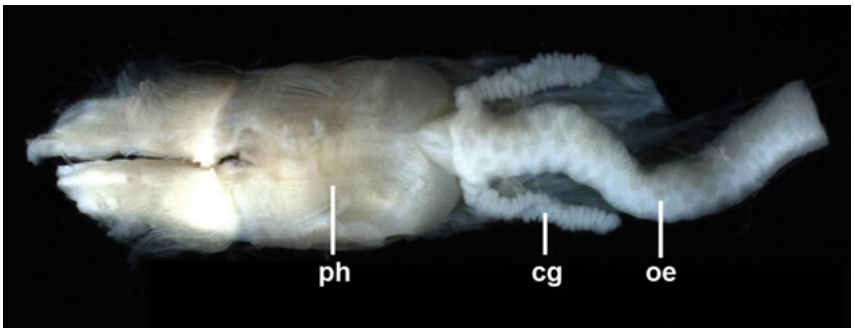


Fig. 7.13.3.3.14: Dissected pharynx and esophagus from *Perinereis mictodonta* (Marenzeller, 1879) showing the cecal glands present in some Nereididae. cg, cecal glands; oe, esophagus; ph, pharynx. Photo from C.J. Glasby.

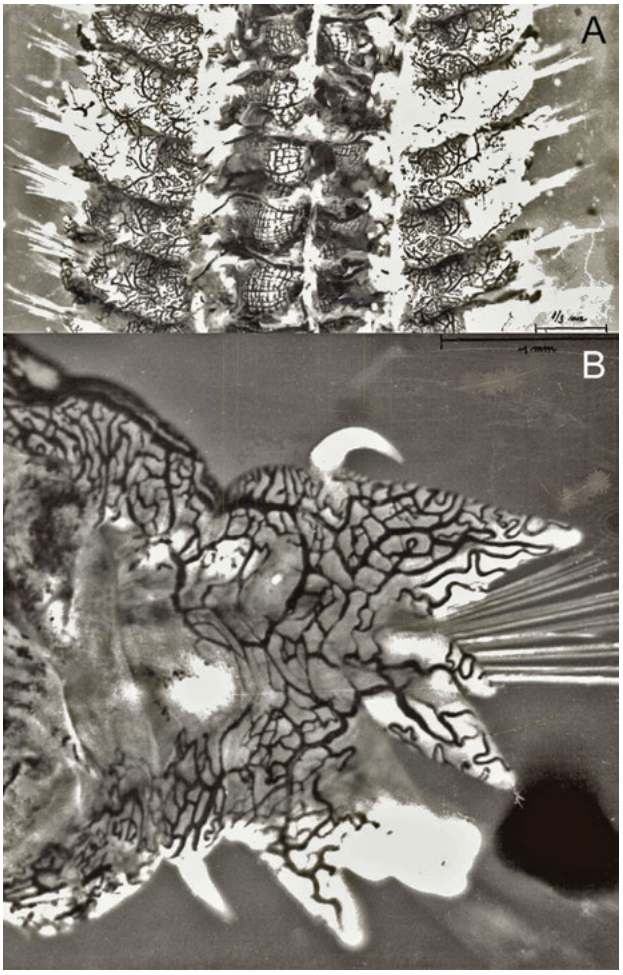


Fig. 7.13.3.3.15: *Hediste diversicolor* circulation preparations, from Kaufmant (1965), stained with Indian ink and cleared with toluene and Canada balsam. A, Ventral view of body dissected to reveal digestive tract (midgut and hindgut) (modified from Kaufmant, 1965 plate 8). B, Parapodium, anterior view (modified from Kaufmant, 1965 plate 12).

have only been found in single species. However, the determination of the stimuli, which the sensory structures mediate, is still in some cases unknown (Orrhage and Müller 2005).

In Nereididae, a single pair of antennae located on the anterior rim of the prostomium (Fig. 7.13.3.3.17) are homologous with lateral antennae in other polychaete families (Acoetidae, Polynoidae, Sigalionidae, Syllidae, Hesionidae, Phyllodocidae, Onuphidae, and Eunicidae) (Orrhage and Müller 2005). They are covered with sensory cells and probably have a tactile role and are innervated by the midbrain.

Palps are sensory organs innervated in the cephalic nervous system, from the mid to posterior part of brain, or partially or wholly from the circumesophageal ring, and are found to be homologous with other structures also termed palps in a range of other polychaetes where studies of the microanatomy of the cephalic system have been undertaken (Orrhage 1993, Orrhage and Müller 2005). Nereididae have paired ventral sensory palps, as do all Aciculata; they are relatively short in comparison and comprise a thick basal portion called a palpophore and a much smaller distal portion, a palpostyle, which is spherical, conical, or oval shaped and covered by sensory cells. Observations on living nereidids show that the palpostyles are eversible, projecting in and out of the palpophores (Harper 1979), although they appear never to invert completely as does the proboscis.

Nuchal organs are present in all Nereididae (and in all polychaetes; Rouse and Fauchald 1997) and are assumed to have a chemosensory role, although this has not been demonstrated (Rouse and Pleijel 2001) (Fig. 7.13.3.3.18). In Nereididae, they are present as small, almost invisible, ciliated pits located on the posterior prostomial corners of the prostomium (Pleijel 2001), innervated to the cephalic nervous system (Orrhage 1993). The ultrastructure of nuchal organs in *Platynereis dumerilii*, a species considered a model organism for developmental biology, is described by Schmidtberg and Dorresteijn (2010) (Fig. 7.13.3.3.18B–H), and although they are similar to those of other polychaetes (Purschke 1997), some interesting structural characteristics of the nuchal organ of *P. dumerilii* have yet to be analyzed. Suggestions that a portion of the

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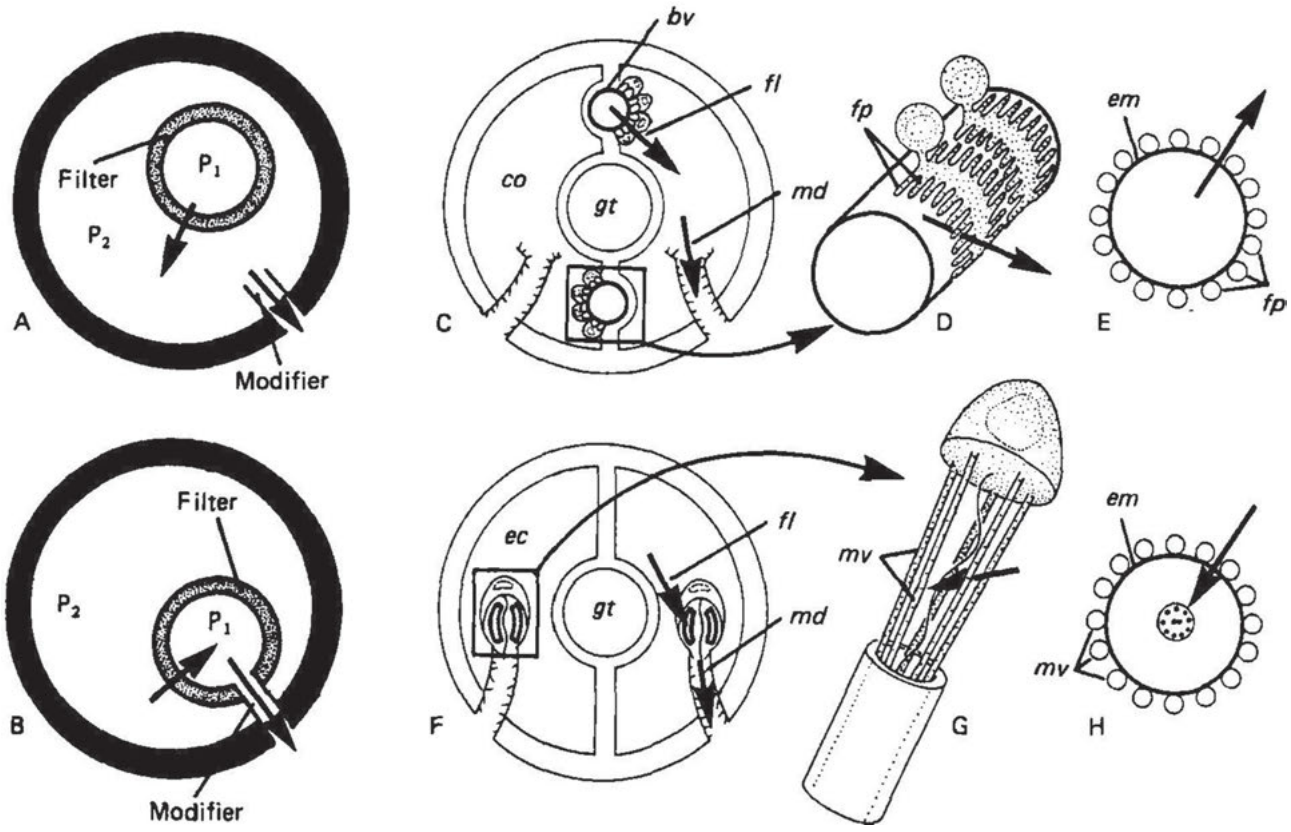


Fig. 7.13.3.3.16: A functional model of proto- and metanephridial systems in polychaetes. bv, blood vessel; co, coelomic fluid; ec, extracellular matrix; em, vascular basal lamina; fl, filtration; fp, foot process of peritoneal podocytes; gt, gut; md, modification of coelomic fluid; mv, microvilli of *Glycera* Lamarck, 1818. From Ruppert and Smith (1988, fig. 2A–H).

nerve fibers of the nuchal nerves are efferent and synapse with the ciliated supporting cells have yet to be verified in *P. dumerilii*. Also, the undefined origin of the cellular swellings in the olfactory chambers and details of the morphology of the modified sensory cilium during its course through the olfactory chamber require clarification. The authors emphasize that future studies should focus on the earlier developmental stages, as the developing nuchal organ has fewer cells than that of the adult and, thus, may be easier to describe fully.

There are various kinds of other photoreceptor-like sensory structures in polychaetes. Nereididae have two pairs of eyes (Figs. 7.13.3.3.1, 7.13.3.3.17, and 7.13.3.3.18B), dorsally located on the prostomium, and innervated in the cephalic microanatomy (Orrhage 1993), but these have not been studied in great detail as for polychaetes in general (Orrhage and Müller 2005, Purschke et al. 2006). These authors did not mention specifically the family Nereididae, but errant forms in the Aciculata were described as possessing true multicellular eyes in the adult stage (Suschenko and Purschke 2009). The two pairs of eyes of adult *Platynereis* show a very characteristic pigment-cup structure with photoreceptoral cell processes traversing the pigment cell layer shared with adult eyes in other carnivorous polychaetes, various molluscs, sipunculans, and onychophorans (Arendt et al. 2002). A distinct lens can be seen to occupy the cup-shaped eye of some but not all species (Purschke et al. 2014, fig. 7D). They represent a second separate type of eye that is distinct from the larval eyes that might equally be phylogenetically conserved, at least among Protostomia.

Nervous system. Mid-nineteenth century studies of nereidid polychaetes were among the first to examine annelid nervous systems. Members of Nereididae have complex neural morphology exemplary of errant polychaetes and are leading research models in the investigation of annelid nervous systems (Winchell et al. 2010).

The cephalic nervous system and innervations of anterior appendages in nereidids has been studied through the examination of the central nervous system

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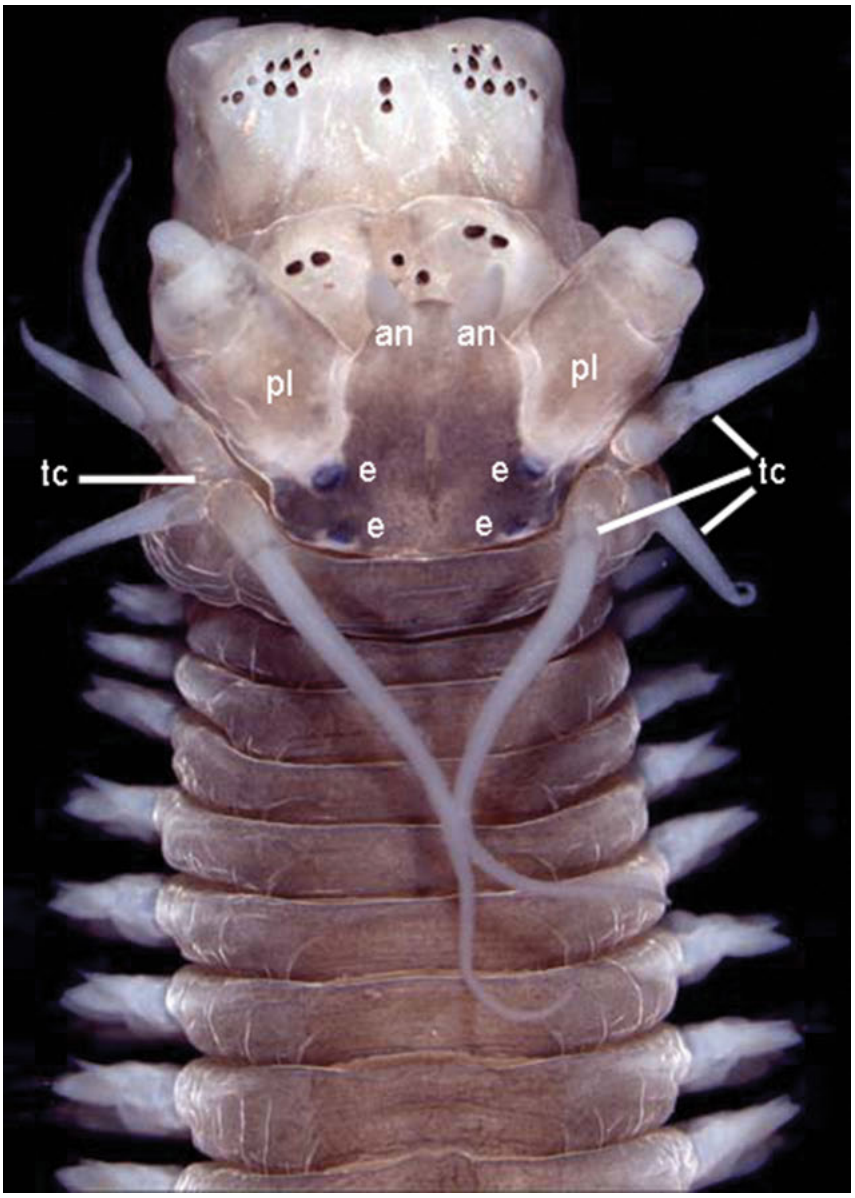
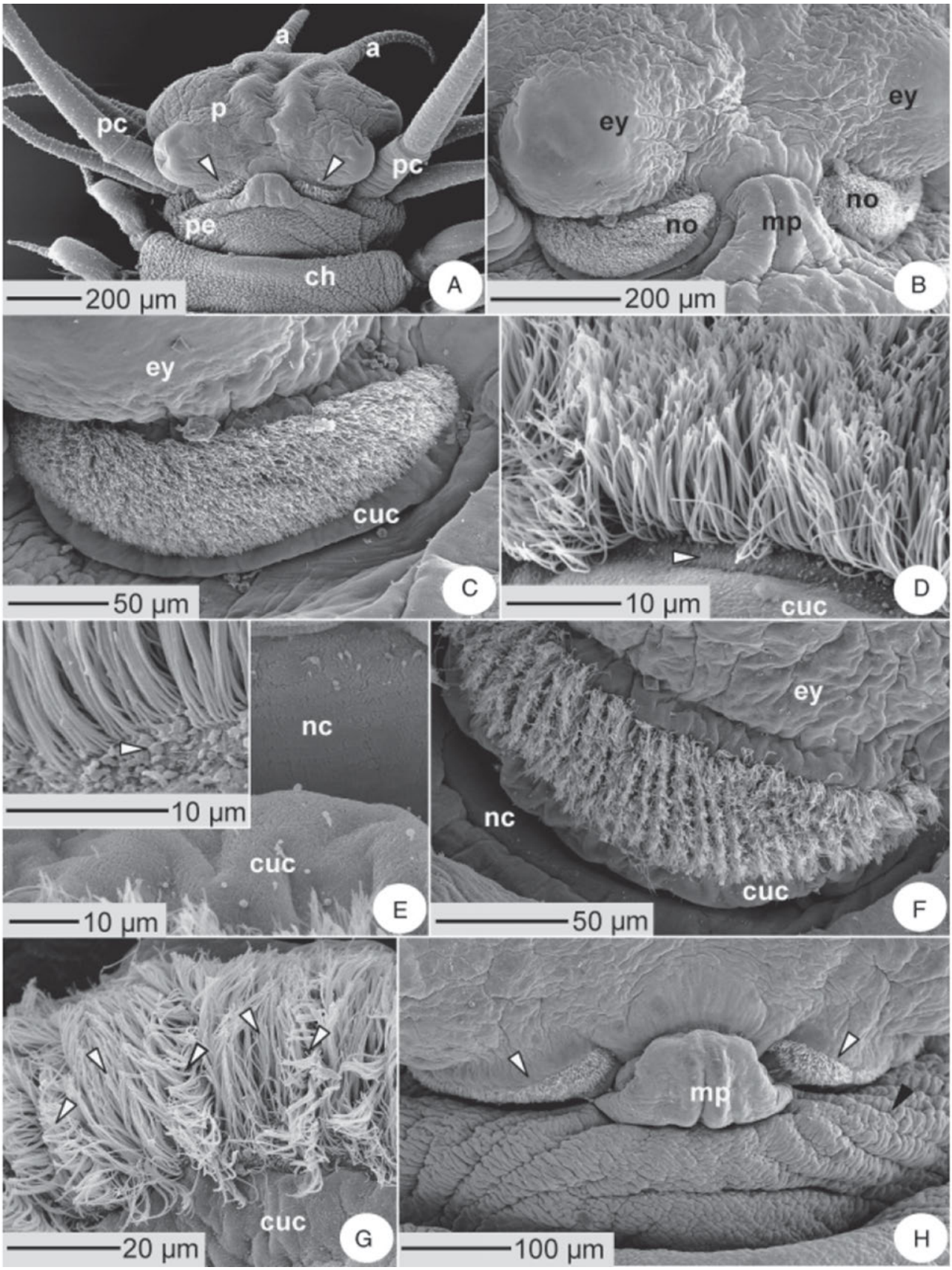


Fig. 7.13.3.3.17: Sensory organs in a nereidid anterior end, *Perinereis aibuhitensis* (Grube, 1878). an, antenna; e, eye; pl, palp; tc, tentacular cirri. Photo from C.J. Glasby.

in selected species. A review by Orrhage (1993) compared new results with previous literature and corroborated as well as clarified misconceptions in earlier studies. Several studies of brain nervous systems have been done, and Orrhage (1993) emphasized the continued relevance of several early studies (Gilpin-Brown 1959). According to Orrhage (1993), the most detailed description for the nervous system of a nereidid species is that of Gilpin-Brown (1959). Orrhage also summarized the main problems and remaining questions about the centralmost part of nervous systems in Nereididae: (1) Is the circumesophageal connective of each side connected with the brain through two or three roots? (2) Is there a ganglion at the lateral junction of the roots of the circumesophageal connectives? (3) Is there a ganglion at the dorsal root of the circumesophageal connectives?

In summary, a complex brain, as seen in Nereididae and other errant forms, is formed by a dorsal brain connected to a ventral nerve cord by two (or three) circumesophageal connectives (Rouse and Pleijel 2001). Three subdivisions are recognized: a forebrain, a midbrain, and a hindbrain. The forebrain has palpal and buccal centers and the anterior roots of the circumesophageal connectives. The midbrain has antennae and optic centers and the posterior roots of the circumesophageal connectives. Nereididae have paired dorsolaterally corpora pedunculata, which are mushroom shaped, consisting of a stalk of

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neuropil and a cap of cell bodies. The hindbrain includes centers for the nuchal organs.

The ventral nerve cord is usually paired and runs the length of the body, varying in thickness and differentiating into a ganglia in each segment. From each ganglion, nerves pass out to the body wall, muscles, and gut (Rouse and Pleijel 2001). Recently, Starunov and Lavrova (2013) described the structure of nervous system of the pygidium in *Alitta virens*. In this region, it is represented by the terminal parts of the ventral nervous system and has the form of two thick longitudinal nerve trunks which enter pygidial filaments and become gradually thinner toward the end. In the anterior pygidium, the trunks are connected to each other by a thin commissure. At the same level, two small nerves come off from the trunks medially, go to the posterior pygidium, and end at the bases of the anal cirri, whereas two nerves come off from it laterally to the dorsal part of the pygidium wall. These nerves ramify and connect at the dorsal part of the pygidium, forming a circumpygidial nerve ring.

The main results of a comprehensive overview of the nervous system in *Neanthes arenaceodentata* Moore, 1903 juveniles support the classic literature on neural architecture in adults, based on methylene blue staining, histologic reconstruction, electron microscopy, and neurophysiology (Winchell et al. 2010). However, Winchell et al. (2010) also revealed additional variability and previously unknown peripheral nerve interconnections and aspects of parapodial muscle innervation, including the presence/absence of lateral nerves, and showed when key features of the cephalic nervous system become morphologically distinguishable in the different stages of juvenile ontogeny. Examples of the latter include, first, portions of the stomatogastric system, consisting of the nerves and ganglia responsible for foregut innervation; second, the corpora pedunculata, prominent structures of the anterior brain thought to integrate information from the various cephalic sensory organs, and that are potential homologs of arthropod mushroom bodies; and third, two pairs of ciliated sense organs: the chemosensory nuchal organs of the posterior head and the poorly understood Langdon's organs of the anterior head (Winchell et al. 2010).

Although the nereidid nervous system exhibits all the hallmarks of complex annelids, it does not show exceptional specialization (Winchell et al. 2010, and references therein). Besides, the generalized morphology is traditionally considered archetypal within Annelida. Furthermore, based on arguments that Aciculata, a modern polychaete clade, including Nereididae, is most closely related to stem annelids, and the nereidid nervous system may be little changed from an early, errant polychaete ancestor.

Biology and ecology

Nereididae are common in a wide range of marine environments from the deep sea to the intertidal; many species also occur in estuaries, and some occur in freshwater, semiterrestrial, and subterranean environments. Nereidids may be infaunal, where they can build burrows and galleries, or epifaunal, inhabiting rock crevices, mangrove roots, or the blades of algae or seagrasses where they may attach flimsy mucous tubes (Fig. 7.13.3.3.19A). The common European gallery builder, *Hediste diversicolor*, is often the dominant animal in estuarine sediments with densities up to 3700 m^{-2} (Scaps 2002).

Species-rich genera show widespread, if not global, distributions. Less diverse genera often show regional fidelity, for example, *Dendronereides* is restricted to the Indian Ocean and adjacent seas; *Laeonereis* is restricted to the Americas; *Leonnates* Kinberg, 1865, *Simplisetia* Hartmann-Schröder, 1985, *Solomononereis* Gibbs, 1971, *Tambalagamia*, and *Tylonereis* Fauvel, 1911 are restricted to the Indo-west Pacific; *Tylorrhynchus* Grube, 1866 is restricted to Asian estuaries; *Cheilonereis* Benham, 1916 is restricted to the Pacific Ocean; and *Hediste* is restricted to the northern hemisphere.

Nereididae have more freshwater and freshwater-tolerant representatives than any other polychaete family with about 61 species, representing 31% of all polychaetes

◂ **Fig. 7.13.3.3.18:** Scanning electron micrographs of nuchal organs in *Platynereis dumerilii* (Audoin & Milne-Edwards, 1833). A, Dorsal view of the anterior end with peristomium and nuchal organs (arrowheads). B, Middorsal process separating the nuchal organs. C, Crescent-shaped nuchal organ as ciliated field surrounded by a smooth cuticular collar. D, Cilia of the supporting cells by the cuticular surface (arrowhead). E, View of the epithelium of the nuchal cleft. F, Cilia of the supporting cells appear to be arranged in longitudinal rows. G, Cilia of the nuchal organ fixed in action, showing metachronous waves of power and recovery strokes (arrowheads). H, Nuchal organs (arrowheads: ciliated region of the nuchal organ) almost hidden in the nuchal cleft. a, antennae; ch, chaetiger; cuc, cuticular collar; ey, eyes; mp, middorsal process; nc, nuchal cleft; no, nuchal organ; p, prostomium; pc, peristomial cirrus; pe, peristomium. From Schmidtberg and Dorresteijn (2010, fig. 1).

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recorded from nonmarine habitats, including caves and other groundwater habitats; the dominant nonmarine taxa are *Namanereis* Chamberlin, 1919 and *Namalycastis* (Glasby et al. 2009); *Hediste* is a well-known freshwater-tolerant taxon. The colonization of terrestrial water bodies by marine polychaetes, including Nereididae, can be attributed to either ancient vicariant events or more recent uplifting of coastal areas (Glasby and Timm 2008, Glasby et al. 2014). Nonmarine and freshwater-tolerant nereidids are most threatened by human activities, and at least one species, *Hediste japonica* Izuka, 1908, has been extirpated from a large part of its range in Japan and Korea as a result of land reclamation and is in danger of extinction (Sato and Sattmann 2009).

Several species, mostly euryhaline estuarine forms, have been accidentally or intentionally introduced throughout the world. Well-documented examples are the North American species *Alitta succinea* and the European species complex *Hediste diversicolor*. The spread of *Alitta succinea* can be attributed to either human introduction into inland saline lakes for aquaculture food (North America and Eastern Europe), or accidental introduction via shipping particularly Asia and the southern hemisphere, where it is generally restricted to ports (Glasby et al. 2009, Sato 2013). Taxonomic studies have documented *Alitta succinea* to be a species complex which demonstrate the need to review the taxonomy of this group, also in lieu of introductions regionally as well as globally (Villalobos-Guerrero and Carrera-Parra 2015). The spread of the *Hediste diversicolor* complex westward across the Atlantic is also complicated as it is composed of several cryptic species that each have different histories of human-mediated colonization (Einfeldt et al. 2014); like *A. succinea*, the species group has also spread eastward with the deliberate stocking of inland saline seas in Eastern Europe (Glasby et al. 2009). Another *Hediste* invader, the Japanese *Hediste diadroma* Sato & Nakashima, 2003, has been introduced multiple times across the Pacific to North America presumably by shipping (Nishizawa et al. 2014, Tosuji and Furota 2016). The westward spread of the marine Indo-Pacific species *Pseudonereis anomala* Gravier, 1899 (Fig. 7.13.3.3.1B) into the Mediterranean, also by shipping, is another well-documented example (D'Alessandro et al. 2016 and references therein). Less well documented is the introduction of freshwater species. The tropical Indo-Pacific species *Namalycastis hawaiiensis* (Johnson, 1903) has been introduced to terrestrial water bodies in Israel via the aquarium trade, and occurrences of this species in other places closer to its native range are also suggestive of a similar introduction method (Goren et al. 2020 and references therein).

Life history characteristics (longevity, spawning season, feeding tactics, and growth) and population dynamics (sex ratio, density, and biomass) vary greatly within the family. A review of reproductive modes in polychaetes described six combinations for 22 species of Nereididae, including different modes for the same species (Wilson 1991): (1) free spawning with planktotrophic larvae, (2) free spawning with lecitotrophic larvae,



Fig. 7.13.3.3.19: A, *Platynereis* sp. builds a mucous tube, a preferred temporal burrow, here pulled out from the tube for study. B, SEM micrograph showing retractable elastic threads in *Platynereis bicanaliculata* (Baird, 1863) used to build mucous tubes. Photos from D. Riek and C. Santos.

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(3) free spawning with entirely benthic development, (4) brooding outside of the body with direct development, (5) brooding inside the tube with direct development, and (6) encapsulation of embryos in a gelatinous mass with release of lecitotrophic larvae. An almost similar degree of variation is also apparent within some species complexes (e.g., *H. diversicolor*, *Perinereis cultrifera*) and between sibling species (e.g., *Platynereis dumerilii/massiliensis* (Moquin-Tandon, 1869) and *Hediste japonica/diadroma* Sato & Nakashima, 2003/*atoka* Sato & Nakashima, 2003) (Schroeder and Hermans 1975, Scaps 2002, Helm et al. 2014, Valvassori et al. 2015), indicating that life history traits may be evolving more rapidly than morphological traits in these groups.

The Nereididae undergo the best known and most complete epigamous metamorphosis, that is, transformation of the entire adult worm into a reproductive epitoke. Almost all species are semelparous, breeding only once during a life time. Death of adults usually follows reproduction as the changes resulting from metamorphosis, such as muscle degradation and body wall rupture for oocyte release, are irreversible. However, in some species, spent worms were observed to be intact (e.g., Ong 1996), which questions the generality of postspawning death. Further, males of *Neanthes acuminata* have been observed to breed up to nine times over 13 months (Reish 1957, Reish et al. 2009, as *Neanthes caudata* and *N. arenaceodentata*). The males of some species release sperm via their pygidial rosette (Schroeder and Hermans 1975, and references therein). Nereidid life spans typically range from 6 months to 3 years or more for larger species (Pagliosa and Lana 2000, Kikuchi and Yasuda 2006).

Almost all Nereididae have separate sexes (dioecious). Reproductive and developmental modes are diverse, but most species studied undergo metamorphosis (epitoky) followed by swarming and spawning in the water column, and a variable period of planktonic larval development (Schroeder and Hermans 1975, Reish 1957). There are many exceptions to this pattern, however, with some species swarming without epitoky (e.g., *Micronereis* species) and others swarming with minor modifications (e.g., *Namalycastis rhodochorde* Glasby, Miura, Nishi & Junardi, 2007). Members of the genus *Micronereis* swarm on vegetation on the seabed without metamorphosing: males fertilize eggs when they are emitted by the female, who then surrounds the eggs in a gelatinous mass and broods them (Fig. 7.13.3.3.20); larvae emerge after about 2 weeks and develop in the water column (Berkeley and Berkeley 1953). Epitoky is minimal in *N. rhodochorde* as in other Namanereidinae: in this case, only the male changes, with minor eye enlargement and acquisition of many fine compound spinigerous chaetae, which strangely appear more similar to syllid natatory chaetae than those of other nereidids (Glasby et al. 2007).

Epitoky involves several changes to the body, including loss of feeding ability as a result of reduction of the gut and septa and breakdown of paragnaths, and increased sensory and swimming abilities. Reorganization of the musculature and regionalization of the body, including the appearance of specialized natatory regions that develop additional lobes on the parapodia and specialized paddlelike natatory chaetae (hairlike in Namanereidinae), enable the worms to swim more effectively for swarming (Fig. 7.13.3.3.4D), and eye enlargement provides additional sensitivity to detect low-light levels, important for queuing reproduction to day length and moon phase (Fig. 7.13.3.3.21). In addition, the dorsal and ventral cirri of anterior body parapodia swell basally, and those of the midbody become scalloped in the males of many species. Lastly, the pygidium in males of some species becomes modified into a rosette with multiple rows of short papillae (Schroeder and Hermans 1975). External epitokal changes are often taxon and sex specific. For example, the anterior part of the prostomium enlarges to form a thin membranous, ventrally directed lobe in some *Platynereis* species (Clark 1961). Further, a single natatory region



Fig. 7.13.3.3.20: Fertilized eggs in a gelatinous egg mass from *Micronereis* sp. Photo from L. Harris.

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is common to most genera, but two different adjoining natatory regions appear to be a feature of *Solomonereis*; also, males often have fewer prenatatory chaetigers than females (Clark 1961, Pamungkas and Glasby 2015, Peixoto and Santos 2016).

In species that do not show epitoky, gender can be determined by body color and presence of gametes in the coelom, as was observed for the estuarine *Laeonereis culveri* (Webster, 1879) whose females are green and males cream in color (Mazurkiewicz 1975). Epitokal stage modifications may also be useful in identifying cryptic species, as shown by Read (2007) who was able to distinguish three species of *Platynereis* in New Zealand from epitokes, whereas the atokes were morphologically indistinguishable.

The metamorphosed worms (epitokes) are well equipped for swimming at night, and in response to seasonal occurring environmental and triggers swim to the surface during night hours to spawn. Typically, spawning involves a nuptial "dance" where the males display circling and accelerated swimming before spawning and sperm emission; females respond by shedding eggs. Spawning is initiated in males by pheromone signaling from the female; the specific pheromone is detected by sensory cells in the modified parapodial cirri (Schroeder and Hermans 1975, Zeeck et al. 1988, Lindsay 2009). Multiple-species spawning in Nereididae is probably more common than the few literature records suggest; in Ambon, Indonesia, seven to nine nereidid species were reported to spawn at the same time as the eunicid *Palola viridis* (Pamungkas and Glasby 2015); in this and other cases, which may involve multiple phyla including corals, one species may be taking chemical cues from the other (Hardege 1999).

Although nereidids as a group are adept at living in waters of reduced salinity, their early embryos and larvae have poor osmoregulatory abilities and are generally incapable of surviving low salinity water. Salinity optima for early development varies considerably between species with about 9–10 parts per thousand being the lower limit for juvenile survival (Schroeder and Hermans 1975, Tosuji and Sato 2006). Nereidids inhabiting estuarine, freshwater, and semiterrestrial environments have developed strategies to protect embryos from osmotic stress, including the following:

1. Catadromy with pelagic larval development (i.e., migration from freshwater to spawn in the sea) e.g., *Hediste diadroma* and *Tylorrynchus* species). Species of *Tylorrhynchus* and *Hediste* undergo metamorphosis and use their increased swimming power (and ebbing tides) to migrate to more saline downstream areas more conducive for early development of embryos and larvae (Yamamoto 1947, Kikuchi and Yasuda 2006).
2. Brooding with direct (nonpelagic) lecithotrophic larvae, either within the adult tube (*Australonereis* Hartman, 1954, *Simplisetia*, some *Hediste*) or in mucous clutches anchored to the substrate (*Namanereis* species, *Perinereis rullieri* Pilato, 1974) (Dorsey 1981, Glasby 1986, Sato 1999, Prevedelli and Cassai 2001, Ezhova 2011).
3. Hermaphroditism (and questionably viviparity), an extreme form of brood protection, is confirmed only for *Hediste limnicola* (Johnson, 1903); *Namanereis quadraticeps* (Blanchard in Gay, 1849); and *Namanereis catarractarum* (Smith 1950, Glasby 1999). Although the data are scarce, they suggest that these species are most likely simultaneous (self-fertilizing) hermaphrodites.

The regulation of reproduction involves a complex system of environmental and endogenous (endocrine) factors. The coordination of spawning and mating by chemical signals is better known in nereidids than other



Fig. 7.13.3.3.21: A fully metamorphosed male epitoke of *Perinereis akuna* Wilson & Glasby, 1993, dorsal view, showing modified parapodia in mid and posterior chaetigers with scalloped dorsal cirri, enlarged eyes, and rosette pygidium. Photo from D. Riek.

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polychaetes (Hardege 1999, Hardege et al. 2004, Lindsay 2009). Cyclical environmental factors, including lunar cycle and day length, provide the impetus for the initiation of gamete production, and water temperature and salinity ensure synchronization to the most favorable conditions (Clark 1961, Schroeder and Hermans 1975, Olive 1984, Bentley and Pace 1992, Lawrence and Soame 2009). Multiple sex hormones and the release of pheromones ensure the coordinated release of gametes in the water (Zeeck et al. 1988, Hardege 1999, Lawrence and Soame 2009). In at least one of the semiterrestrial namanereidine species, reproduction appears to be synchronized to the beginning of the Wet Season presumably to reduce the risk of desiccation to the embryos (Ezhova 2011).

In most cases, nereidid larvae are lecithotrophic, and development occurs in the benthos. The development of larvae to a demersal juvenile stage of three to six segments may occur in 4–40 days (Reish 1957). Juvenile development is highly variable in terms of the sequence and the development of parapodia and tentacular cirri, and in its timing, which may vary from 19 to 40 chaetiger stage for the adult form to be reached (Mazurkiewicz 2009).

Most nereidids are omnivores. They exhibit a range of feeding strategies, including both microphagous (surface deposit feeding) and macrophagous (plant grazing, predation, and scavenging) (Riisgård and Kamermans 2001). This is because of flexibility in their ingestion (the jaws are equally capable of grasping large prey items or gathering sediments) and digestion (Jumars et al. 2015). *Hediste* and possibly also *Australonereis*, which often inhabit highly productive estuaries, are inclined to be detritivore, ingesting organic matter at the sediment surface and also switching to a type of suspension feeding (=facultative filter feeding) with the aid of a mucus net bag suspended within the tube (Dorsey 1981, Riisgård 1991, Kanaya et al. 2008, Toba and Sato 2013) (Fig. 7.13.3.3.22). Another estuarine species, *Alitta succinea*, is equally adept at macrophagous or deposit feeding (Dauer 1980, Pardo and Dauer 2003). The obligate algal and plant grazers, including *Platynereis dumerilli* and *Neanthes rubicunda* (Ehlers, 1868), are an exception to the general rule of omnivory in the group: individuals of the latter species attach algae to their tube opening and display gardening behavior (Gambi et al. 2000, Cosentino et al. 2014).

Most species of Nereididae are highly motile, crawling over the surface of substrates in search of food, often during the night, or moving up and down burrows/tubes/galleries to ventilate them to transport water and associated particles and solutes through their enclosure. The tube-dwelling *Nereis vexillosa* Grube, 1851 and *Platynereis bicanaliculata* Baird, 1863 may defend their tubes against intruders and the loser is cannibalized (Roe 1975).

Locomotion has been studied in the UK populations of *Hediste diversicolor*, which show two forms of crawling: a slow one involving rotation strokes of the parapodia and grasping of the substratum by the chaetae and a more rapid one involving sinuous waves of the body from anterior to posterior (Gray 1939) (see also comments above in the section on muscles).

Most nereidids are free living. Commensalism is relatively uncommon in the group, but there are some well-documented examples, including the northern European *Neanthes fucata* and the east Asian *Cheilonereis cyclurus* Harrington, 1897, which are both commensal on species of hermit crabs where they scavenge food of the host crab (Martin and Britayev 1998). Parasitism by nereidids on other organisms is unknown. Several groups of

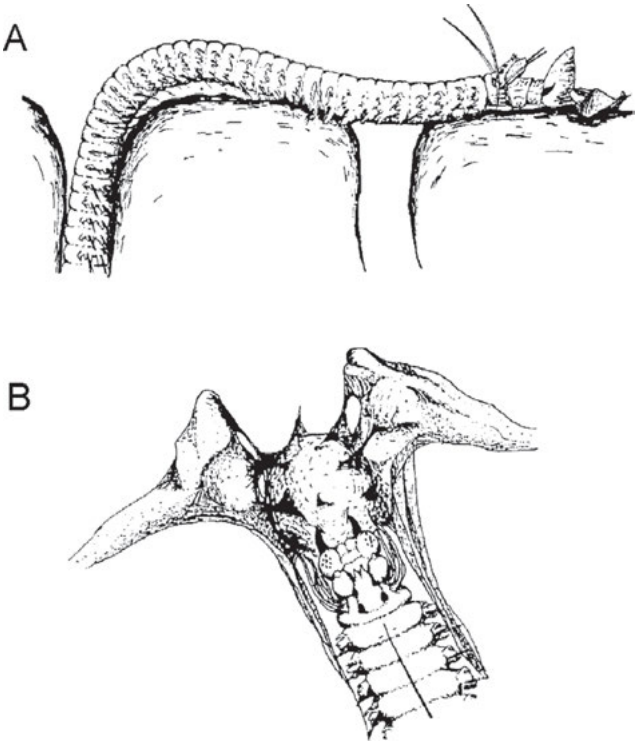


Fig. 7.13.3.3.22: Searching behavior of *Hediste diversicolor* (O.F. Müller, 1776). A, Prospecting tactic without mucous secretion, immediate ingestion of food particles. B, Prospecting tactic with mucous secretions collecting food particles brought back in a pellet form to the opening of the burrow. After Esnault et al. (1990); reproduced from Scaps (2002, fig. 2).

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animals parasitize nereidids, including endoparasitic ciliate protozoans and the oenonid polychaete *Labrorostratus* Saint-Joseph, 1888, which both live in the body cavity and feed on gametes (Scaps 2002, Arias et al. 2013, Hernández-Alcántara et al. 2015).

Nereididae have a high ecosystem value. As active predators, they can regulate infaunal benthic populations; their burrowing activities can modify biogeochemical cycles of nutrients and contaminants, and as suspension feeders, they control phytoplankton biomass. It has been estimated that in Danish fjords, *Hediste diversicolor* populations can filter the entire water mass about three times per day, reducing the phytoplankton biomass by 50% within less than 5 h (Riisgård et al. 2004). Larger intertidal forms such as *Hediste*, *Neanthes* and *Perinereis* are important prey items for shorebirds (Shin 2001, Iwamatsu et al. 2007), and fishes (especially flatfish), crustaceans (especially prawns), and cephalopods also feed on them. The high nutritional value of nereidids, specifically the high fatty acid content, makes them the preferred diet of several species, both in nature (Valls et al. 2015) and in cultivation of hatchery-reared prawns and fish (Olive 1994, 1999). They are also used by humans for fishing bait, as aquaculture feed, and for sewage waste treatment (Kurihara 1983, Gambi et al. 1994, Idris et al. 2012). The bait worm *Alitta virens* is one of the most valuable wild-harvested polychaetes worldwide, worth £33 per kilogram in the UK and £62 per kilogram in the United States (Watson et al. 2017). Trade in live worms for bait has increased the risk of accidental introductions; at least one case of translocation has been reported — the east Asian species, *Perinereis linea* Treadwell, 1936, has been introduced recently to western Europe (Gambi et al. 1994, Arias et al. 2013).

A lesser known value of nereidids is human consumption. In many countries of East and Southeast Asia, the reproductive forms (epitokes) of nereidid species are consumed, either as a targeted species in the case of the east Asian *Tylorrhychus heterochaetus* Quatrefages, 1866 or as "by-catch" as part of traditional, festival-based harvest of *Palola viridis* (Eunicidae) in Ambon, Indonesia and Timor-Leste (Pamungkas and Glasby 2015, Glasby personal observation).

Finally, some Nereididae, including *Platynereis dumerilii*, *Alitta succinea*, *Hediste diversicolor*, and *Neanthes acuminata*, have become model species for developmental, environmental, and chemical ecology studies (Hardege 1999, García-Alonso et al. 2011, Helm et al. 2014). Their ubiquity in coastal environments, well-known neurohormone regulated reproduction, and development makes them particular useful in toxicity tests and bioassays and for developing biomarkers.

Phylogeny and taxonomy

Rag worms were mentioned in pre-Linnaean writing (Fauchald and Rouse 1997). *Nereis pelagica* Linnaeus, 1758 and *Nereis caerulea* Linnaeus, 1758 were the first two nereidid species described, and *Nereis pelagica* Linnaeus, 1758 was subsequently designated by Hartman (1948) as type species of the genus *Nereis*, the type genus of the family (Hartman 1959). Early nineteenth century authors described several species-level taxa in *Nereis*, many of which are now known to belong to other families (Hartman 1959).

As one of the first standard works on polychaetes, Johnston (1865) has often been given as author of the family as he was the first to use and write Nereididae as the family name. According to the nomenclatorial rules, unlatined usage of the name should be taken into account, and it was argued that Lamarck, 1818 should be the author (Bakken and Wilson 2005). It appears that Lamarck did not include *Nereis* in his systematic account, unlike Blainville (1818) who should therefore be the author of the family (Read and Fauchald 2019).

Kinberg (1865) used his pharyngeal identification system (Fig. 7.13.3.3.12) to erect new families from nereidid taxa. This was emended when Malmgren (1867) published a comprehensive work on North Atlantic polychaetes. Malmgren synonymized several of Kinberg's new families with Nereididae, and he presented a key, as a chart, with brief diagnoses in Latin to nereidid genera found in the North Atlantic. This was in large based on parapodial features but also included paragnath characters (Fig. 7.13.3.3.23).

Although neither Kinberg nor Malmgren discussed classification of Nereididae as such, their contemporary works are interesting in the way they had contact or at least had their respective papers available. For example, Kinberg (1865) and Malmgren (1865) were published in consecutive pages in the same volume, in which Malmgren cited Kinberg's work. Malmgren (1867) must have studied Kinberg's work in detail and used Kinberg's description of pharyngeal armature, although he did not use the numbering system of the pharynx. It seems that it was Malmgren who coined the word "paragnaths" (Malmgren 1867).

Ehlers (1868) was of the opinion that Kinberg and Malmgren had recognized too many genera to encompass the diversity of nereidid morphology and synonymized

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all genera having paragnaths with *Nereis*. Claparède (1870) compromised and placed species he described in respective subgenera of *Nereis*; and later Saint-Joseph (1898) emended descriptions for some genera and recognized them as subgenera, but he kept others with rank of genus.

A formal systematic classification delineating nereidid groups was not suggested until Corrêa (1948) erected the first subfamily, which she named Lycastinae. Hartman (1959) reviewed this group, showed that *Lycastis* did not have generic status, and redescribed and gave the subfamily the new name Namanereinae, placing Lycastinae in synonymy. Reduced notopodia was a key diagnostic character for taxa included in the subfamily, along with lack of papillae and paragnaths on the pharynx (Hartman 1959).

Another subfamily was erected for taxa possessing parapodial branchiae and included *Dendronereis*, *Dendronereides*, and *Tambalagamia*. Named Dendronereinae from the type genus, Pillai (1961) argued that this group of taxa should be included in a subfamily of their own because of the presence of the aberrant nereidid character notopodial branchiae being a synapomorphy for the group. This subfamily was, however, rejected by Banse (1977b) who showed that the "branchiae" as then termed were not homologous structures across Nereididae, for example, the "branchiae" of *Tambalagamia* are expanded notopodial ligules, and the genus must be related to *Ceratocephale* and *Gymnonereis*. Earlier, Southern (1921) had shown that the "branchiae" of *Dendronereis* and *Dendronereides* were convergent characters.

Banse (1977a) erected the subfamily Gymnonereidinae, which he hypothesized to be a monophyletic group, including taxa with two shared characters not found in other Nereididae: bifid neuropodial cirri and numerous chaetae in anterior chaetigers. He also included other characters in the diagnosis for the group but emphasized the homoplasious condition in many of these characters. By this definition, Gymnonereidinae included *Ceratocephale*, *Gymnonereis*, *Micronereides*, and *Tambalagamia* (Banse 1977a). Before this, Pettibone (1971) had revised a large number of taxa by the examination of type material, belonging to a group of nereidids without paragnaths but with or without soft papillae on the pharynx. She did not discuss phylogeny or classification as such, but her detailed description of parapodial morphology provided many new characters in a group lacking pharyngeal characteristics. The group

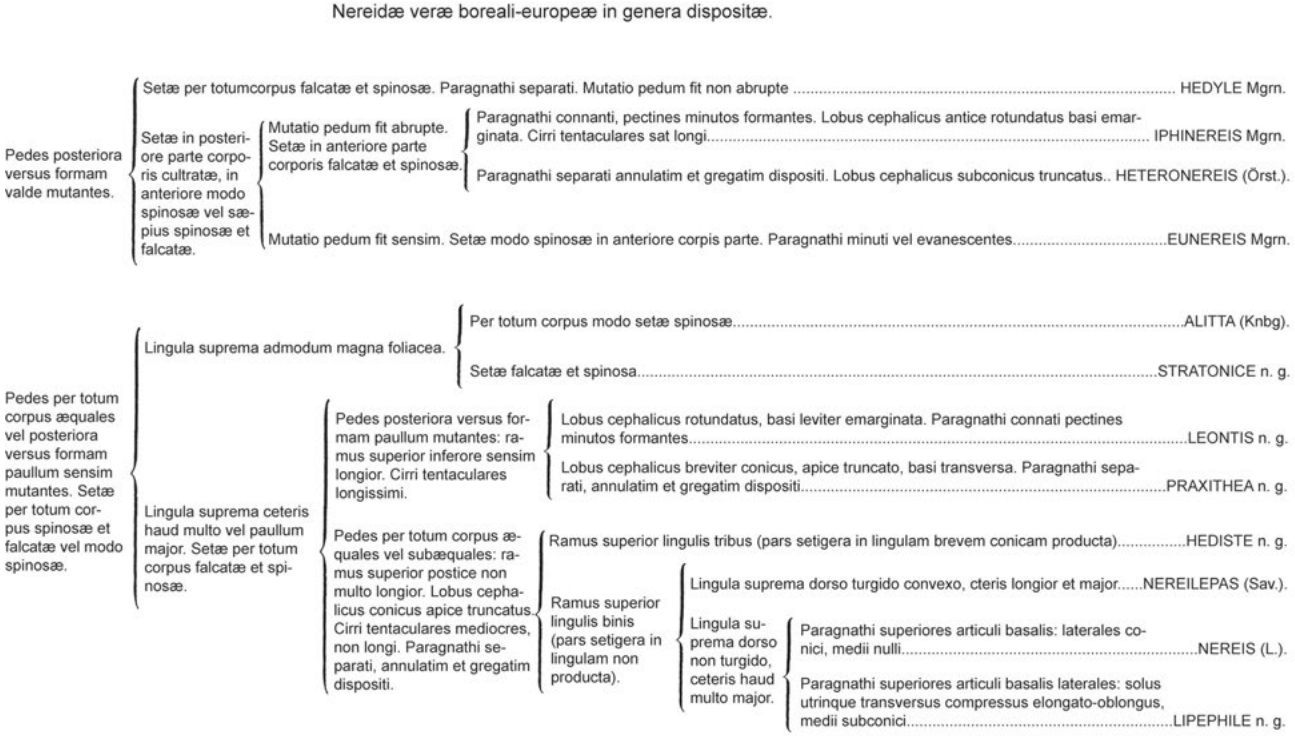


Fig. 7.13.3.3.23: An early identification chart for all North European genera of Nereididae where both parapodial characters and character variation using paragnaths were used as distinguishing features (modified from Malmgren 1867).

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Banse (1977a) included in Gymnonereidinae consisted of taxa without paragnaths but with a diverse range of parapodial structures.

A fourth subfamily, Notophycinae, was described for minute specimens belonging to *Micronereis* and *Quadricirra* (Banse 1977b). *Quadricirra* was later synonymized with *Micronereis* (Paxton 1983), which left *Micronereis* a single genus in Notophycinae. Several unique characters for Notophycinae were given (Banse 1977b): absence of antennae, pharynx not differentiated in two rings, absence of dorsal cirri in the first two chaetigers, and presence of copulatory hooks in males. On taxonomic grounds, *Micronereis* was justified as a group of species being nereidids, but the phylogenetic position of the genus within the family was left open based on a discussion of possible neotenic characters (Banse 1977b).

Khlebovich (2001) proposed that cecal or esophageal glands (Wu et al. 1985) provided novel additional characters of phylogenetic significance in nereidids. Khlebovich's study found cecal glands to be present in taxa with paragnaths but absent in taxa with a combination of papillae and paragnaths, although cecal glands were also found in species in *Nicon*. Based on the presence or absence of cecal glands, two tribes in the subfamily Nereidinae were erected, Nereidini and Leonnatini (Khlebovich 2001). Khlebovich (1996) recognized the original definition of Gymnonereidinae (Banse 1977a), leaving all other taxa in Nereidinae. The conclusions and suggested classification was not based on a phylogenetic analysis and has received little attention in the literature, and his cecal glands have not been used in any study using parsimony or other phylogenetic methods.

Nereididae was recognized as a monophyletic group defined by the presence of autapomorphies with distinct notopodia, usually with flattened lobes (also called ligules), and notochaetae with compound falcigers and/or spinigers (Glasby 1993). Nereididae can be pragmatically diagnosed from other family-level polychaete taxa as follows: "foregut with one pair of lateral jaws; head discrete and compact, dorsal to mouth; prostomial antennae paired arising anterolaterally; capillary chaetae absent; pygidial appendages present" (Glasby and Fauchald 2003).

It is well established that Nereididae is a part of Phyllodocida (Rouse and Pleijel 2001). Apart from the study of the superfamily Nereidoidea (Glasby 1993), which studied the interrelationships of the group, no phylogenetic analyses to assess the position of the family within Phyllodocida has been undertaken. However, nereidid species have been a part of phylogenetic studies aiming at resolving questions in relationships of specific taxa, usually represented by one or two terminals.

The study of Nereidoidea found Nereididae as sister-group to Chrysopetalidae and Hesionidae, the three forming one clade, which was the sister-group of another consisting of Pilargidae, Nautiliniellidae, and Syllidae (Glasby 1993). Pleijel and Dahlgren (1998) supported Glasby's (1993) result with a Chrysopetalidae, Hesionidae, and Nereididae sister-group relationship, which was supported by molecular analyses of the same taxa (Dahlgren et al. 2000). In their analyses of morphological data for polychaete relationships, Rouse and Fauchald (1997) found Nereididae being sister-group to a clade, including Glyceridae, Goniadidae, Paralacydoniidae, Pisionidae, Lacydonidae, and Phyllodocidae. Worsaae et al. (2005) obtained a group consisting of Nereididae, Syllidae, and Hesionidae in a combined morphological and molecular analysis.

The first phylogenetic study of relationships within Nereididae was that of Fitzhugh (1987), using genera as terminals represented by type species based on original descriptions. The most parsimonious of the two resulting trees was used to present a new classification of Nereididae, with three monophyletic subfamilies (Namanereidinae, Gymnonereidinae, and Nereidinae Blainville, 1818, including Notophycinae Knox & Cameron, 1970) (Fitzhugh 1987). One subfamily, Gymnonereidinae, had to be expanded to include all genera without paragnaths, excluding Namanereidinae that was retained unchanged; the newly defined Gymnonereidinae thus encompassed a more diverse group of taxa. Glasby (1991) supported Fitzhugh's (1987) concept of Namanereidinae but differed in the status and synapomorphies defining other subfamilies. Santos et al. (2005) conducted a further parsimony analysis using morphological data, also with genera represented by single representative species; their analysis found support for Namanereidinae and for a restricted Gymnonereidinae (sensu Banse 1977a), but most other nereidid subfamily previously proposed were unresolved. Bakken and Wilson (2005) almost simultaneously published results of another phylogenetic study, also using parsimony methods and morphological data. Bakken and Wilson's study was restricted to Nereididae with paragnaths but with most genera represented by multiple species; they failed to find support for most currently accepted genera with the most species-rich genera (*Neanthes*, *Nereis*, and *Perinereis*) in particular recognized as polyphyletic. A study using a fragment of the COI gene for

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22 species representing eight genera was the first study to test nereidid phylogeny using molecular techniques, which found the family paraphyletic (Liu et al. 2012). Currently, recognized subfamilies were also found not monophyletic in a study where complete mitochondrial genomes were used to test phylogenetic relationships in the family (Alves et al. 2020). They found that mitochondrial gene order data may be phylogenetically informative, and that the current classification does not reflect the evolutionary history of the family, which should be addressed with broader taxon sampling.

There are currently 43 genera and about 705 accepted names of species or subspecies ranks in the family Nereididae (Read and Fauchald 2019). Many of the most species-rich genera of Nereididae are heterogeneous assemblages of species (Bakken and Wilson 2005, and discussion above) and for convenience have been divided into informal, artificial groups based on morphological characters. Fauchald (1972) defined such groups within *Neanthes* Kinberg, 1865 solely based on chaetal and parapodial characteristics, and Wilson (1984) updated that system. Hutchings et al. (1991) devised a similar informal subdivision of species within the genus *Perinereis* Kinberg, 1865 based on paragnath and parapodial characters, where the number of smooth bar-shaped paragnaths in area VI was a key feature. Another Kinberg genus, *Ceratonereis* Kinberg, 1865, had been widely recognized as representing a heterogeneous grouping of species (Fauchald 1972, Perkins 1980, Hutchings and Turvey 1982), and many species have been assigned to that genus based solely on the absence of oral ring paragnaths. Fauchald (1972) stated this was a catchall genus for species with poorly developed paragnaths. Hartmann-Schröder (1985) reviewed species assigned to *Ceratonereis* and formally erected three subgenera: *Ceratonereis* (*Ceratonereis*) for species with indented prostomium and distinctive sesquigomph falcigers, *Ceratonereis* (*Simplisetia*) for species with fused heterogomph falcigers in neuropodial positions, and *Ceratonereis* (*Composetia*) for the remaining species. Khlebovich (1996) elevated these subgenera to full generic status, which has been followed since (e.g., Wilson 2000, Bakken and Wilson 2005, Glasby 2015, Pamungkas and Glasby 2015). Groups of species of *Nereis*, with morphological similar characters, have been compared in detail (Fauchald 1972, Hutchings and Turvey 1982, Hilbig 1992), although no authors have systematically reviewed morphological diversity across this large genus, which includes more than 150 species.

In the absence of an accepted phylogenetic analysis of relationships within Nereididae (see discussion above), and despite universal support for a monophyletic Namanereidinae (Fitzhugh 1987, Glasby 1991, Santos et al. 2005, Alves et al. 2020), we list the 42 currently accepted nominal genera alphabetically.

Nereididae Blainville, 1818

Type genus: *Nereis* Linnaeus, 1758.

Diagnosis: Body shape vermiform; segments numerous (more than about 15); regionalization absent. Pygidium simple ring or cone. Pygidial appendages present; one pair of cirri. Head discrete and compact, dorsal to mouth. Prostomium bluntly conical to trapezoidal (narrow end anteriorly) (sometimes called an inverted T-shape). Eyes present (rarely absent); two (rarely three) pairs; situated on prostomium; compound with lenses. Prostomial antennae present, paired (rarely absent or single); arising anterolaterally; smooth. Palps paired; biarticulated (robust basal part and spherical or oval-shaped terminal part, which is rarely absent) (excepting *Micronereis* in which palps comprise a single article); ventrolateral. Nuchal organs indistinct, paired, dorsolateral patches. Peristomial ring absent (rather, an enlarged fused annulus present behind head). Foregut a muscular axial pharynx; with one pair of lateral, fanglike jaws (often serrated); without paragnaths (rarely), or with paragnaths present in distinct areas; surface smooth, or with soft papillae; papillae in distinct areas. First segment with tentacular cirri. Tentacular cirri three to four pair(s); arise on a single segment (which is fused to s); internal aciculae absent. First chaetiger with neurochaetae only, or with both notochaetae and neurochaetae. Parapodia uniramous throughout (rarely), or biramous with prominent parapodial lobes (up to five lobes per parapodium); notopodial lobes represented by at least one chaetal lobe, or absent; neuropodial lobes represented by at least one chaetal lobe. Dorsal cirri more or less cirriform, or flattened and foliaceous (rarely), or basally dendritically branched (rarely). Ventral cirri present, cirriform, or tapering. Branchiae absent, or present (rarely); arise from parapodia; occur on at least some chaetigerous segments; digitiform (resemble cirri; one or more per parapodium) or branched. Notochaetae absent (rarely) or present. Aciculae present; in both dorsal and ventral positions (=noto- and neuroaciculae, although notoaciculae may be absent from chaetigers 1 and 2 in some genera). Compound chaetae present; appendage distally tapering to slender tips (=spinigerous) or distally curved (=falcate); appendage not canaliculated; appendage without hoods

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or guards; joint more or less symmetrical (=homogomph; includes also hemigomph/sesquigomph) or distinctly asymmetrical (=heterogomph); joint effected by ligament(s) (double), although occasionally absent in case of a fused joint; shaft tapering slightly or evenly thick from emergence to joint; shaft with camerated core. Compound falcigers present in most or all chaetigers. (Following Wilson et al. 2003.)

Alitta Kinberg, 1865

Type species: *Nereis virens* Sars, 1835.

Diagnosis: Prostomium with entire anterior margin, two antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment larger than length of chaetiger 1. Maxillary ring of pharynx with conical paragnaths; areas I–IV, present. Oral ring with conical paragnaths and occasionally P-bar or pyramidal paragnaths; area V, present or absent; VI–VIII, present. Dorsal ligule elongated pennant-like or wide cordate in posterior chaetigers. Prechaetal notopodial lobe long on anterior chaetigers, present at least on anterior and middle chaetigers. Dorsal cirri middorsally to terminally attached to dorsal ligule in posterior chaetigers. Neuropodial postchaetal lobe projecting beyond end of acicular ligule, present throughout, digitiform. Notoaciculae absent or present from chaetigers 1 and 2. Neurochaetae upper fascicle with homogomph spinigers; heterogomph falcigers on anterior chaetigers present, on posterior ones absent or present. Neurochaetae lower fascicle with heterogomph spinigers and heterogomph falcigers present. Heterogomph falcigers may have terminal tendon. (Following Villalobos-Guerrero and Carrera-Parra 2015, p. 160.)

Remarks: Kinberg (1865) erected *Alitta* for the single species, *Alitta virens*, emphasizing the "foliose" dorsal ligules of the parapodia, which distinguished this taxon from other taxa possessing parapodia with similar appearance (Fig. 7.13.3.3.12). In the same year, Malmgren (1865) assigned *Alitta brandti* to the same genus. Most authors have since treated *A. virens* and *A. brandti* as species of *Neanthes* and, hence, regarded *Alitta* as a synonym of *Neanthes*. Khlebovich (1996) resurrected *Alitta* for a group of closely related species: *A. virens*, *A. brandti*, and *Alitta grandis*, a complex of species. *Alitta* was found to be monophyletic in phylogenetic analyses (Bakken and Wilson 2005), with foliose dorsal notopodial ligule as one of the synapomorphic characters.

Villalobos-Guerrero and Carrera-Parra (2015) emended the generic diagnosis. Further, they did not accept transfer of *Alitta succinea* to *Neanthes*, which was proposed by Sato (2013), as this was not justified on a suite of phylogenetic characters. Villalobos-Guerrero and Carrera-Parra (2015) briefly discussed the other species in the genus and suggested these, with *A. virens*, comprise a species complex, for a part was revised comprising species with a north Pacific distribution (Villalobos-Guerrero and Bakken 2018). Eight species are considered valid in this genus (Villalobos-Guerrero and Bakken 2018).

Australonereis Hartman, 1954

Type species: *Nereis* (*Leonnates*) *ehlersi* Augener, 1913.

Diagnosis: Prostomium with anterior margin indented, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx with papillae (sometimes with horny tips). Oral ring bare, papillae, and paragnaths absent. Ventrum of anterior chaetigers with rows of papillae connecting with base of each neuropodium. Dorsal notopodial ligule similar in size and shape throughout. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph and sesquigomph spinigers present, sesquigomph falcigers present, blades serrated. Neurochaetae, ventral fascicle: sesquigomph falcigers and sesquigomph spinigers present. (Following Bakken and Wilson 2005, p. 517.)

Remarks: The genus is monotypic and only known from Australia.

Ceratocephale Malmgren, 1867

Type species: *Ceratocephale loveni* Malmgren, 1867.

Diagnosis: Pair of frontal antennae displaced nearby the basis of palps; proboscis with conical papillae on oral ring, maxillary ring bare; parapodia with noto and neuroaciculae supporting noto- and neuropodia, respectively; notopodial ligulae absent; dorsal cirri with cirrophore, that might be expanded; double ventral cirri; notopodia with supra-acicular chaetae homogomph spinigers throughout and subacicular sesquigomph spinigers; neuropodia with homogomph and sesquigomph spinigers, sesquigomph falcigers may be present. (Following Santos 2007, p. 373.)

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Remarks: Banse (1977a) revised the genus and Santos (2007) emended the generic diagnosis with first observations of sesquigomph chaetae for species in this genus. Hylleberg and Nateewathana (1988) argued that *Tambalagamia orientalis* Hartman, 1976 should be transferred to *Ceratocephale*, which is also referred to by León-González and Góngora-Garza (1992). It seems that the questions raised in the papers cited above show that *Ceratocephale* is in need of revision. As there are doubts concerning some species, *T. orientalis* is here kept in *Tambalagamia*. There are currently 12 recognized species in *Ceratocephale*.

Ceratonereis Kinberg, 1865

Type species: *Ceratonereis mirabilis* Kinberg, 1865.

Diagnosis: Prostomium with anterior margin indented, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. Maxillary ring of pharynx: area I, conical or minute rodlike paragnaths in a compact cluster present or absent; II–IV, conical paragnaths present. Oral ring bare. Dorsal notopodial ligule markedly reduced, or not, on posterior chaetigers. Prechaetal notopodial lobe and acicular process absent. Dorsal cirrus middorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, arising from basal cirrophore. Basal cirrophore cylindrical throughout. Neuropodial postchaetal lobe present, restricted to limited number of anterior chaetigers, projecting strongly beyond end of acicular ligule. Notoaciculae present on chaetigers 1 and 2. Notochaetae: sesquigomph spinigers and falcigers present, blade in falcigers distally bifid or with single distal tooth. Neurochaetae, dorsal fascicle: sesquigomph spinigers present, heterogomph falcigers present or absent. Neurochaetae, ventral fascicle: sesquigomph falciger blade distally bifid or with single distal tooth, heterogomph spinigers, and heterogomph falcigers present, latter with long blade, terminally bifid or with single terminal tooth. (Following Bakken and Wilson 2005, p. 518.)

Remarks: *Ceratonereis* as previously defined has been a large and diverse genus that has been described as a catchall group for nereidids with poorly developed paragnaths (Fauchald 1972). An important redescription of the type species *C. mirabilis* and related species was provided by Perkins (1980). *Ceratonereis mirabilis* had previously been reported as a cosmopolitan, but Perkins redefined the status of species and their distribution. Later, Hartmann-Schröder (1985) formally revised the genus, recognizing three subgenera: *Ceratonereis*, *Simplisetia*, and *Composetia*. The subgenera were widely used in the literature until given status of full genera (Khlebovich 1996). The status of separate genera was confirmed in a phylogenetic analysis and *Ceratonereis sensu stricto* was found to be monophyletic (Bakken and Wilson 2005). The diagnosis of the genus was emended according to the phylogenetic results (Bakken and Wilson 2005).

A total of 14 species belong in *Ceratonereis sensu stricto* in addition to 13 species that could not be placed by Hartmann-Schröder (1985) and remain as *Ceratonereis incertae sedis*.

Cheilonereis Benham, 1916

Type species: *Nereis cyclurus* Harrington, 1897.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Ventral peristomial flap present, covering areas VII–VIII when proboscis everted. Maxillary ring of pharynx, conical paragnaths: areas I–IV, present. Oral ring, conical paragnaths: area V, absent; VI, present; VII–VIII, present. Dorsal notopodial ligule markedly elongate, broader on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, restricted to a limited number of anterior chaetigers. Dorsal cirrus middorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers and falcigers. Neurochaetae, dorsal fascicle: homogomph spinigers, heterogomph falcigers, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers, heterogomph falcigers with long blades on anterior chaetigers, medium blades on posterior chaetigers. (Following Bakken and Wilson 2005, p. 519.)

Remarks: The genus was diagnosed based on the unique ventral peristomial flap (Benham 1916). Later He and Wu (1989) described the monotypic *Laevispinereis* He & Wu, 1989 with a feature they regarded as similar, although an alternative explanation is that the distorted peristomium region is a preservation artifact; we follow Read and Fauchald (2019) in regarding it as a junior synonym of *Leonnates*. Details on the relationship between these two taxa are unknown (Bakken and Wilson 2005). Two species of *Cheilonereis* are known.

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Composetia Hartmann-Schröder, 1985

Type species: *Nereis costae* Grube, 1840.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: area I, present or absent; II–IV present. Oral ring, paragnaths absent. Dorsal notopodial ligule similar in size on anterior and posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus basally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe present, at least on some anterior chaetigers. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers present, sesquigomph spinigers, and falcigers present or absent. Neurochaetae, ventral fascicle: sesquigomph falcigers present or absent, homogomph spinigers present, heterogomph falcigers present or absent, homogomph falcigers on anterior chaetigers absent, posterior chaetigers present or absent. (Following Bakken and Wilson 2005, pp. 520–521.)

Remarks: When first defined, *Composetia* included notopodial homogomph falcigers in the description (Hartmann-Schröder 1985), but this is not recorded for any of the species assigned to the genus, hence, this character is removed from the description. When *Ceratonereis* was restricted and redescribed (Perkins 1980, Hartmann-Schröder 1985) and other species were transferred to *Simplisetia*, *Composetia* became the catch-all genus that *Ceratonereis* used to be. The group is in need of revision; 25 species have been assigned to the genus.

Dendronereides Southern, 1921

Type species: *Dendronereides heteropoda* Southern, 1921.

Diagnosis: Prostomium with anterior margin indented, one pair of antennae, palps biarticulated with transverse groove on palpophore and conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. One apodous anterior segment. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary and oral rings of pharynx with papillae, solitary. Dorsal notopodial ligule divided into numerous branchial filaments. Dorsal cirri single. Ventral cirri single. Notochaetae: homogomph spinigers present, sesquigomph spinigers present or absent. Neurochaetae: dorsal fascicle heterogomph spinigers present or absent, homogomph spinigers present; sesquigomph spinigers present or absent. Neuropodial dorsal fascicle heterogomph falcigers on anterior chaetigers present or absent; homogomph falcigers on anterior chaetigers present or absent. Neurochaetae, ventral fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent; neuropodial ventral fascicle heterogomph falcigers and homogomph falcigers present or absent. (Following Wilson et al. 2003, with minor emendation).

Remarks: There are currently three accepted species in this genus. All appear to have overlapping distributions in the Indo-Pacific area (Hutchings and Reid 1990, Chan 2009).

Dendronereis Peters, 1854

Type species: *Dendronereis arborifera* Peters, 1854.

Diagnosis: Prostomium with anterior margin indented, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Eyes present, two pairs. One apodous anterior segment. Maxillary ring of pharynx with or without papillae and paragnaths. Oral ring papillae present. Dorsal cirrus basally divided into numerous branchial filaments. Dorsal notopodial ligule present, similar in size on anterior and posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Ventral neuropodial ligule of anterior chaetigers present, up to half length of acicular neuropodial ligule; on posterior chaetigers absent. Neuropodia of branchial chaetigers divided into five lobes, plus ventral cirrus, plus two smaller cirri on ventral neuropodial lobe (not arising from same location as ventral cirri); posteriorly, eventually with single neuropodial lobe and ventral cirrus. Notochaetae: homogomph spinigers present. Neurochaetae, dorsal fascicle: homogomph spinigers present. Neurochaetae, ventral fascicle: homogomph spinigers present. (Following Wilson et al. 2003).

Remarks: There are currently five accepted species in this genus, which appear to be restricted to the Indian Ocean and Indo-Malay Archipelago. A recent addition with a new species from Taiwan also contributed to insight to the morphological characteristics of this group (Hsueh 2019a).

Eunereis Malmgren, 1865

Type species: *Nereis longissima* Johnston, 1840.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical

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palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx without paragnaths. Oral ring, conical paragnaths: area V, present or absent; VI, present or absent, smooth bars present or absent; VII–VIII, present or absent. Dorsal notopodial ligule present, similar in size or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent; when present, restricted to limited number of anterior chaetigers. Acicular process present or absent. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers present, homogomph falcigers present or absent. Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers present. Neurochaetae, ventral fascicle: heterogomph spinigers and heterogomph falcigers with long blades present. (Following Bakken and Wilson 2005, p. 523).

Remarks: Species of *Eunereis* resemble species of *Neanthes* and *Nereis*. *Eunereis* is separated from *Nereis* by the presence of paragnaths on the oral ring only. Types and distribution of chaetae are similar for the two genera, and the description of the genus includes several characters being scored as "absent or present," indicating a heterogeneous assemblage of species (Bakken and Wilson 2005). A review of the genus is necessary, which includes nine species.

Gymnonereis Horst, 1919

Type species: *Gymnorhynchus sibogae* Horst, 1918.

Diagnosis: Body elongated, depressed, attenuated posteriorly. Prostomium with frontal margin deeply incised between bases of antennae. Eversible pharynx with jaws having cutting edge smooth or serrated, with papillae on oral ring. Notopodia with accessory dorsal cirri attached to dorsal cirrophores in anterior region only, with prechaetal ligules and short, rounded postchaetal lobes. Median segments with dorsal cirrophores greatly elongated and highly vascularized (except in *Gymnonereis crosslandi*) and lacking accessory cirri. Dorsal transverse ridges present or absent. Chaetae homogomph or sesquigomph spinigers and homogomph or sesquigomph falcigers may be present. Chaetae very numerous in anterior chaetigers. (Following Hutchings and Reid 1990, p. 86.)

Remarks: Phylogenetic analysis placed *Gymnonereis* in a monophyletic group with *Micronereides*, *Ceratocephale*, and *Tambalagamia* based on the presence of double ventral cirri and subacicular notochaetae (Santos et al. 2005). Several characters justified the monophyly of the genus, but the double ventral dorsal cirri is the most characteristic. Species in *Gymnonereis* are close to *Tambalagamia* species, which is evident from literature records synonymizing *Tambalagamia* with *Gymnonereis* (Pettibone 1970, Banse 1977a, Hylleberg and Nateewathana 1988, Hutchings and Reid 1990). Six species are currently assigned to *Gymnonereis* (Darbyshire 2014).

Hediste Malmgren, 1867

Type species: *Nereis diversicolor* O. F. Müller, 1776.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: area I, present or absent; II–IV, present. Oral ring, conical paragnaths: area V, absent; VI–VII, present. Dorsal notopodial ligule similar in size throughout. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, restricted to limited number of anterior chaetigers. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers present, blades serrated; fused (simple) falcigers present. Neurochaetae, ventral fascicle: heterogomph spinigers and heterogomph falcigers with long blades present. (Following Bakken and Wilson 2005, p. 524.)

Remarks: Species of *Hediste* are diagnosed by the large fused falcigers in posterior neuropodia, a type of chaeta often termed simple falcigers in descriptions. These chaetae are similar to those found in *Simplisetia* species, but the two genera are distinguished by the absence of oral ring paragnaths in *Simplisetia*. The two groups were found to be related (Bakken and Wilson 2005). A complex of species was described and revised based on material from Japan (Sato and Nakashima 2003). The distinct fused falcigers were not described for *Hediste kermadeca* (Kirkegaard 1995), retaining five species in this genus. It has been shown that *Hediste diversicolor* is a complex of species and has deep phylogeographic splits over large geographic distances, as well as sympatrically separate genetic lineages (Audzijonyte et al. 2008, Virgilio et al. 2009, Einfeldt et al. 2014, Tosuji et al. 2018).

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***Imajimainereis* León-González & Solís-Weiss, 2000**

Type species: *Imajimainereis pacifica* León-González & Solís-Weiss, 2000.

Diagnosis: Prostomium pentagonal, with one pair of frontal antennae and two pairs of eyes. Apodous anterior segment with four pairs of tentacular cirri. Pharynx with chitinous paragnaths in both pharyngeal rings, and in area VII–VIII one row of soft papillae intercalated with conical paragnaths. Parapodia of first two chaetigers subbiramous, the rest biramous. Dorsal cirri inserted medially; notopodium with dorsal and median ligule, and small superior lobe; neuropodium formed by one postchaetal and ventral ligule. Notochaetae homogomph spinigers. Neurochaetae homogomph and heterogomph spinigers, and heterogomph falcigers. (Following León-González and Solís-Weiss 2000, pp. 552–553.)

Remarks: This genus is monotypic and was erected based on the presence of both paragnaths and soft papillae in area VII–VIII, which is unique in nereidines (León-González and Solís-Weiss 2000, p. 554). In other respects, *Imajimainereis* is similar to *Leonnates* (Qui and Qian 2000) and *Wuinereis* Klebovitch, 1996 (see Remarks for *Leonnates* and *Wuinereis* below).

***Kainonereis* Chamberlin, 1919**

Type species: *Kainonereis alata* Chamberlin, 1919

Diagnosis: Two antennae, separate (not fused) or sometimes basally fused in male epitokes, articulated in some species. Four pairs of articulated anterior cirri. Pharynx bare. Chaetigers 1 and 2 with neuroacicula only. Notopodial prechaetal lobes present, subconical to digitate in atokes, rounded in epitokes. Body of epitokes divided into two regions (one prenatatory and one natatory). Chaetigers 5–7 with dorsal cirri modified into elytriform structures or dorsal discs in epitokes. Males with notopodial homogomph falcigers and spinigers in chaetigers 1–7. Females with notopodial homogomph spinigers in chaetigers 1–7. Notopodial dorsal ligule present from chaetiger 4 in males, chaetiger 3 in females (Conde-Vela et al. 2018, p. 3).

Remarks: Originally described as monotypic this genus was revised, including descriptions of new species and evaluation of morphological characteristics (Conde-Vela et al. 2018), to currently include five species. The revision included important insight into epitokous characters.

***Kinbergineris* Pettibone, 1971**

Type species: *Nereis* (*Leptonereis*) *inermis* Hoagland, 1920

Diagnosis: Prostomium with anterior margin indented. Cirriform frontal antennae present. Eyes present. Apodous anterior segment with four pairs of tentacular cirri with distinct cirrophores. Oral ring with papillae in area VI papillae present. Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule with single dorsal cirrus. Neuropodial postchaetal flattened lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule. Ventral neuropodial ligule of anterior chaetigers present, up to half length of acicular neuropodial ligule; on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single. Notoaciculae present on segments 1 and 2. Notochaetae: homogomph spinigers present. Neurochaetae: dorsal fascicle homogomph spinigers present. Neurochaetae, ventral fascicle: heterogomph spinigers present, in anterior chaetigers with blades coarsely serrated proximally. (Following Wilson et al. 2003.)

Remarks: Pettibone (1971) erected this genus for *Kinbergineris inermis*, which is the only species in the genus. *K. inermis* is similar to *Tylonereis*, another monotypic genus.

***Laeonereis* Hartman, 1945**

Type species: *Nereis culveri* Webster, 1879

Diagnosis: Prostomium subpyriform, with paired frontal antennae, palps biarticulate, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Pharynx with paired jaws, without paragnaths; with tufts of papillae on maxillary and pair of large papillae on oral ring, area VI. Parapodium of first two chaetigers subbiramous, notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at base of upper notopodial ligules. Notopodia with two ligules and additional prechaetal lobe in anterior parapodia. Neuropodia with lower ligules and additional prechaetal and postchaetal lobes in anterior parapodia. Ventral cirri very short. Notochaetae homogomph spinigers only. Neurochaetae homogomph spinigers and, more posteriorly, some homogomph falcigers, with rather long blades. Pygidium with paired anal cirri. (Following Pettibone 1971, pp. 13–14.)

Remarks: Pettibone (1971) reviewed the genus, and synonymized *Laeonereis brunnea* Hartmann-Schröder, 1959 with *Laeonereis culveri* (Webster, 1879), which was later resurrected by Dean (2001). The recent review of Jesus-Flores et al. (2016) argued that Pettibone (1971) did not give enough emphasis on the parapodial features present in these species, and they reviewed the validity of the species assigned to the genus. No new generic description was presented. As a result, Jesus-Flores et al. (2016) recognized four valid species and provided a key to distinguish them. Although morphological examination

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was performed between different populations along the western Atlantic Coast, the COI barcodes revealed seven highly divergent clades in *Laeonereis*, indicating they might constitute separate species (Sampieri et al. 2021).

Leonnates Kinberg, 1865

Type species: *Leonnates inducus* Kinberg, 1865.

Diagnosis: Prostomium with pair of antennae, palps biarticulated and two pairs of eyes. Eversible pharynx with pair of jaws, soft papillae and occasionally paragnaths on oral ring, paragnaths and occasionally soft papillae on maxillary ring. Apodous anterior segment with four pairs of tentacular cirri. Parapodia biramous, except first two pairs. Notopodia with dorsal notopodial ligule, infra-acicular ligule, and often supra-acicular ligule. Neuropodia with prechaetal acicular lobe or ligule, postchaetal lobe or ligule, and ventral ligule. Notochaetae homogomph spinigers and occasionally homogomph falcigers. Neurochaetae homogomph or heterogomph spinigers and homogomph or heterogomph falcigers. Chaetal shafts distally with large solitary tooth and circular fringe of small teeth. (Following Qui and Qian 2000, pp. 1112–1113.)

Remarks: *Leonnates* was revised by Qui and Qian (2000), who discussed taxonomic challenges they could not solve due to the limited material available. One species, *Leonnates simplex* Monro, 1939, had previously been transferred to *Wuinereis* (Khlebovich 1996) as type species, which Qui and Qian (2000) were apparently unaware. *Leonnates* has many characters in common with *Paraleonnates*, *Imajimainereis*, and especially *Laevispinereis* He & Wu, 1989 (Bakken and Wilson 2005); the latter is considered by Read and Fauchald (2019) to be a synonym of *Leonnates*, as there are no obvious differences between the two taxa apart from the oddly inflated peristomial region of its only species, *Leonnates fujianensis* He & Wu, 1989. Relationships between species and how they might be grouped are unclear and require further revisionary studies. *Wuinereis* with its single species formerly placed in *Leonnates* should be a part of such a revision. *Leonnates* currently includes 10 valid species.

Leptonereis Kinberg, 1865

Type species: *Leptonereis laevis* Kinberg, 1865.

Diagnosis: Prostomium subpyriform, with paired frontal antennae, palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Pharynx with paired jaws, without paragnaths or papillae. Dorsal cirri at bases of upper notopodial ligules in anterior region. Notopodia with two ligules, upper one gradually increasing in size, becoming greatly enlarged, oval, scalelike, with minute dorsal cirri inserted terminally in middle and posterior parapodia. Neuropodia with chaetigerous lobe and lower ligule. Ventral cirri short, tapered. Notochaetae spinigers only. Neurochaetae homogomph and heterogomph spinigers and heterogomph falcigers with rather long blades. (Following Pettibone 1971, pp. 6–7.)

Remarks: Two valid species are recognized in this genus as revised by Pettibone (1971).

Lycastonereis Rao, 1981

Type species: *Lycastonereis indica* Rao, 1981

Diagnosis: Prostomium with anterior margin entire. One pair of antennae and two pairs of eyes. Three pairs of anterior cirri. Pharynx with rounded papillae present in both oral and maxillary ring, in all areas except area V. Chaetigers 1 and 2 with neuroaciculae only. Notopodial dorsal ligules, notopodial prechaetal lobes, and neuroacicular ligules bilobed present in anterior chaetigers; notopodial dorsal ligules, notopodial prechaetal lobes, and neuropodial postchaetal lobes absent in posterior chaetigers. Neuropodial ventral ligules absent throughout body. Notochaetae homogomph spinigers; neurochaetae homogomph spinigers and falcigers in supra-acicular fascicles, homogomph and sesquigomph spinigers and homogomph falcigers in subacicular fascicles. (Following Conde-Vela 2019a, p. 452).

Remarks: The original description (Rao 1981) of this monotypic genus did not include all characters used in most other modern generic treatments of Nereididae. It was suggested to belong in Gymnonereidinae (Glasby 1991) from the presence of papillae. Papillae on both rings of the pharynx was described in a revision (Conde-Vela 2019a), that also demonstrated lack of ventral ligules as a unique feature. The revision also found the name spelling Rao to be author of this genus, rather than Nageswara Rao as has commonly been used (Conde-Vela 2019a). *Lycastonereis* has never been assessed in a phylogenetic framework.

Micronereides Day, 1963

Type species: *Micronereides capensis* Day, 1963

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles. Eyes absent or indistinct and likely to be missed. Two apodous anterior segments, equal to or less than length of chaetiger 1. Tentacular segments separate; two distinct segments carry four pairs of tentacular

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cirri. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae or paragnaths. Oral ring papillae present. Median body region without vascularized dorsal cirrophores, transversal dorsal flaps, or long neuropodial prechaetal lips. Single notopodial acicular ligule present, dorsal cirrus single, present on an enlarged cirrophore. Ventral neuropodial ligule of anterior chaetigers present, similar in length in posterior chaetigers. Ventral cirri of some chaetigers double. Dorsal notopodial ligule elongate, exceeding length of dorsal cirrus. Notochaetae: homogomph spinigers present. Neurochaetae: dorsal fascicle homogomph spinigers present. Neurochaetae, ventral fascicle: homogomph and sesquigomph spinigers present (possibly, chaetae need reexamination). (Following Banse 1977a, pp. 623–624, Wilson et al. 2003.)

Remarks: This monotypic genus was included in Gymnonereidinae when Banse (1977a) erected the subfamily, due to the presence of bifid neuropodial cirri (=double ventral cirri). Its phylogenetic position was also supported by Santos et al. (2005).

Micronereis Claparède, 1863

Type species: *Micronereis variegata* Claparède, 1863.

Diagnosis: Frontal antennae absent; palps not articulated, palpophores spherical to subconical, palpostyles absent. Prostomium with entire anterior margin, sometimes weakly bilobed. Four pairs of tentacular cirri lacking cirrophores. Two pairs of eyes. One apodous anterior segment. Maxillary ring not divided into discrete areas. Maxillary ring of pharynx with two paragnaths in total, present on undivided proboscis. Oral ring paragnaths present as regular crown-shaped rows. Dorsal notopodial ligule absent throughout; single major notopodial acicular ligule present, dorsal cirrus on enlarged cirrophore. Prechaetal notopodial lobe and ventral notopodial ligule absent. Dorsal cirri single. Neuropodial postchaetal lobe and ventral neuropodial ligule absent. Ventral cirri single. Notoaciculae absent from chaetigers 1 and 2 (only confirmed as yet for *Micronereis bansei* (Hartmann-Schröder, 1979)). Notochaetae: homogomph spinigers present, homogomph falcigers present or absent. Neurochaetae, dorsal fascicle: homogomph spinigers and homogomph falcigers present. Neurochaetae, ventral fascicle: homogomph spinigers present. (Following Wilson et al. 2003.)

Remarks: The genus now includes 10 species according to the revision of Paxton (1983). *Micronereis* was found to be the most highly derived genus within Nereididae (Paxton 1983) and was considered the only member of the subfamily Notophycinae. The absence of antennae may suggest that *Micronereis* represents either the most ancestral or the most derived nereidid group, although the presence of antennae in the closely related families Hesionidae and Syllidae suggests that the absence of antennae is a derived character in *Micronereis*. In the first phylogenetic analyses of the whole family (Fitzhugh 1987), *Micronereis* was included in Nereidinae due to the presence of paragnaths in some species.

Namalycastis Hartman, 1959

Type species: *Lycastis abiuma* Grube, 1872.

Diagnosis: Long body, usually with more than 150 chaetigers. Prostomium trapezoidal, shallowly cleft anteriorly (usually); paired antennae short and subconical; palps biarticulated, with spherical palpostyles; two pairs of eyes, usually with posterior pair slightly smaller. Four pairs of tentacular cirri. Pharynx with pair of dentate jaws with single terminal tooth, lacking papillae or paragnaths. Dorsal cirri usually increasing in size posteriorly showing cylindrical cirrophores in anterior region and flattened cirrophores in posterior region; notochaetae present in most species; preacicular neurochaetae as heterogomph falcigers (rarely sesquigomph or heterogomph spinigers); postacicular neurochaetae as sesquigomph spinigers in supra-acicular fascicle and heterogomph spinigers in subacicular fascicle; pygidium button-shaped (rarely tripartite). Oocytes small (less than 150 μm), spherical (Following Glasby 1999, Alves and Santos 2016, pp. 501–502.)

Remarks: The genus was redescribed after a revision and phylogenetic analyses where its monophyly was demonstrated (Glasby 1999). A phylogenetic analysis (Alves and Santos 2016), which corroborated earlier results (Glasby 1999), but also indicated the group to have few informative characters for resolving evolutionary relationships between species (Alves and Santos 2016). Currently, 28 valid species are assigned to the genus (Glasby et al. 2016).

The generic diagnosis was recently emended by Conde-Vela (2013) to accommodate a new species from Mexico, *Namalycastis occulta* Conde-Vela, 2013. The emendations included the absence of eyes, jaws, having bifid terminal teeth and lacking teeth along the cutting edge, the presence of heterogomph pseudospingers (referred to as long-bladed heterogomph falcigers by Conde-Vela), and the presence of large oocytes (not explicitly stated, but implied). Although Conde-Vela (2013) noted that his new species shared several features with groundwater inhabiting *Namanereis* Chamberlin, 1919, he rather argued in favor of placing it in *Namalycastis* because it shared with this genus features such as having four pairs of tentacular cirri, dorsal cirri that increase in length and

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become foliose posteriorly, presence of heterogomph falcigers, and a pygidium with a tripartite rim; but these features are shared by members of both *Namalycastis* and *Namanereis* (Glasby 1999). Although many species of *Namalycastis* do have dorsal cirri that increase in length and become dramatically foliose posteriorly, the important difference between the two genera appears to be the presence of a distinct cirrophore on the anterior dorsal cirri of *Namalycastis* and its absence (or indistinctness) in *Namanereis*. Indeed this feature was identified as the only unequivocal synapomorphy for the genus *Namalycastis* by Alves and Santos (2016). Considering the general resemblance of *N. occulta* to the groundwater forms of *Namanereis*, and its lack of a distinct cirrophore on anterior dorsal cirri, the position of this species needs to be reassessed.

Namanereis Chamberlin, 1919

Type species: *Lycastis quadraticeps* Blanchard in Gay, 1849.

Diagnosis: Body small, few chaetigerous segments (<150). Prostomial cleft generally absent; antennae generally cirriform (rarely subspherical or absent). Palps biarticulated with spherical palpostyles. Tentacular cirri, three pairs (rarely four pairs); cirrophores usually indistinct. Pharynx lacking papillae or paragnaths, with pair of dentate jaws with single terminal tooth, or bifid smooth-bladed jaws. Dorsal cirri short and similar in length throughout; cirrophores absent. Notochaetae usually absent. Neurochaetae present, although type and arrangement variable. Supraneuroacicular chaetae: sesquigomph spinigers (rarely heterogomph spinigers or absent) in postacicular fascicle; heterogomph falcigers in preacicular fascicle. Subneuroacicular chaetae: usually absent in postacicular fascicle, rarely heterogomph spinigers (e.g., *Namanereis tiriteae* (Winterbourn, 1969)); heterogomph falcigers (or heterogomph falcigers, pseudospinigers, and spinigers in a graded series) in preacicular fascicle. Pygidium tripartite (usually), with two large lateral lobes and a smaller pointed dorsal one. Monoecious or dioecious. Oocytes large (417 ± 112 µm), ovoid (rarely spherical). (Following Glasby 1999, p. 73.)

Remarks: *Namanereis* was revised by Glasby (1999), including a review of the taxonomic history of the included taxa). There are currently 22 species belonging to this genus, including two new subterranean species recently described from the Canary Islands (Alves et al. 2018, Núñez at al. 2020). The genus is probably the best represented polychaete group in terrestrial groundwater.

Neanthes Kinberg, 1865

Type species: *Neanthes vaalii* Kinberg, 1865.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx with paragnaths, area I–IV conical paragnaths present or absent, area IV smooth barlike paragnaths present or absent. Oral ring paragnaths present or absent, area V and VI present as distinct groups, or not separated, area V–VIII conical paragnaths present or absent. Dorsal notopodial ligule present, similar in size on anterior and posterior chaetigers or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, present throughout all chaetigers or restricted to limited number of anterior chaetigers. Acicular process present or absent, present on anterior chaetigers, reducing in size posteriorly. Dorsal cirrus basally or middorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae homogomph spinigers. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present or absent. Neurochaetae, ventral fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent, heterogomph falcigers present. (Following Bakken and Wilson 2005, p. 527.)

Remarks: *Neanthes* is a heterogeneous group of species, and the only phylogenetic analysis indicates the genus as presently conceived is polyphyletic (Bakken and Wilson 2005). Informal groups defined by morphological characters were created as an identification convenience (Fauchald 1972, Wilson 1984), but these groupings were not supported by Bakken and Wilson (2005). This large group includes about 90 valid species (Read and Fauchald 2019), species are being revised and transferred to other genera or more are described (e.g., Hsueh 2019b).

Nectoneanthes Imajima, 1972

Type species: *Nereis* (*Alitta*) *oxypoda* Marenzeller, 1879.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, two pairs of eyes. Eversible proboscis with conical paragnaths on both maxillary and oral rings. Four pairs of tentacular cirri. Parapodia of first two chaetigers

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subbiramous, all following parapodia biramous. Subbiramous parapodia with thin notoacicula and thick neuroacicula. Notopodia consisting of dorsal cirrus, dorsal ligule, prechaetal lobe, and ventral ligule in biramous parapodia; notopodial dorsal ligule expanded with prominent ovoid lobe developing above dorsal cirrus in middle and posterior parapodia even in atokes. Neuropodia consisting of inferior lobe, postchaetal lobe, ventral ligule, and ventral cirrus throughout; all neuropodial lobes and ligule slender and conical. Notochaetae homogomph or sesquigomph spinigers. Neurochaetae in both upper and lower fascicles consisting of homogomph or sesquigomph spinigers and heterogomph spinigers. Falcigers absent except for neurochaetae in juveniles. (Following Sato 2013, p. 3.)

Remarks: *Nectoneanthes* was synonymized with *Neanthes* by Wilson (1988), and with *Alitta* (Bakken and Wilson 2005), but later resurrected (Sato 2013). The recent revision included two species in *Nectoneanthes* (Sato 2013).

Nereis Linnaeus, 1758

Type species: *Nereis pelagica* Linnaeus, 1758.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: areas I–III, present or absent; IV, present, smooth barlike paragnaths present or absent. Oral ring: conical paragnaths present or absent. Dorsal notopodial ligule similar in size in anterior and posterior chaetigers or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers, homogomph falcigers present. Neurochaetae, dorsal fascicle: homogomph spinigers present, heterogomph falcigers on anterior chaetigers present or absent, on posterior chaetigers present. Neurochaetae, ventral fascicle: heterogomph spinigers present or absent, heterogomph falcigers present or absent. (Following Bakken and Wilson 2005, p. 529.)

Remarks: *Nereis* is the largest genus in Nereididae and the type genus of the family. Currently, *Nereis* includes 252 species and subspecies (Read and Fauchald 2019). There has been no attempt to delineate species into informal subgroups as has been done for other genera, although the genus is equally diverse morphologically. No clear groupings were supported by the phylogenetic analysis of Bakken and Wilson (2005). Many nominal species are described from epitokous specimens and may be junior synonyms.

Nicon Kinberg 1865

Type species: *Nicon maculata* Kinberg, 1865.

Diagnosis: Prostomium pyriform to subpyriform, with two pairs of eyespots, paired frontal antennae and biarticulate palps. Four pairs of tentacular cirri with distinct cirrophores, smooth, or articulated. Pharynx with paired mandibles, without paragnaths or papillae. Parapodia of first two chaetigers subbiramous, notopodium represented by single ligule with dorsal cirri at its base. Subsequent notopodia with dorsal and ventral ligules with or without small notopodial prechaetal lobe decreasing in far posterior parapodia. Neuropodia with superior and inferior prechaetal lobes, digitiform or conical postchaetal lobe present or absent along body, and ventral ligule which can be reduced in posterior parapodia; ventral cirri short, tapered. All notochaetae homogomph spinigers; neurochaetae homogomph, heterogomph, or sesquigomph falcigers, may be accompanied by homogomph and heterogomph spinigers, and simple chaetae. Pygidium with paired anal cirri. (Following León-González and Trovant 2013, p. 69–70.)

Remarks: The generic diagnosis of Pettibone (1971), with updates provided by Hutchings and Reid (1990), was further emended by León-González and Trovant (2013). *Nicon* currently includes 10 species, which can be divided into two informal groups based on the presence or absence of a notopodial prechaetal lobe (León-González and Trovant 2013).

Olganereis Hartmann-Schröder, 1977

Type species: *Ceratocephala edmondsi* Hartman, 1954.

Diagnosis: Prostomium subpyriform, with two pairs of eyes. Palps biarticulated. Tentacular cirri with distinct cirrophores. Pharynx with papillae on both maxillary and oral rings. First two chaetigers uniramous subsequent chaetigers biramous. In anterior notopodia, dorsal cirri at bases of dorsal notopodial ligule. Notopodia with two ligules and superior lobe. Neuropodia with conical or bilobed acicular lobes and ventral ligules. Ventral cirri tapered. Notochaetae homogomph and heterogomph spinigers and heterogomph falcigers. (Following Hutchings and Reid 1990, p. 90.)

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Remarks: Hartman (1954) described *Ceratocephale edmondsi* from South Australia and emended the description of *Ceratocephale* to accommodate the new species, as it possessed soft papillae on both rings instead of the oral ring only as in *Ceratocephale*. *Olganereis* was erected for the single species *Olganereis edmondsi* by Hartmann-Schröder (1977) in the course of her treatment of *Ceratocephale*. She based this on the presence of papillae on both rings of the pharynx, single instead of double ventral cirri, and the presence of both homo- and heterogomph chaetae instead of only homogomph chaetae.

Paraleonnates Khlebovich & Wu, 1962

Type species: *Paraleonnates uschakovi* Khlebovich & Wu, 1962.

Diagnosis: Prostomium with deep cleft on anterior edge, one pair of antennae, palps biarticulated, and two pairs of eyes. Eversible proboscis with transverse rows of paragnaths or partly sclerotized papillae on both dorsal and ventral surfaces of maxillary ring, and with sharply pointed soft papillae on both dorsal and ventral surfaces of oral ring. Parapodia of first two chaetigers subbiramous, all following parapodia biramous. Subbiramous parapodia with both notoacicula and neuroacicula. Notopodia consisting of dorsal cirrus, dorsal ligule, and ventral ligule in biramous parapodia, lacking prechaetal lobe throughout; notopodial dorsal ligule flattened, leaflike, with small additional lobe developing above dorsal cirrus in posterior parapodia, even in sexually immature stage (atokes). Neuropodia consisting of superior lobe, inferior lobe, postchaetal lobe, ventral ligule, and ventral cirrus throughout; postchaetal lobe digitate with tapering tip in anterior parapodia, becoming round in posterior parapodia. Notochaetae consisting of homogomph or sesquigomph spinigers with long blades; few additional heterogomph spinigers with short, poorly serrated blades in several anteriormost notopodia. Upper neurochaetae consisting of homogomph or sesquigomph spinigers with long blades and heterogomph spinigers with short, poorly serrated blades. Lower neurochaetae consisting of heterogomph spinigers with long blades and heterogomph spinigers with short, poorly serrated blades. Falcigers absent throughout. (Following Hong et al. 2012, p. 51.)

Remarks: *Paraleonnates* resembles *Leonnates* but can be distinguished by the spinigerous chaetae, which are present only in species of *Paraleonnates* (Wu et al. 1985, Qui and Qian 2000). The presence of both pointed and blunt papillae on the oral ring is also diagnostic for *Paraleonnates*, whereas in *Leonnates*, species have only blunt papillae on the oral ring (Qui and Qian 2000). There are consistent differences in the neuropodial ligules and lobes between species in the two genera. The genus description was recently emended based on published species descriptions (Hong et al. 2012). From this revision, *Periserrula leucophryna* Paik, 1977 was synonymized with *Paraleonnates uschakovi* Khlebovitch & Wu, 1962, leaving the monotypic *Periserrula* as a synonym of *Paraleonnates*. Another monotypic genus *Ganganereis* was synonymized with *Paraleonnates* from the revision of its single member *Ganganereis sootai*, which was transferred to *Paraleonnates* (Conde-Vela 2019a,b). Amoureux (1985) described *Paraleonnates* as a new genus, a homonymy that was dealt with by Hong et al. (2012). Four species are assigned to this genus (Glasby et al. 2009, Hong et al. 2012, Conde-Vela 2019a,b).

Perinereis Kinberg, 1865

Type species: *Perinereis novaehollandiae* Kinberg, 1865.

Diagnosis: Prostomium with entire anterior margin. Frontal antennae present, one pair. Palps biarticulated; palpophore with transverse groove present; palpostyles conical. Eyes present, two pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Jaws with smooth or slightly crenulate cutting edge or with dentate cutting edge. Maxillary ring of pharynx with conical paragnaths. Oral ring conical and bar-shaped paragnaths present. Dorsal notopodial ligule present. Prechaetal notopodial lobe present or absent. Ventral notopodial ligule present. Dorsal cirrus simple, lacking basal cirrophore. Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent or present. Ventral neuropodial ligule of anterior chaetigers present. Ventral cirri single. Notoaciculae absent from segments 1 and 2. Notochaetae are homogomph spinigers. Neurochaetae dorsally are homogomph spinigers, heterogomph falcigers; blades serrated. Neurochaetae ventrally heterogomph spinigers (may be absent), heterogomph falcigers; blade lacking distinct tendon on terminal tooth. Anal cirri cirriform or conical. (Following Glasby 2015, p. 226.)

Remarks: Species in *Perinereis* are recognized by the smooth, bar-shaped paragnaths in area VI. Phylogenetic analyses indicated that *Perinereis* could be polyphyletic (Bakken and Wilson 2005). An informal grouping of species proposed by Hutchings et al. (1991) had some support in phylogenetic analyses (Bakken and Wilson 2005) but was not conclusive. Several important taxonomic treatments of *Perinereis* species include those by Hutchings et al. (1991), Wilson (1993), Wilson and Glasby (1993), and Glasby and Hsieh (2006). Other important

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studies include closely related species with molecular techniques (Glasby et al. 2013, Sampértegui et al. 2013) and regional treatments (León-González and Geothel 2013, Glasby 2015), and a detailed description of *Perinereis nuntia* as a species complex revising members of the group (Villalobos-Guerrero 2019). There are 92 species currently assigned to *Perinereis*.

Platynereis Kinberg, 1865

Type species: *Platynereis magalhaensis* Kinberg, 1865.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, rodlike paragnaths: areas I–II, absent; III–IV, present. Oral ring, rodlike paragnaths: area V, absent; VI, present; VII–VIII, present, arranged in isolated patches or in one or more irregular lines forming a continuous band. Dorsal notopodial ligule similar in size on anterior and posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus middorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe present or absent. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers present; homogomph falcigers present or absent, present as a simple chaeta or articulated throughout. Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present, heterogomph falcigers with long blades of anterior chaetigers present. (Following Bakken and Wilson 2005, p. 533.)

Remarks: Diagnostic characters of species in *Platynereis* are typical rodlike paragnaths arranged in tight lines (Bakken et al. 2009). Shape and form of the blade on notopodial homogomph falcigers may be characteristic, although similar chaetae are found in other genera. There is no current taxonomic treatment and overview of species in this genus. About 35 species are assigned, most in need of revision. Many original descriptions may be inadequate to recognize cryptic species, and there is no global equivalent to the study of reproductive morphology and behavior of New Zealand taxa (Read 2007), who point out that some species can be only differentiated in epitoke stages. Despite the extensive use of "*Platynereis antipoda*" Hartman, 1954 from widespread localities in laboratory studies, there are no molecular studies of likely species complexes. A start to resolve a difficult taxonomic history of species were studied with population genetic tools from southern Africa (Kara et al. 2020) and the Mediterranean (Wäge et al. 2017), which will need to be followed in other regions to accurately characterize all names described. Descriptions of species in regional accounts include Hutchings and Reid (1991), León-González et al. (2001), and Read (2007).

Pseudonereis Kinberg, 1865

Type species: *Pseudonereis gallapagensis* Kinberg, 1865.

Diagnosis: Prostomium with anterior margin complete, antennae present. Two pairs of eyes, lenticulate. Four pairs of tentacular cirri. Achaetous ring without ventrolateral projections. Pharyngeal areas with paragnaths only. Area I with cones. Areas II and III with pointed bars (P-bars), sometimes also cones, arranged in comblike series. Area IV with P-bars arranged in comblike series; cones and merged paragnaths usually present. Area V, when paragnaths present, conical. Area VI with bars (shield shaped or crescent shaped) or cones. Areas VII–VIII with P-bars and cones arranged in one or two bands. Dorsal cirrus attached terminally or subterminally (*Pseudonereis multisetosa* and *Pseudonereis anomala*) to dorsal ligule on posterior chaetigers. Dorsal ligules foliose, pennantlike or barely enlarged, short (*P. multisetosa*) on posterior chaetigers. Notopodial prechaetal lobe absent. Neuropodial superior lobe present or absent (*Pseudonereis palpata* and *Pseudonereis pseudonoodti*). Neuropodial postchaetal lobe absent throughout, or present on at least some anterior chaetigers. Ventral cirri single. Notoaciculae absent from chaetigers 1–2. Notochaetae homogomph spinigers present; homogomph falcigers absent or present (*P. anomala* and *P. multisetosa*). Neuropodial supra-acicular spinigers homogomph only. Neuropodial subacicular spinigers heterogomph only or absent (*Pseudonereis noodti* and *Pseudonereis podocirra*). Neuropodial supra-acicular and subacicular falcigers all heterogomph, or with also homogomph falcigers on supra-acicular fascicle (*P. multisetosa*); blades short, serrated, lacking distinct tendon on terminal tooth. (Following Villalobos-Guerrero and Idris 2020, p. 1562.)

Remarks: The genus was revised and was found be monophyletic, although with low support (Bakken and Wilson 2005, Bakken 2007). Characteristic features are the paragnath types P-bars in areas VII–VIII, and groups of comb-shaped paragnaths in areas II–IV (Villalobos-Guerrero and Idris 2020). A limitation to the first revision (Bakken 2007) was only a single specimen for many species was known. This has been improved in recent studies as

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more information has been provided and contributed to intraspecific variation through revisions of species. This has led to an improvement in understanding of species delineations and distribution (Conde-Vela 2018, Villalobos-Guerrero and Tovar-Hernandez 2013, Kara et al. 2018, Villalobos-Guerrero and Idris 2020). Variation, especially in paragnath characters, seems to be valuable in species delimitation (Bakken 2007, Villalobos-Guerrero and Tovar-Hernández 2013, Glasby et al. 2013, Conde-Vela 2018, Villalobos-Guerrero and Idris 2020).

Among the 19 species recognized in the genus, closely related species seem to represent species groups or cryptic species with only very small morphological differences, where molecular techniques would be helpful to reveal true identity (Glasby et al. 2013, Kara et al. 2018).

Rullierinereis Pettibone, 1971

Type species: *Leptonereis zebra* Rullier, 1963.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, biarticulated palps with conical palpostyles, and four pairs of tentacular cirri with distinct cirrophores. Eyes present or absent. Pharynx with paired jaws; maxillary ring without papillae and paragnaths; oral ring without paragnaths, with or without papillae (papillae present in *Rullierinereis bahamensis* (Hartmann-Schröder, 1958)). Parapodia of first two chaetigers uniramous; notopodium with dorsal cirrus; single notopodial ligule present or absent. Notopodia of following chaetigers with dorsal cirrus and ventral ligule; dorsal ligule and prechaetal lobe present or absent. Neuropodia with acicular lobe, postchaetal lobe, ventral ligule, and ventral cirrus; prechaetal lobe absent. Notochaetae: homogomph spinigers and falcigers present; falcigers often replacing spinigers on posterior chaetigers. Neurochaetae: homogomph spinigers present in upper neurochaetae, together with heterogomph falcigers or spinigers; heterogomph falcigers present in lower neurochaetae, with or without heterogomph spinigers. (Following Tanaka and Sato 2017, pp. 428–429.)

Remarks: A total of 16 species are currently assigned to *Rullierinereis*, nine of which have been described since Pettibone (1971) erected the genus. There has been no revision since Pettibone (1971). Tanaka and Sato (2017) emended slightly the diagnosis of the genus.

Simplisetia Hartmann-Schröder, 1985

Type species: *Nereis (Ceratonereis) aequisetis* Augener, 1913.

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, palps biarticulated with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. Maxillary ring of pharynx, with conical paragnaths: area I, present or absent; II, present; III, present or absent; IV present. Oral ring, paragnaths absent. Dorsal notopodial ligule markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Acicular process present or absent. Dorsal cirrus basally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent, or present at least on some anterior chaetigers. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent (only in *Simplisetia lizardensis*), homogomph spinigers and heterogomph falcigers present, fused falcigers present. Neurochaetae, ventral fascicle: heterogomph spinigers present, heterogomph falcigers with long blades of anterior chaetigers present, with long or short blades of posterior chaetigers present or absent. (Following Bakken and Wilson 2005, p. 535.)

Remarks: Originally described as a subgenus of *Ceratonereis*, *Simplisetia* was given full genus status by Khlebovich (1996). This was given support by the phylogenetic analyses of Bakken and Wilson (2005), although the position within Nereidinae was not resolved. The characteristic fused falcigers are also found in species in *Hediste*, and the two genera were grouped together in some analyses (Bakken and Wilson 2005). Considerable differences in morphology of simple falcigers across different species may group different species in informal subgroups (Bonyadi-Naeini et al. 2017). A total of 10 species are assigned to this genus.

Sinonereis Wu & Sun, 1979

Type species: *Sinonereis heteropoda* Wu & Sun, 1979.

Diagnosis: Prostomium with entire anterior margin. Four pairs of anterior cirri. Pharynx surface smooth. Upper notopodial ligule present from chaetiger 4 in atokes and epitokes. Notopodial prechaetal lobe present throughout body. In males, chaetigers 5 to 7 with napiform dorsal cirri (i.e., cirrophores globose or ovoid, cirrostyles cirriform); parapodia of natatory region with four lamellar processes (dorsal lamella, ventral lamella, upper and lower lamellae of ventral cirri); females without heteronereid transformation. Notochaetae homogomph spinigers; neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and

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falcigers in subacicular fascicles. (Following Conde-Vela and Wu 2019, p. 154)
Remarks: This monotypic genus was originally placed in Nereidinae (Wu et al. 1985) but was transferred to Gymnonereidinae due to the absence of paragnaths and papillae (Glasby 1991). The genus was revised combining epitokous and atokous characters for the currently single recognized species (Conde-Vela and Wu 2019), which was originally described from epitokous specimens only.

Solomononereis Gibbs, 1971

Type species: *Solomononereis marauensis* Gibbs, 1971.
Diagnosis: Prostomium with anterior margin indented, one pair of antennae, palps biarticulated, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. Maxillary ring of pharynx with paragnaths, minute, rodlike in compact cluster present in areas II–IV. Oral ring, paragnaths absent. Dorsal notopodial ligule markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent. Dorsal cirrus basally attached to dorsal notopodial ligule on posterior chaetigers. Neuropodial postchaetal lobe present or absent. Notoaciculae present on chaetigers 1 and 2. Notochaetae: sesquigomph spinigers present; sesquigomph falcigers present or absent; homogomph falcigers present or absent, if present multidentate blades. Neurochaetae, dorsal fascicle: sesquigomph spinigers present, heterogomph falcigers on anterior chaetigers present or absent, on posterior chaetigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present, heterogomph falcigers present or absent. (Following Bakken and Wilson 2005, p. 536.)
Remarks: This genus with two species was found to be monophyletic based on the synapomorphy minute rodlike paragnaths in areas II–IV, and the diagnosis was emended (Bakken and Wilson 2005). The species in this genus show similarities with species of *Ceratonereis* and *Unanereis* Day, 1962.

Stenononereis Wesenberg-Lund, 1958

Type species: *Stenononereis martini* Wesenberg-Lund, 1958.
Diagnosis: Prostomium with anterior margin cleft. Antennae and eyes present. Four pairs of anterior cirri. Pharynx bare. First two chaetigers with neuroacicular ligules and ventral cirri only. Anterior chaetigers with dorsal cirrophores and notopodial dorsal ligules ciliated. Dorsal cirri with distinct cirrophores and cirrostyles throughout body. Notopodial dorsal ligules present in anterior and middle chaetigers, disappearing in posteriormost ones; neuropodial ventral ligules absent throughout body. Notochaetae sesquigomph spinigers; neurochaetae sesquigomph spinigers and falcigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in subacicular fascicles. Pygidium with two platelike lobes. (Following Conde-Vela 2019b, p. 97).
Remarks: The dorsal cirri with elongate cirrophore and short distal style make this genus unique among nereidid genera (Pettibone 1971). A revision of the genus gave new insight into morphological characters (Conde-Vela 2019b) and emended the genus diagnosis following an earlier update (León-González and Solís Weiss 1997). Four species are currently assigned to the genus (Conde-Vela 2019b).

Tambalagamia Pillai, 1961

Type species: *Tambalagamia fauveli* Pillai, 1961.
Diagnosis: Gymnonereidinae with papillae on oral ring of proboscis. Jaws without teeth. Some dorsal cirri in anterior body region with one accessory cirrus each. Median body region with dorsal cirri on elongated vascularized cirrophores, conspicuous transversal dorsal folds, and long neuropodial prechaetal lips. Double ventral cirri. (Following Banse 1977a, p. 625.)
Remarks: This genus was found to have phylogenetic relationships with *Gymnonereis*, *Micronereides*, and *Ceratocephale* (Santos et al. 2005), with the double ventral cirri as one of the most characteristic synapomorphies. Earlier *Tambalagamia* has been treated as a separate genus or been synonymized with *Gymnonereis*, first following a revision of several related species (Pettibone 1970). It was later retained (Banse 1977a) because of the presence of dorsal transversal folds. Hylleberg and Nateewathana (1988) agreed with Pettibone's opinion and emended the diagnosis of *Gymnonereis* so that *Tambalagamia* again was synonymized. Hutchings and Reid (1990) retained *Tambalagamia* although they had doubts of the validity of the genus. Three species belong to *Tambalagamia*.

Tylonereis Fauvel, 1911

Type species: *Tylonereis bogoyawlenskyi* Fauvel, 1911.
Diagnosis: Prostomium with anterior margin indented, one pair of cirriform antennae palps biarticulated with conical palpostyles, one apodous segment with four pairs of tentacular cirri with distinct cirrophores. Eyes present, two pairs. Maxillary and oral rings of pharynx with long papillae. Dorsal notopodial ligule present; markedly elongate on posterior chaetigers and markedly broader on posterior chaetigers. Dorsal cirri single. Ventral neuropodial

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ligule of anterior chaetigers present, up to half length of acicular neuropodial ligule; on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single. Neuropodial acicular ligule has three to four distinct lobes. Notoaciculae absent from segments 1 and 2. Notochaetae: homogomph spinigers present. Neurochaetae: dorsal fascicle homogomph spinigers present. Neurochaetae, ventral fascicle: homogomph spinigers present. (Following Wilson et al. 2003).

Remarks: Three species are assigned to the genus, which is restricted to the gulfs and seas of the Indian Ocean and the Indo-Malay Archipelago (Lee and Glasby 2015b).

Tylorrhynchus Grube, 1866

Type species: *Nereis heterocheta* Quatrefages, 1866.

Diagnosis: Prostomium subpyriform, with paired frontal antennae, palps biarticulated, and two pairs of eyes. Tentacular segment achaetous and apodous, four pairs of tentacular cirri with distinct cirrophores. Pharynx with paired jaws, without paragnaths but with soft papillae on both maxillary and oral rings Parapodia of first two chaetigers subbiramous, notopodium with dorsal cirrus and ligule. Dorsal cirri with large thick cirrophores, enclosing large parapodial glands, and distal styles. Notopodia with low, rounded acicular lobes and subarticular ligules. Neuropodia thick, bilobed distally forming small rounded supra-acicular and subacicular lobes, without ligules. Ventral cirri short and subulate. Notochaetae sesquigomph spinigers. Neurochaetae sesquigomph and heterogomph spinigers and heterogomph falcigers with relatively long blades. Pygidium with paired anal cirri. (Following Pettibone 1971, pp. 42–43.)

Remarks: Three species are currently assigned to this genus, which was revised by Pettibone (1971).

Typhlonereis Hansen, 1879

Type species: *Typhlonereis gracilis* Hansen, 1879.

Diagnosis: Prostomium with entire anterior margin. One apodous segment with four pairs of tentacular cirri. Notoaciculae from chaetiger 3. Maxillary and oral rings of pharynx without paragnaths and papillae. Parapodia of first four chaetigers with dorsal cirrus and notopodial ventral ligule, all subsequent notopodia with dorsal cirrus and two ligules, dorsal notopodial ligule reduced in posterior chaetigers. Notopodial prechaetal and neuropodial postchaetal lobes absent. Notochaetae absent in first four chaetigers, thereafter homogomph spinigers only. Neurochaetae in dorsal fascicle homogomph spinigers, in ventral fascicle heterogomph spinigers and heterogomph falcigers. (Following Bakken 2003, pp. 347–350.)

Remarks: *Typhlonereis* is a name that had been overlooked due the incomplete original description until Bakken (2003) redescribed the type species and resurrected the genus. *Typhlonereis gracilis* resembles species in *Rullierinereis* and *Nicon* but has a remarkable feature in lacking a notopodial ligule and notochaetae in the first four chaetigers, a character not known in any other nereidines aside from the namanereidines. In addition, the dorsal ligule is strongly reduced in posterior chaetiger (Bakken 2003), which also occurs in species from a number of seemingly unrelated nereidines (Wilson et al. 2003, Bakken and Wilson 2005). The single species in this genus should be included in assessments of similar species in *Rullierinereis* and *Nicon*.

Unanereis Day, 1962

Type species: *Unanereis macgregori* Day, 1962.

Diagnosis: Prostomium with entire anterior margin, one unpaired cirriform median antenna, one pair biarticulated palps, conical palpostyles; four pairs of tentacular cirri with distinct cirrophore. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, with conical paragnaths: area I absent. Oral ring, paragnaths absent. Dorsal notopodial ligule markedly elongate on posterior chaetigers. Prechaetal lobe absent, acicular process absent. Dorsal cirrus terminally attached to dorsal notopodial ligule on posterior chaetigers, arising from a basal cirrophore. Neuropodial postchaetal lobe present, at least on some anterior chaetigers. Notoaciculae present on chaetigers 1 and 2. Notochaetae: homogomph spinigers; sesquigomph falcigers, blade distally bifid. Neurochaetae, dorsal fascicle: sesquigomph spinigers, heterogomph falcigers. Neurochaetae, ventral fascicle: heterogomph spinigers, heterogomph falcigers present, terminally bifid. (Following Bakken and Wilson 2005, p. 536.)

Remarks: *Unanereis* was erected based on the unique occurrence of a single median antenna on the prostomium (Day 1962). Similar features in *Unanereis macgregori* were observed in species of *Ceratonereis* and *Solomononereis* (Day 1962), and the three groups were grouped together in phylogenetic analyses (Bakken and Wilson 2005, Santos et al. 2005). There are reports in the literature documenting malformations in Nereididae, including fused and single antennae (Coutinho and Santos 2014), and therefore, there is a possibility that specimens currently identified as *Unanereis* could be malformed members of *Ceratonereis*

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and *Solomononereis*. Currently, two species are described, which are very different in shape of parapodia.

Websterinereis Pettibone, 1971

Type species: *Nereis tridentata* Webster, 1879.

Diagnosis: Prostomium subpyriform to pentagonal, one pair of frontal antennae, palps biarticulate, globulose, two pairs of eyes of different shape. Apodous anterior segment with four pairs of short tentacular cirri. Pharynx with pair of jaws. Maxillary ring unarmed, oral ring with papillae on areas VI and VII–VIII. First two parapodia uniramous, remainder biramous. Notopodium represented by dorsal cirri with dorsal and median ligulae, notopodial prechaetal lobe present on anterior parapodia. Neuropodium with superior and inferior lobe forming prechaetal area; postchaetal lobe subulate to triangular, ventral ligule generally subulate. Ventral cirri short. Notochaetae homogomph spinigers; neurochaetae homogomph and heterogomph spinigers and heterogomph falcigers, those in posterior parapodia with short to long blades; anchylosed chaetae may be present. Pygidium with pair of anal cirri. (Following León-González and Balart 2016, p. 17.)

Remarks: Pettibone (1971) revised the genus, whereas León-González and Balart (2016) described a new species and provided an important redescription of *Websterinereis foli* Fauvel, 1930 that led to a modified diagnosis of the genus. Five species are currently recognized for this genus.

Wuinereis Khlebovich, 1996

Type species: *Leonnates simplex* Monro, 1939.

Diagnosis: Prostomium oval or pear shaped. One pair of antennae. Palps biarticulated. Four pairs of peristomial cirri. Maxillary ring of proboscis with chitinous paragnaths, oral ring with soft papillae. First two chaetigers have uniramous parapodia. Notopodia with two lobes. Notopodial chaetae homogomph spinigers. Neuropodia has clear heterogomph falcigers with a short and bent distal part. (Following Khlebovich 1996, p. 100).

Remarks: The genus is monotypic and is close to *Leonnates* and *Paraleonnates*, with both paragnaths and soft papillae present on the proboscis. It differs from the first by lacking the middle lobe of notopodia and by having clear heterogomph falcigers and from the second by the presence of falcigers (Khlebovich 1996). The original description does not include characters used in most other modern generic treatments of Nereididae, and it is presently not possible to differentiate *Wuinereis* from *Imajimainereis* or *Leonnates* (Wilson et al. 2003).

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7.13.3.4 Pilargidae Saint-Joseph, 1899

Introduction

The family Pilargidae Saint-Joseph, 1899 is currently placed in Nereidiformia: Phyllodocida (Rouse and Fauchald 1997, Read and Fauchald 2021). Historically, the affinities of the group have been uncertain with family acceptance not recognized until the mid-twentieth century (Hartman 1947b, Pettibone 1966). Morphology-based phylogenetic analyses found support for a sister grouping with either Syllidae or Nautiliniellidae (Fitzhugh and Wolf 1990, Glasby 1993), Sphaerodoridae (Rouse and Fauchald 1997), and either Chrysopetalidae, Nereididae, and Hesionidae or the genus *Microphthalmus* (Dahlgren et al. 2002). Molecular phylogenetic studies place Pilargidae as a sister group to Nephtyidae (Zrzavý et al. 2009, Struck and Halanych 2010). An exclusive nautiliniellid sister-group relationship can be dismissed because of the recent finding that this family is nested within Chrysopetalidae (Aguado et al. 2013), although pilargids were not included in their analysis.

Morphologically diverse, Pilargidae have few, if any, unique features. Typically, pilargids are slender and elongate and slightly inflated anteriorly (Fig. 7.13.3.4.1); the body surface may be smooth or papillated. A ventrolateral palpal papilla (Fig. 7.13.3.4.2) is almost always present and apparently unique to the family. Chaetae are all simple (noncompound) and include hooks, spines, and various capillary-like forms. Other distinctive features include the presence of simple neurochaetae in upper and lower positions of the neuropodia and a bilobed to multiple-lobed brain.

Members of Pilargidae are distributed worldwide in marine and estuarine soft sediments; they can be found at all depths but are less common in intertidal and low salinity environments. They are seldom frequent or abundant, which accounts for our poor knowledge of them. Some genera (*Litocorsa*, *Synelmis*, *Hermundura*) are far more diverse in tropical waters than in waters of higher latitudes (Salazar-Vallejo and Solís-Weiss 1992).

Within Pilargidae, there are currently 19 nominal genera, but only 11 are regarded as valid, and about 100 species (Salazar-Vallejo 2011); *Antonbruunia* is here included in the family following Salazar-Vallejo (1986), Glasby (1993), and Mackie et al. (2015). Two subfamilies have been proposed, Synelminae and Sigambrinae (see Salazar-Vallejo 1986); they were later corrected to Kynephorinae Ehlers, 1920 and Pilargidae Saint-Joseph, 1899, respectively (Salazar-Vallejo and Rizzo 2009). The subfamilies are not considered in the Classification section because they have not been corroborated by phylogenetic analyses, and besides, they provide little utility in a family with only 11 genera.

Morphology

Form and color of living material

Most pilargids are white to red-yellow, being lighter anteriorly and pigmentation increasing posteriorly. Pigmented subdermal gland cells (chromatophores) are distributed along the lateral body of many species (Figs 7.13.3.4.1 and 7.13.3.4.3) and/or on the pygidium. Their function is unknown.

External morphology

Body shape and surface. Adults can be 1–10 cm long and range in size from short (less than 100 segments) to very elongate (several hundred segments); width varies from uniform throughout to posteriorly tapering (*Sigambra*), in cross section from cylindrical (*Hermundura*, *Litocorsa*, and *Synelmis*), subcylindrical (*Antonbruunia*, *Cabira*), to ribbonlike (*Otopsis*, *Pilargis*, *Glyphohesione*). Taxa with a cylindrical body may have thick oblique muscular bundles, which make the body appear trilobed in cross section and produces a deep midventral groove running longitudinally (*Litocorsa*, *Sigambra*, *Synelmis*) (Fig. 7.13.3.4.4); other taxa with cylindrical bodies lack a ventral groove and have the parapodia ventrally displaced (*Antonbruunia*). The anterior body may be inflated (*Cabira*, *Glyphohesione*, and *Hermundura*) (Fig. 7.13.3.4.5) or not. The body surface is covered with scattered papillae/verrucae, mostly on the dorsal surface of the head, body segments, and pygidium (*Pilargis*, *Ancistrosyllis*, and some *Cabira* species) (Fig. 7.13.3.4.6A, B), or papillae are restricted to one or a few anterior segments (*Sigambra*) (Fig. 7.13.3.4.7). Other genera (*Antonbruunia*, *Glyphohesione*, *Hermundura*, *Otopsis*) have a smooth to slightly rugose appearance, whereas *Litocorsa* and *Synelmis* have a very smooth, shiny body surface.

Head. The head comprises a more or less distinct prostomium, which is rectangular to rounded, paired palps showing various degrees of fusion, and a remnant peristomium is confined to an area around the mouth (Fauchald and Rouse 1997). Palp fusion varies from

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https://doi.org/10.1515/9783110647167-011

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Fig. 7.13.3.4.1: *Hermundura gladstonensis* (Marks & Hocknull, 2006), complete, right lateral view. Adapted from Glasby and Hocknull (2010, fig. 1).

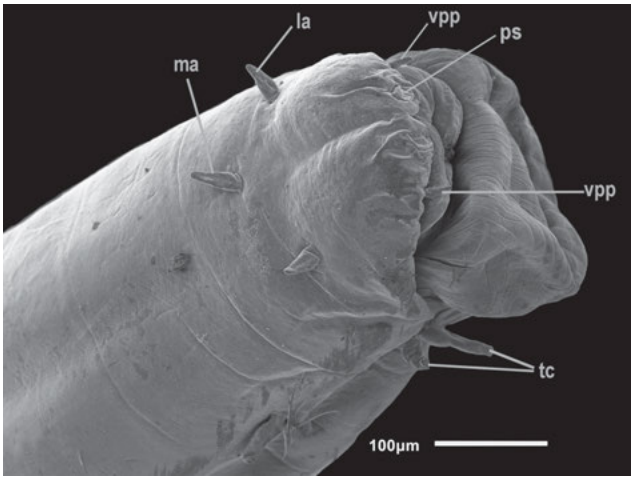


Fig. 7.13.3.4.2: *Litocorsa seychellensis* Darbyshire & Mackie, 2003, anterior end, dorsofrontal view. la, lateral antenna; ma, median antenna; ps, palpostyle; tc, tentacular cirri; vpp, ventral palpal papilla. Specimen in collection of Museum and Art Gallery Northern Territory.

unfused (*Pilargis*) (Fig. 7.13.3.4.8), almost totally fused medially (*Litocorsa*, *Synelmis*) or palps may be merged with the prostomium (*Glyphohesione*). Palps are biarticulate comprising a basal palpophore and a minute distal palpostyle; the palpostyle may be small and buttonlike as in *Cabira* sp. (Fig. 7.13.3.4.9) or cirriform as in *Glyphohesione* sp. (Fig. 7.13.3.4.10). Paired ventrolateral palpal papillae are present in most genera and are usually much smaller than the palps (Figs. 7.13.3.4.2, 7.13.3.4.6B, 7.13.3.4.9, and 7.13.3.4.10); in the past, they have been mistaken for palps or palpostyles in the literature (e.g., fig. 1.84a in Glasby 2000, figs 21.2 and 21.2 in Rouse and Pleijel 2001, Glasby 2003). The homology of this structure needs further clarification. In *Glyphohesione*, for example, the two pairs of cirriform appendages extending distally from the palps could be interpreted as either ventrolateral papillae or palpostyles; similarly, the anteroventral projections in *Antonbruunia* may be either palps or palpal papillae; in *Hermundura*, bifid palpostyles have been reported (Glasby and Marks 2013), but it is conceivable that one represents the palpostyle and the other the palpal papilla. Two or three antennae are present or, rarely, antennae are absent (*Hermundura*); when present, the lateral ones can be positioned either anteriorly (*Sigambra*), on the mid-prostomium, or posteriorly (*Litocorsa*, *Otopsis*); the median one is positioned posteriorly between the posterior prostomial margin and the anterior edge of segment 1. Antennae are either cirriform (*Glyphohesione* and *Sigambra*; Fig. 7.13.3.4.10) or short, papilliform to fusiform (*Litocorsa*, *Otopsis*, *Synelmis;* Fig. 7.13.3.4.9). Eyes may be present as one or two simple, unlensed pairs or may comprise a group of smaller ocelli (some *Synelmis*); they either occur on the surface of the prostomium, sunken on the prostomium (some *Ancistrosyllis;* Fig. 7.13.3.4.6B) subdermally on the midbrain (some *Hermundura*), or may be absent (some *Cabira*). As the presence and form of the eyes are variable within genera, they are not included in the generic diagnoses.

Segment 1. An achaetous segment 1, which has been reported in the older literature as the peristomium, may be distinct (*Glyphohesione*) or more or less fused to the

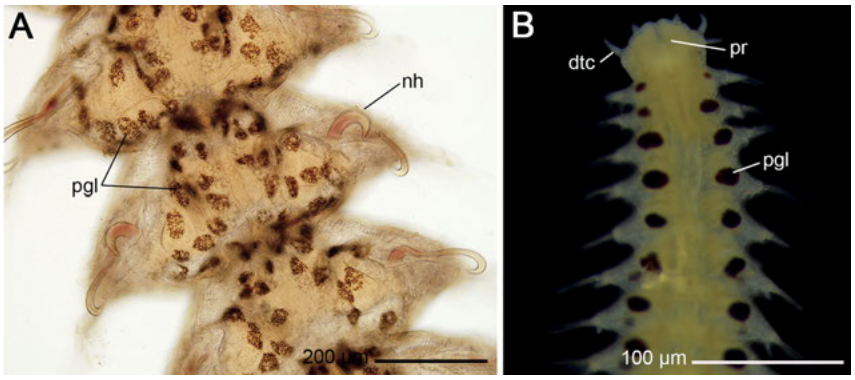


Fig. 7.13.3.4.3: Pigmented glands of Pilargidae. A, *Ancistrosyllis* cf. *groenlandica* McIntosh, 1878, midbody segments, dorsal view. B, *Pilargis* sp., anterior end, dorsal view. nh, notopodial hook; tdc, dorsal tentacular cirri; pgl, pigmented gland; pr, prostomium. Adapted from Ribeiro et al. (2020: figs 2e, 7b).

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Fig. 7.13.3.4.4: *Sigambra hanaokai* (Kitamori, 1960), midbody region, ventral view. Specimen H02-2, 21/6 in Zoological Reference Collection of the National University of Singapore.

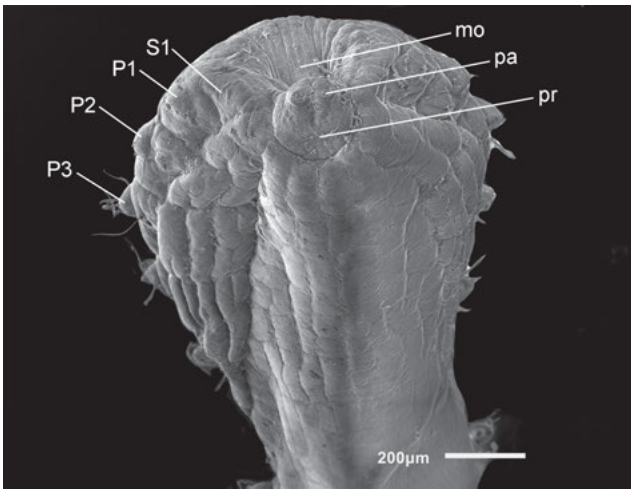


Fig. 7.13.3.4.5: *Hermundura* sp., anterior end, dorsal view. Specimen in Zoological Reference Collection of the National University of Singapore.

prostomium (*Litocorsa*, *Pilargis*). It carries two (rarely one) pairs of cirriform to fusiform tentacular cirri, or cirri are absent (*Hermundura*); the dorsal tentacular cirri are similar in length or slightly longer than the dorsal cirri of the following segment. In *Cabira*, the first segment is sharply divided from the first chaetiger by a deep constriction (Fig. 7.13.3.4.11). Segments are pseudo-annulated in some genera (*Cabira*, *Sigambra)*, with each segment having up to five annulations anteriorly (Figs. 7.13.3.4.11 and 7.13.3.4.12).

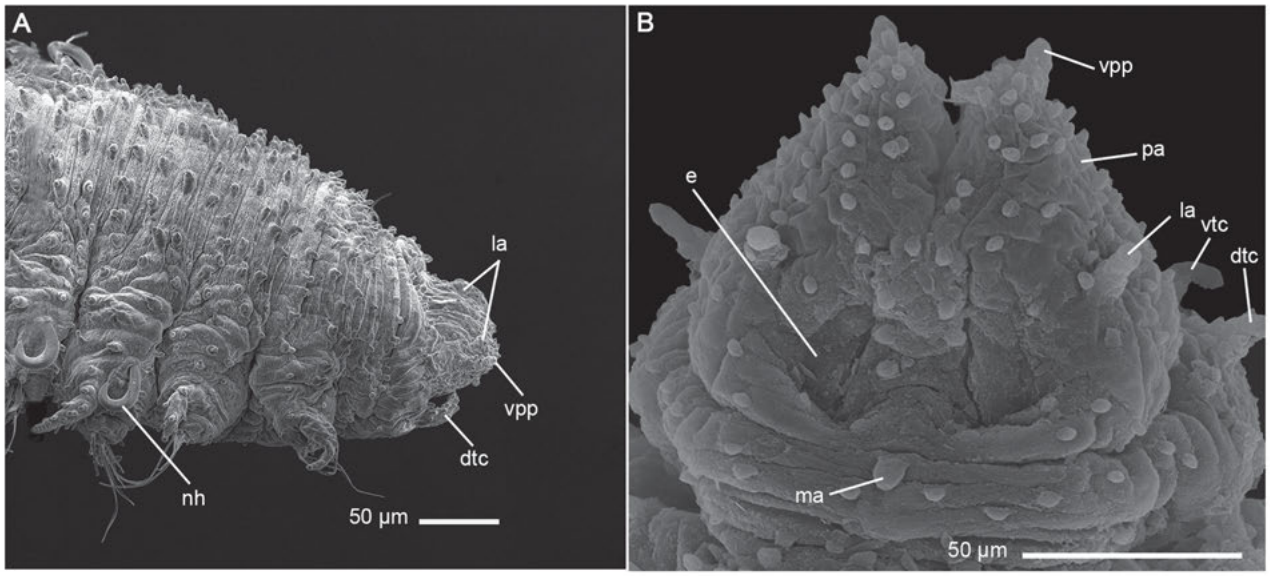


Fig. 7.13.3.4.6: Anterior ends of Pilargidae. A, *Ancistrosyllis* sp., anterior end, dorsolateral view. Specimen H02-2 9/5 in Zoological Reference Collection of the National University of Singapore. B, *Ancistrosyllis hartmanae* Pettibone, 1966, anterior end, dorsal view; adapted from Ribeiro et al. (2020, fig. 4b). dtc, dorsal tentacular cirrus; e, eye; la, lateral antenna; ma, median antenna; nh, notopodial hook; pa, palp; vpp, ventrolateral palpal papilla; vtc, central tentacular cirrus.

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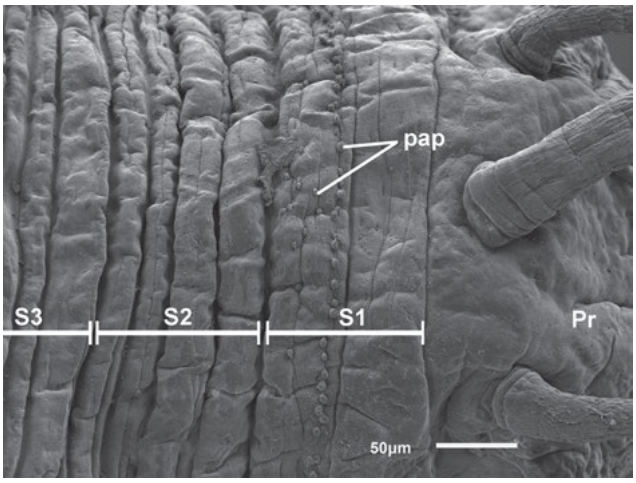


Fig. 7.13.3.4.7: *Sigambra hanaokai* (Kitamori, 1960), close-up of dorsal surface of prostomium (Pr) and first three segments (S1–S3). (S1, S2, S3, segments 1, 2, 3; pr, prostomium; pap, papilla). Specimen H02-2, 21/6 in Zoological Reference Collection of the National University of Singapore.

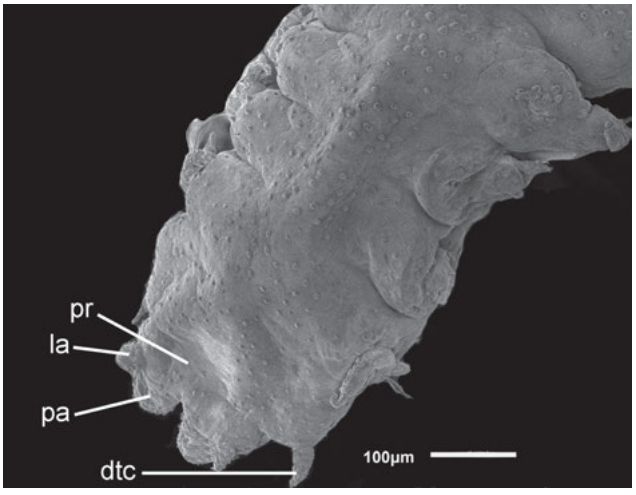


Fig. 7.13.3.4.8: *Pilargis mohri* Gallardo, 1968, anterior end, dorsal view. dtc, dorsal tentacular cirrus; la, lateral antenna; pa, palp; pr, prostomium. Specimen St 30A, (Indonesia) in collection of Museum and Art Gallery Northern Territory.

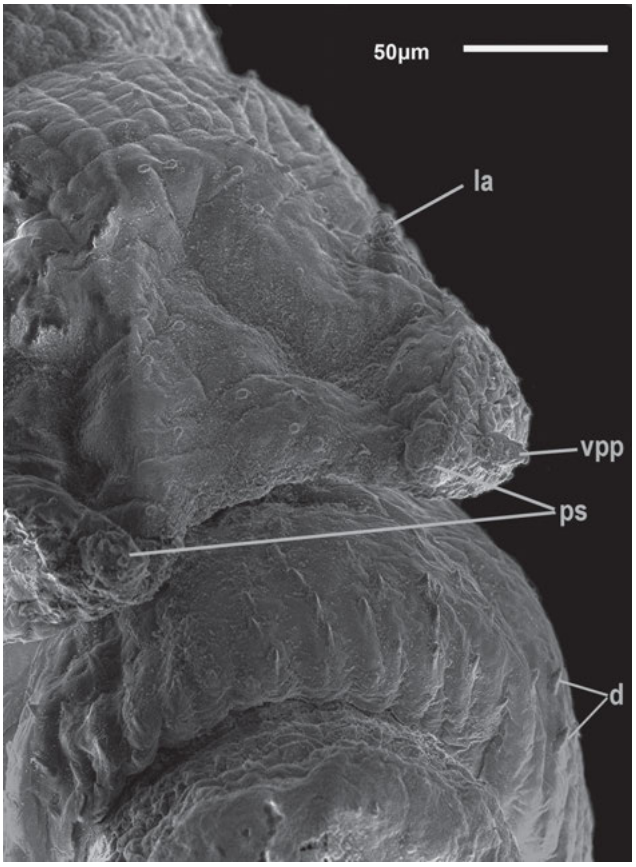


Fig. 7.13.3.4.9: *Cabira* sp., close-up of head and pharynx d, denticles; la, lateral antenna; ps, palpostyle; vpp, ventral palpal papilla. Specimen H04-1, 22/5 in Zoological Reference Collection of the National University of Singapore.

Parapodia and chaetae. Parapodia are typically subbiramous with notopodial elements reduced; they range from well developed (*Pilargis*, *Sigambra*) to barely extending beyond the body wall (*Cabira*). Notopodial lobes are short and rounded (*Ancistrosyllis*, *Glyphohesione*, *Synelmis;* Fig. 7.13.3.4.13A) or absent (*Cabira*, *Hermundura*). Notoacicula are present, usually singular (Fig. 7.13.3.4.13B) or absent (*Hermundura*, *Otopsis*). Notochaetae are usually present except in the first few parapodia, although occasionally they do not appear until the mid or posterior body, as in some *Sigambra* and *Synelmis*, or they are absent (some *Antonbruunia*, *Otopsis*, *Pilargis*; Fig. 7.13.3.4.13B); they include stout hooks (*Sigambra;* Fig. 7.13.3.4.13C), straight to slightly curved spines (*Glyphohesione*, *Litocorsa*, *Synelmis;* Fig. 7.13.3.4.13A, D) or, more rarely, capillaries (*Hermundura*). The notoaciculae and the notochaetae are either positioned ventral to the dorsal cirri (Fig. 7.13.3.4.13A) or dorsal to the dorsal cirri (Fig. 7.13.3.4.13C). The first occurrence of notospines appears to be body-size dependent in some genera (*Sigambra*), but not others (*Hermundura*), and may also vary between species (Paterson and Glover 2000, Glasby and Marks 2013).

Neuropodia are low and rounded (*Hermundura*, *Litocorsa*, *Synelmis;* Fig. 7.13.3.4.13D) or more obvious conical to quadrangular projections (Fig. 7.13.3.4.13A, C); neuroacicula are always present, often several, and may be tapered or knobbed distally (*Hermundura*). Neurochaetae are present, usually both above and below the neuroacicula. They are

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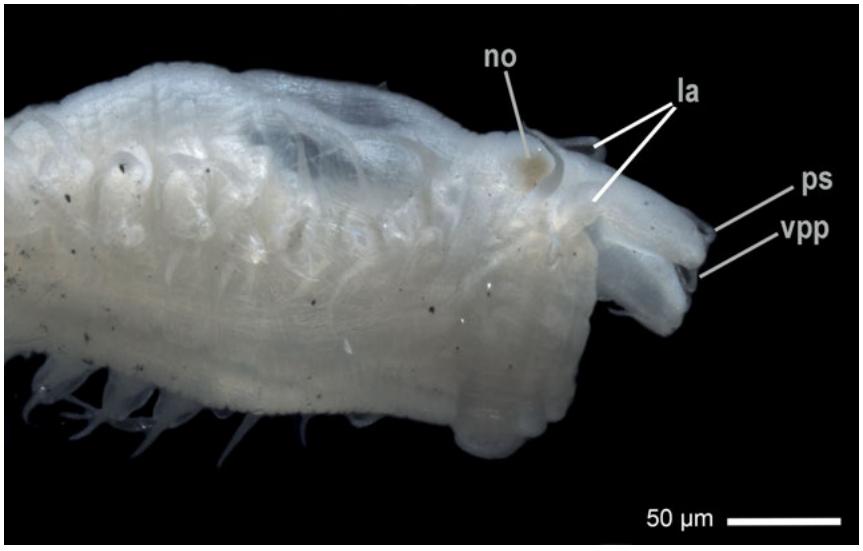


Fig. 7.13.3.4.10: *Glyphohesione* sp., anterior end, right lateral view (la, lateral antenna; no, nuchal organ; ps, palpostyle; vpp, ventral palpal papilla). Specimen St 9B, (Indonesia) in collection of Museum and Art Gallery Northern Territory.

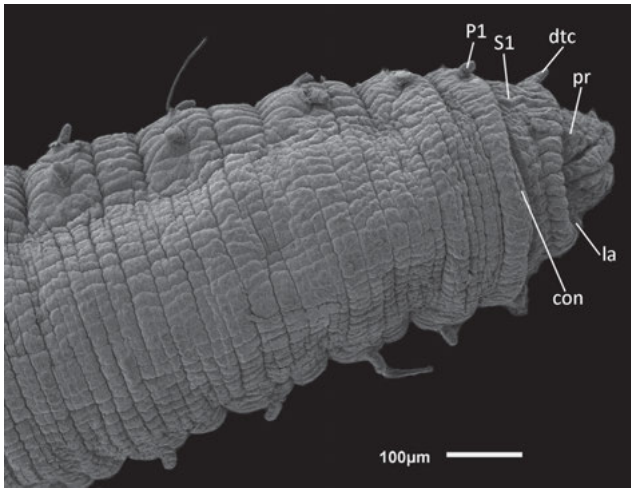


Fig. 7.13.3.4.11: *Cabira* sp., anterior end, dorsal view. con, constriction between S1 and first chaetiger; dtc, dorsal tentacular cirrus; la, lateral antenna; P1, parapodium 1; pr, prostomium; S1, segment 1. Specimen J03-3, 18/1 in Zoological Reference Collection of the National University of Singapore.

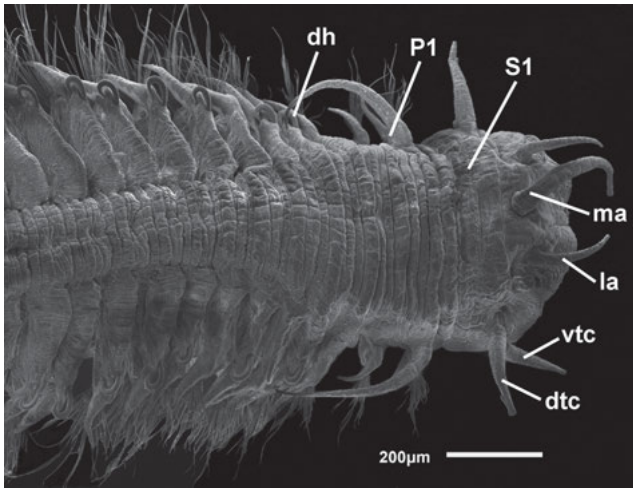


Fig. 7.13.3.4.12: *Sigambra hanaokai* (Kitamori, 1960), anterior end, dorsal view. dh, dorsal hook; dtc, dorsal tentacular cirrus; la, lateral antenna; ma, median antenna; P1, parapodium 1; S1, segment 1; vtc, ventral tentacular cirrus. Specimen H02-2, 21/6 in Zoological Reference Collection of the National University of Singapore.

noncompound, of various lengths, and include smooth limbate capillaries, finely to coarsely serrated along one edge (*Glyphohesione*, *Litocorsa*, *Synelmis;* Fig. 7.13.3.4.14A, D), or having a whorl of fine hairs (*Hermundura;* Fig. 7.13.3.4.14C). Other neurochaetae are hooked or bifid terminally (*Antonbruunia*, *Ancistrosyllis*), whereas in the *Litocorsa* species, some capillaries are replaced by spines (smooth or distally denticulate) and/or short, denticulate, limbate forms (Fig. 7.13.3.4.14B) in median and posterior chaetigers. Furcate neurochaetae are present in species of *Synelmis* and *Pseudexogone* (Fig. 7.13.3.4.14D).

Dorsal cirri are rarely absent as in some *Cabira* and *Hermundura* (Fig. 7.13.3.4.13D). When present, they are highly variable in form ranging from triangular (*Otopsis*), uniformly tapered to papilliform (*Cabira*) or foliaceous (*Synelmis*), and have more or less distinct cirrophores and cirrostyles (*Ancistrosyllis*, *Otopsis*, *Pilargis*). Dorsal cirri on the first chaetiger are often larger than those on subsequent chaetigers. Ventral cirri, by contrast, are often absent from one or a few anterior chaetigers even in species within the same genus; they range from short papilliform to well developed and foliaceous (*Synelmis*), or large and

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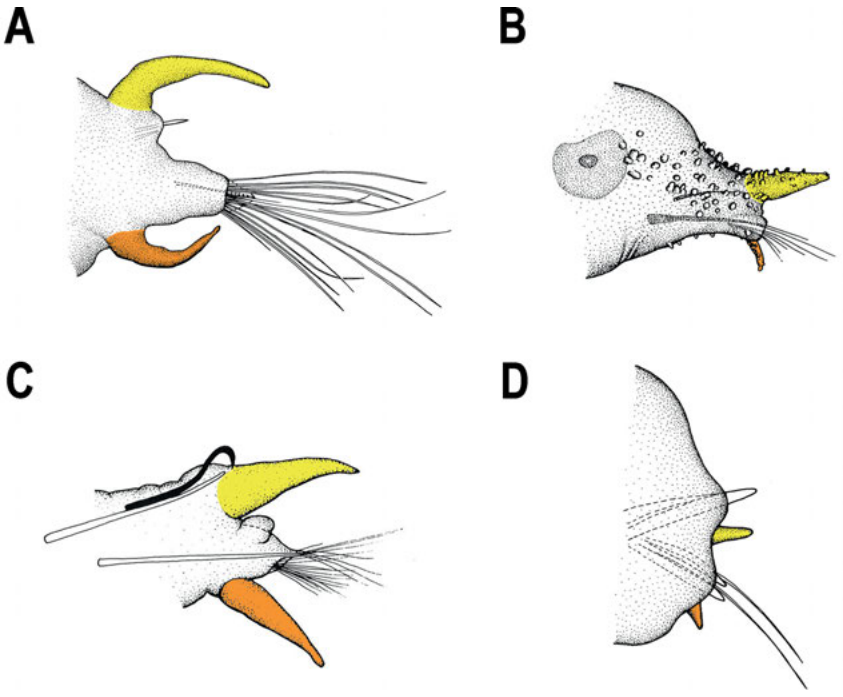


Fig. 7.13.3.4.13: Parapodial morphology. A, *Glyphohesione klatti* Friedrich, 1950. B, *Pilargis verrucosa* Saint-Joseph, 1899. C, *Sigambra parva* (Day, 1963). D, *Litocorsa stremma* Pearson, 1970. Dorsal and ventral cirri colored (yellow, orange resp.) to facilitate visualization of position of notochaetae and notoaciculae. A, C, D after Parapar et al. (2004).

cirriform to triangular, and may extend beyond the neuropodial lobe (*Pilargis*, *Otopsis*, *Sigambra*).

Pygidium. The pygidium ranges in form from simple, conical (*Ancistrosyllis*, *Cabira*) to bilobed (*Cabira*) to flattened and platelike (*Hermundura*, *Litocorsa*). Anal cirri are usually present as a pair or, less commonly, singly, ranging from 1 to 5 in number; paired cirri are lateral or ventrolateral (*Ancistrosyllis*, some *Cabira*). The anus is terminal and may be adorned with anal papillae (*Litocorsa*, *Pilargis*).

Tube. There are no published records of pilargid species living inside tubes; however, some specimens of *Litocorsa acuminata* (Wolf, 1986) and *Litocorsa dentata* Imajima, 1987, were found inside tube fragments (Salazar-Vallejo and Glasby in preparation). These tubes are proteinaceous, fragile, and transparent in juveniles and thicker and pale brown in larger specimens.

Internal morphology

Brain and nuchal organs. The pilargid brain typically comprises three regions: a long, bifurcated forebrain; an undivided midbrain; and a hindbrain with two to five lobes extending posteriorly through the first few chaetigers (Fitzhugh and Wolf 1990, Dean 1998). Pigment spots often occur on the midbrain (*Hermundura*) or the posterior ends of the hindbrain (*Litocorsa*, *Ancistrosyllis*, *Sigambra;* Fig. 7.13.3.4.15A, B). Paired nuchal organs, innervated from the hindbrain, are visible externally on the posterolateral margin of the prostomium as ciliated grooves or slits (Fitzhugh and Wolf 1990, Mackie et al. 2015); sometimes they are also pigmented (Fig. 7.13.3.4.10; *Sigambra*, *Cabira*, *Glyphohesione*).

Alimentary canal. The alimentary canal is usually straight and comprises an eversible muscular pharynx, an esophagus, stomach, and intestine, with minor morphological differences between each region. The pharynx may be differentiated to various degrees (Salazar-Vallejo 2003, Rouse and Pleijel 2001) and can be very long and muscular, sometimes looped (*Ancistrosyllis*), or short (*Cabira*). At its junction with the buccal tube, there is a narrow, light-refractive band of soft tissue encircling the opening, which was referred to as "denticulated bands" by Salazar-Vallejo et al. (2001). When fully everted, the eversible pharynx can take several forms, for example, a short muscular cylinder with terminal papillae (*Sigambra;* Fig. 7.13.3.4.16) or a long, straight muscular cylinder (*Hermundura*), or divided into two or three rings (*Ancistrosyllis*, *Cabira*), and sometimes this eversion is partial, giving a false impression of a different type of pharynx (as indicated for *Ancistrosyllis*). Further, the pharynx can be divided into basal and proximal parts (at least in *Litocorsa*) and may be smooth, slightly rugose, or carry a few papillae, denticles or jawlike structures (*Hermundura*, *Sigambra*, *Cabira;* Figs. 7.13.3.4.9, 7.13.3.4.17A, B). In *Sigambra* and some *Ancistrosyllis*, a ring of terminal papillae, bearing sensory cells, is present at the distal tip of the buccal tube (Pettibone 1966, Tzetlin and Purschke

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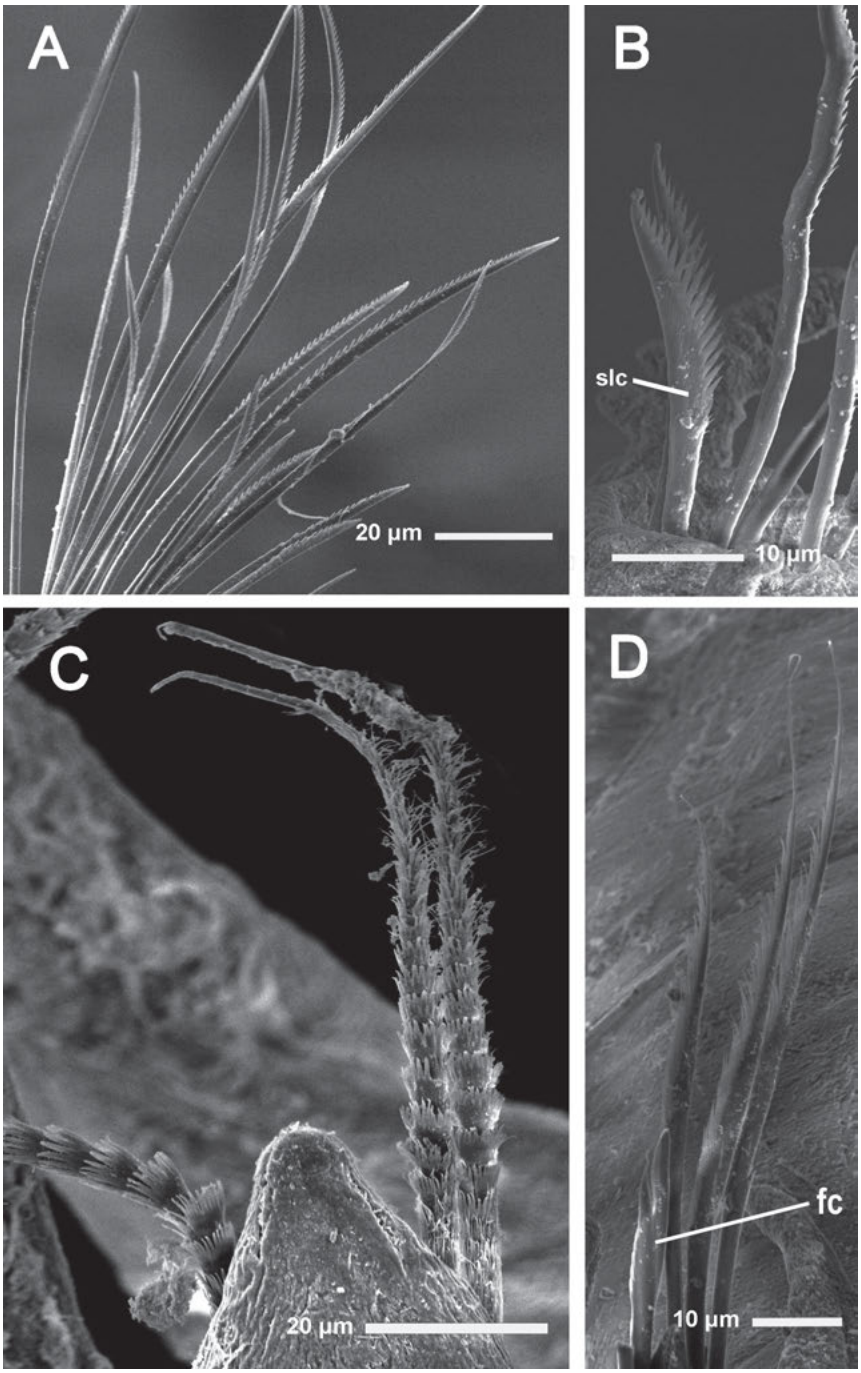


Fig. 7.13.3.4.14: Chaetal morphology, SEM photographs. A, *Glyphohesione* sp., chaetiger 1, specimen St 9B, (Indonesia) in collection of Museum and Art Gallery Northern Territory. B, *Glyphohesione* sp., chaetiger 6, specimen St 9B, (Indonesia) in collection of Museum and Art Gallery Northern Territory (slc, short limbate chaeta). C, *Hermundura* sp. posterior chaetiger, ZRC unreg. 'Serene'. D, *Synelmis sergi* Glasby & Marks, 2013; midbody chaetiger, specimen in collection of Museum and Art Gallery Northern Territory. fc, furcate chaeta.

2005; Fig. 7.13.3.4.16), whereas in *Litocorsa* and *Synelmis*, terminal papillae are absent, replaced by a terminal ciliated ring (Fig. 7.13.3.4.18). True jaws are absent.

Intestinal caeca (or gut diverticula) are present in some groups. Müller (1858) and later Salazar-Vallejo (1990, fig. 1) described them for *Sigambra grubii* Müller, 1858, and they were included in the diagnosis for the genus by Pettibone (1966). She also used this feature in the diagnosis of *Ancistrosyllis* and suggested that the presence of gut diverticula is restricted to pilargids with well-developed parapodia. Their presence was confirmed for *Pilargis* (Salazar-Vallejo and Harris 2006) and has also been noted in *Otopsis longipes pacifica* Uschakov, 1950 and *Cabira* (Salazar-Vallejo personal observation), although in the latter they are reduced because the parapodia barely project from the body wall.

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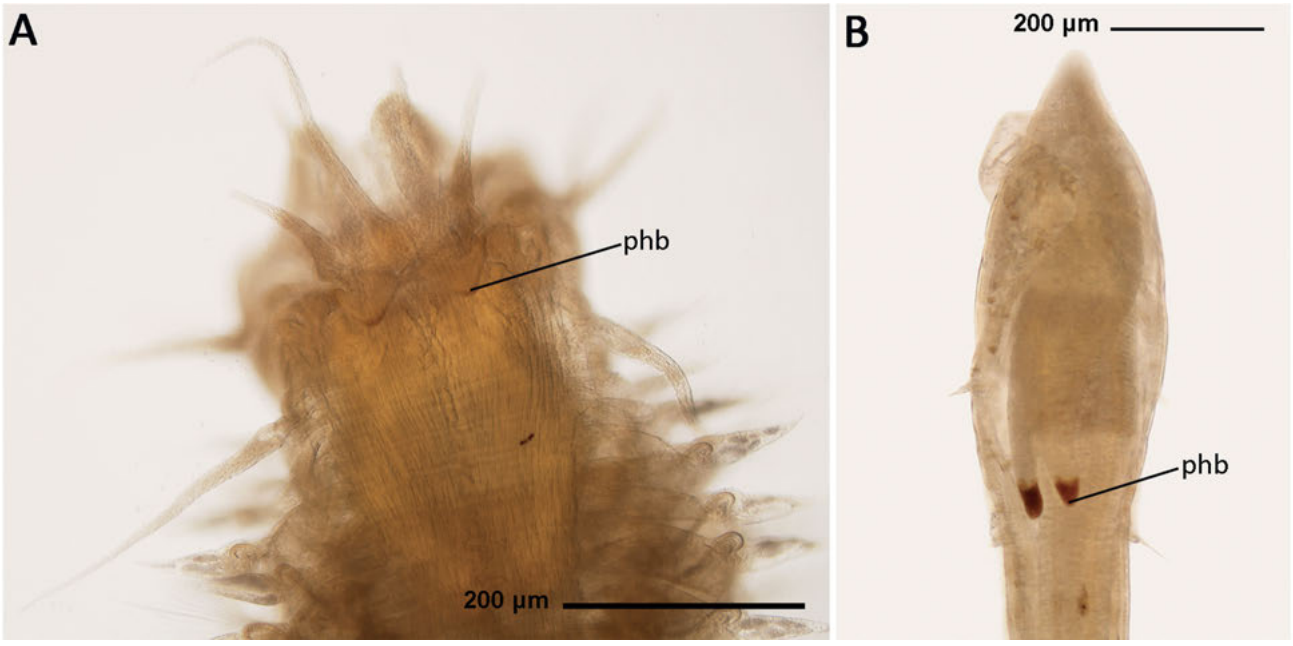


Fig. 7.13.3.4.15: A, *Sigambra* sp. prostomium and first segments, dorsal view showing pigmented nuchal organs. B, *Litocorsa* sp. prostomium and first segments, dorsal view, showing pigmented hindbrain. Specimens in collection of Museum of Rio de Janeiro (MNRJP-2732 and MNRJP-2744, respectively) phb, pigmented hindbrain.

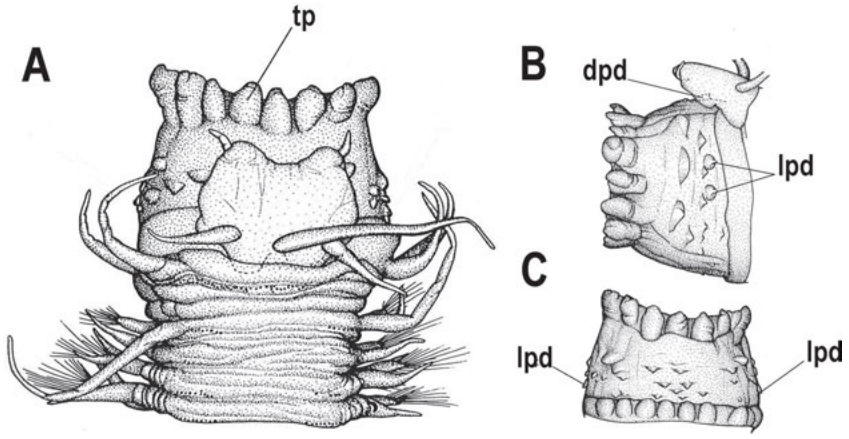


Fig. 7.13.3.4.16: *Sigambra tentaculata* (Treadwell, 1941), pharyngeal papillae and teeth. A, Anterior end, dorsal view. B, Same, lateral view. C, Pharynx, ventral view. lpd, lateral proboscideal denticles; dpd, dorsal proboscideal denticles; tp, terminal papilla. After Parapar et al. (2004).

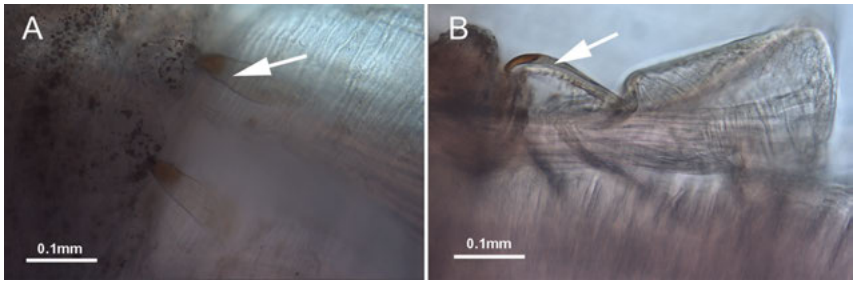


Fig. 7.13.3.4.17: *Hermundura* sp., jaws. A, Jawlike pieces seen by compound light microscopy. B, Pharynx exposed, jaw fully exposed (arrows point to jaws). Adapted from Glasby and Hocknull (2010, figs 2a, c).

Nephridia. Parapodial associated nephridial papillae (originally thought to be branchiae in *Hermundura aberrans* (Monro, 1936)) have been reported in two species of *Hermundura* (Salazar-Vallejo 1998, Glasby and Hocknull 2010).

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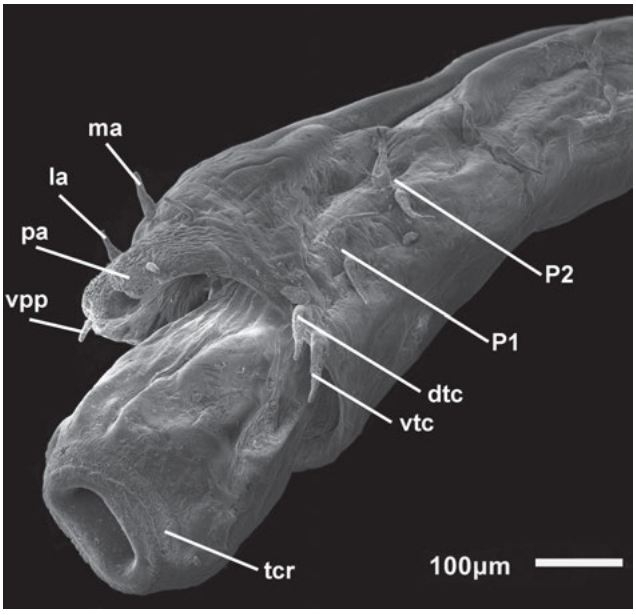


Fig. 7.13.3.4.18: *Synelmis sergi* Glasby & Marks, 2013, anterior end, pharynx fully exposed, left-frontal view. dtc, dorsal tentacular cirrus; la, lateral antenna; ma, median antenna; pa, palp; P1-2, parapodia 1, 2; tcr, terminal ciliated ring; vtc, ventral tentacular cirrus; vpp, ventrolateral palpal papilla. Specimen in collection of Museum and Art Gallery Northern Territory.

Reproductive system. Reproduction in Pilargidae is poorly known. Sexes are separate (Pettibone 1982), and known larvae are planktonic. The development of juveniles has been documented in some species of *Ancistrosyllis* and *Sigambra*, and juvenile ciliation was found to continue until at least the 16-chaetiger stage (Bhaud 1973, Blake 1975, Achari 1975).

Excretory, Circulatory, Sensory, and Nervous Systems. Unknown.

Biology and ecology

Pilargidae has a cosmopolitan distribution, and its members are associated mainly with soft sediments from the intertidal zone to the deep sea; they appear to be most common at shelf and slope depths (Parapar et al. 2004, Hocknull and Glasby 2009). *Sigambra* is notable for preferring coastal and estuarine environments, and some species are tolerant of hypoxic and freshwater conditions (Glasby et al. 2009, Lim et al. 2006). With the exception of some *Sigambra* species, which may be the dominant invertebrate in coastal subtidal sediments (Ong-Che and Morton 1991), pilargids are rarely abundant.

Pilargidae are active burrowers, presumably carnivores, but no further details are available on feeding or diet (Jumars et al. 2015). Early studies suggested that pilargids were symbiotic with other invertebrates on the assumption that the dorsal hooks of many species were used to adhere to their symbionts, as indicated for some specialized *Microphthalmus* (see Westheide 1982). However, only in 4 of the 11 genera are there reports of symbiotic species: *Ancistrosyllis, Antonbruunia*, *Sigambra*, and *Pilargis*. *Ancistrosyllis commensalis* Gardiner, 1976 inhabits burrows of *Notomastus lobatus* Hartman, 1947a. *Ancistrosyllis groenlandica* McIntosh, 1878 was recorded as an enteric commensal with the burrowing holothuroid *Molpadia* (see Rullier 1960), and a species reported as *Pilargis berkeleyae* Monro, 1933 (but that may instead be *Pilargis pacifica*; cf. Salazar-Vallejo and Harris 2006) is commensal in the tubes of *Chaetopterus cautus* Marenzeller, 1879 (Martin and Britaev 1998). *Sigambra commensalis* (Misra, 1999) was found attached to the gastric region of the hemichordate, *Saccoglossus* sp. from the Hooghly-Matla estuary, West Bengal, India (Misra 1999). Inclusion of *Antonbruunia* in the family gives the group an endosymbiotic representation among chemosynthetic bivalves.

Phylogeny and taxonomy

The first phylogenetic studies of the group suggested that *Glyphohesione* was the most plesiomorphic pilargid and that it and all other pilargids evolved from a juvenile stage of a large-bodied hesionid; therefore, the group should be included in the Hesionidae (Licher and Westheide 1994, 1997). Some adult hesionids also have pilargid-like characteristics — for example, *Microphthalmus simplicichaetosus* Westheide & Purschke, 1992, which was up until recently considered a hesionid, also has simple, pilargid-like chaetae and the first two segments are achaetigerous and carry tentacular cirri or enlarged anterior cirri (Westheide and Purschke 1992). Licher and Westheide (1994) consider the direction of evolution to be one of simplification of the body plan involving reduction in the size and complexity of the prostomium and prostomial appendages, loss of tentacular cirri, and simplification of parapodia. Pleijel and Dahlgren (1998) rejected the idea that pilargids (including *Glyphohesione*) belong with hesionids, and subsequent analyses have shown that pilargid and hesionid taxa are clearly separate clades and, therefore, that the two families should be maintained (Pleijel 1998, Pleijel and Dahlgren 1998, Dahlgren et al. 2002).

Recently, the relationship between pilargids and the two chemosynthetic bivalve symbionts *Antonbruunia* and Nautiliniellidae has become clearer, although confirmatory studies are necessary. Since its original description,

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Antonbruunia has been regarded as resembling pilargids. Based on morphological similarities, Salazar-Vallejo (1986) placed the genus together with the pilargid subfamily Sigambrinae (now Pilarginae) (Salazar-Vallejo and Orensanz 1991), and Glasby (1993) formally synonymized the family Antonbruunidae Fauchald, 1977 with Pilargidae. The molecular phylogenetic study of Mackie et al. (2015) supported its position within Pilargidae, specifically as sister group of the pilargids *Ancistrosyllis* and *Sigambra*, although support depended on the analysis type (pilargid sister relationship only supported in the Bayesian analyses, but not in the less-resolved Maximum Likelihood analyses). Such a relationship implies a possible homology between the "palps" of *Antonbruunia* and the palps or palpal papillae of other pilargids. By contrast, Nautiliniellidae, which were thought to be allied to either Pilargidae or Syllidae on morphological grounds (Glasby 1993), are now regarded as being nested within Chrysopetalidae (Aguado et al. 2013).

Saint-Joseph (1899a) described the family based on *Pilargis verrucosa* from France; however, the family was not universally accepted until the revisionary studies of Hartman (1947b) and Pettibone (1966). There are 11 valid genera of Pilargidae; there are no recognized fossil taxa. Pilargids present two distinct morphotypes, which are reflected in the subfamily taxonomic division proposed by Salazar-Vallejo (1986) and modified by Salazar-Vallejo and Rizzo (2009), viz. Kynephorinae and Pilarginae. Kynephorinae, typified by *Litocorsa*, *Synelmis*, and *Hermundura*, have a cylindrical body shape, straight notopodial spines, several gross morphological similarities of the brain, and lack pharyngeal papillae (Fitzhugh and Wolf 1990, Licher and Westheide 1994). Pilarginae, typified by *Cabira*, *Pilargis*, and *Ancistrosyllis*, have a slightly to markedly depressed body that is papillated; falcate notopodial hooks are present in some genera, and they have a hindbrain with either three or five lobes. The other genera do not fall readily into these two groups so, in addition to the reasons outlined earlier, the subfamily classification is not used, and the genera are listed below alphabetically.

Pilargidae Saint-Joseph, 1899

Type genus: *Pilargis* Saint-Joseph, 1899a: 42.

Synonyms: Otopsidae Ditlevsen, 1917: 67.

Kynephoridae Ehlers, 1920: 27 (name now used at subfamily level in Pilargidae).

Antonbruunidae Fauchald, 1977: 91.

Talehsapiidae Misra, 1999: 144.

Diagnosis: Nereidiform polychaetes with cylindrical to ribbonlike bodies; integument smooth or papillose to verrucose. Prostomium bearing paired dorsolateral antennae and a single posteromedial one (may be absent), or antennae entirely absent; anteroventral palps biarticulated or simple, variably fused to each other, rarely absent; usually with an accessory palpal papilla. Tentacular segment with two pairs of cirri, rarely one pair, or without cirri; chaetae absent. Dorsal and ventral cirri variable, short, cirriform, or lobulated. Parapodia lateral but may appear ventrally displaced in cylindrical forms, usually subbiramous or uniramous, notopodia reduced to dorsal cirri, neuropodia distinct. Chaetae simple. Notochaetae include emergent hooks or spines, usually positioned above the dorsal cirri, rarely with capillary chaetae, or without chaetae (one genus with emergent notaciculae below the dorsal cirri). Neurochaetae include limbate capillaries, hirsute or distally bifid falcate spines, distally smooth spines, and delicate furcate chaetae. Alimentary canal includes tubular, muscular pharynx lacking true jaws, and gut diverticula (caeca) variably developed throughout most of body.

Comments: The derivation of the name Pilargidae, based on the type genus *Pilargis*, is not known for sure. Although a few explanations have been offered, perhaps the simplest is that it was derived from the Latin "pila," meaning ball, in reference to the wartlike body surface ornamentations on the type species, *Pilargis verrucosa* Saint-Joseph, 1899b (Salazar-Vallejo and Rizzo 2009, Read and Fauchald 2021). As indicated above, we regard Antonbruunidae as a junior synonym of Pilargidae and thus include the genus *Antonbruunia* in the family Pilargidae.

Ancistrosyllis McIntosh, 1878

(Figs. 7.13.3.4.3A and 7.13.3.4.6A, B)

Type species: *Ancistrosyllis groenlandica* McIntosh, 1878: 502, by monotypy.

Synonyms: *Harpochaeta* Korschelt, 1893: 279.

Ancistargis Jones, 1961: 2.

Diagnosis: Pilargids with body depressed, integument papillose to verrucose, present on both segmental and nonsegmental regions. Antennae, 0–3. Palps unfused, biarticulated; palpostyle minute. Paired ventrolateral palpal papillae present. Pharynx distally with terminal papillae (or absent); proximally smooth or, rarely, with denticles. Two pairs of tentacular cirri. Dorsal and ventral cirri digitate to lobate. Notochaetae are hooks, present from chaetigers 3 to 13 and continuing throughout body. Neurochaetae smooth, or spinulose capillaries, often with bidentate tips. Free living in sediments from intertidal to deep sea, or commensal with other invertebrates.

Comments: *Ancistrosyllis*, first revised by Pettibone (1966: 164), contains 14 named species worldwide (Fiege and Böggemann 1999, Salazar-Vallejo 2011), including the questionable *Ancistrosyllis cingulata* (Korschelt, 1893,

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originally as *Harpochaeta*), a 13-chaetiger form originally described from the Bay of Trieste (northern Adriatic). The synonymy of *Ancistargis* with *Ancistrosyllis* follows the suggestion of Licher and Westheide (1994). However, the presence of a globular, saclike proboscis in *Ancistargis* is a feature that appears to set this genus apart from *Ancistrosyllis* (muscular pharynx present); in other *Ancistrosyllis* species, Gardiner (1976, fig. 9) has shown that the pharynx can be as long as the region extending from the palps to chaetigers 4–12. Further, the most recent species described in the genus *Ancistrosyllis matlaensis* Mandal & Deb, 2018 is also reported to have a soft, globular proboscis, but in this case, it is armed with denticles, a feature not been reported in other members of the genus. Therefore, the phylogenetic significance of pharyngeal features, including its ornamentation, needs to be properly assessed prior to any further taxonomic changes.

Antonbruunia Hartman & Boss, 1965

Type species: *Antonbruunia viridis* Hartman & Boss, 1965: 177, by monotypy.

Diagnosis: Pilargids with body subcylindrical (slightly flattened ventrally), integument smooth. Three antennae; palps unfused, simple, tapered. Paired ventrolateral palpal papillae apparently absent. Pharynx smooth, lacking terminal or proximal papillae. Two pairs of tentacular cirri. Dorsal and ventral cirri tapered. Notochaetae absent. Neurochaetae small, thin hooks, distally bifid. Dimorphic, males dwarf, living inside lucinid bivalves.

Comments. Aguado (this volume) treats *Antonbruunia* in its own family, Antonbruunidae Fauchald, 1977.

Cabira Webster, 1879

(Figs. 7.13.3.4.9 and 7.13.3.4.11)

Type species: *Cabira incerta* Webster, 1879: 67, by monotypy.

Synonyms: *Paracabira* Britaev & Saphronova, 1981: 1322.

Diagnosis: Pilargids with body cylindrical, integument with few verrucae, larger and more numerous in anterior and posterior ends. Lateral antennae papilliform, median antenna absent. Palps unfused, biarticulated, palpostyle minute. Paired ventrolateral palpal papillae present. Pharynx lacking terminal papillae; proximally with soft papillae or hardened denticles arranged in rows. Two pairs of tentacular cirri, minute. Deep constriction between the first segment and the first chaetiger. Dorsal and ventral cirri papilliform; the latter from chaetigers 1 or 3. Notochaetae are hooks, from chaetigers 6 to 8. Neurochaetae are a variety of capillaries, limbate or nonlimbate, smooth or finely serrated. Free living in shelf sediments.

Comments: *Cabira* Webster, 1879 was first revised by Pettibone (1966). Britaev and Saphronova (1981) expanded membership of the genus and created a new genus, *Paracabira* for *Cabira capensis* (Day, 1963), but this genus was subsequently been synonymized by Mandal et al. (2007). *Cabira* presently comprises eight species worldwide (Mandal et al. 2007).

Glyphohesione Friedrich, 1950

(Figs. 7.13.3.4.10, 7.13.3.4.13A, and 7.13.3.4.14A, B)

Type species: *Glyphohesione klatti* Friedrich, 1950: 171, by monotypy.

Diagnosis: Pilargids with body cylindrical, integument smooth. Median and lateral antennae present. Palps unfused, biarticulated, palpostyles cirriform (resemble antennae), ventrally directed. Paired ventrolateral palpal papillae absent. Pharynx lacking terminal papillae; proximally smooth. Two pairs of tentacular cirri, cirriform. Dorsal and ventral cirri tapered. Notochaetae are spines, emergent below dorsal cirri, starting in chaetigers 4–10, continued throughout body. Neurochaetae short or long limbate (laterally spinulose) capillaries. Free living in shelf sediments.

Comments: *Glyphohesione* Friedrich, 1950, containing four species, was originally described as a hesionid based on the type species, *Glyphohesione klatti* from Helgoland, but considered as a pilargid by both Eliason (1962) and Pettibone (1966), although they did not agree on the genus (*Ancistrosyllis* and *Synelmis*, respectively). Its pilargid affinities were strengthened when *G. klatti* was found to have a brain morphology similar to *Sigambra* (see Fitzhugh and Wolf 1990), and the hesionid relationship was finally quashed by the findings of the combined morphological and molecular analysis of Dahlgren et al. (2002).

Hermundura Müller, 1858

(Figs. 7.13.3.4.1, 7.13.3.4.5, 7.13.3.4.14C, and 7.13.3.4.17A, B)

Type species: *Hermundura tricuspis* Müller, 1858: 216, by monotypy.

Synonyms: *Talehsapia* Fauvel, 1932: 251.

Loandalia Monro, 1936: 193.

Parandalia Emerson & Fauchald, 1971: 19.

Diagnosis: Pilargids with body cylindrical, integument smooth. Antennae absent. Palps unfused, biarticulated, palpostyles minute, sometimes double. Paired ventrolateral palpal papillae absent. Pharynx distally with terminal papillae; proximally smooth or with hardened denticles. Tentacular cirri absent. No dorsal cirri, ventral cirri minute, distal. Notochaetae include spines and smooth capillaries. Neurochaetae all hirsute capillaries. Free living in sediments from the intertidal to shelf depths mainly.

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Comments: Glasby and Hocknull (2010) revised the genus, and resurrected Müller's (1858) name. *Hermundura* was one of the first pilargid genera described but quickly fell into synonymy. The type species of *Hermundura*, *H. tricuspis* (as *Parandalia tricuspis*), was redescribed by Salazar-Vallejo (1990), and a neotype designated; he established unequivocally that it represented a senior synonym of *Parandalia*. When Salazar-Vallejo (1998) synonymized *Parandalia* with *Loandalia*, *Hermundura* became the senior synonym of both *Parandalia* and *Loandalia*, but because Salazar-Vallejo (1990) recommended the continuing use of the junior synonym name (*Parandalia*), the name *Hermundura* was effectively suppressed until Glasby and Hocknull (2010) argued against the suppression and resurrected the senior synonym name *Hermundura* as the valid name. Finally, *Talehsapia* was also synonymized with *Hermundura* by Glasby and Hocknull (2010), who established that the supposedly unique feature of the presence of denticulate bands (originally interpreted as jaws) also occurred in other species of *Hermundura*. Seventeen species of *Hermundura* are currently known, but because some were originally described under other genera, a revision of species is needed to clarify its composition.

Litocorsa Pearson, 1970

(Figs. 7.13.3.4.2, 7.13.3.4.13D, and 7.13.3.4.15B)

Type species: *Litocorsa stremma* Pearson, 1970: 69, by monotypy.

Diagnosis: Pilargids with body cylindrical, integument smooth. Antennae present or absent; palps fused dorsally to varying degrees, palpostyles sometimes present. Paired ventrolateral palpal papillae present. Pharynx smooth, terminal papillae absent. Two pairs of tentacular cirri. Dorsal and ventral cirri digitate. Notochaetae are spines, capillaries absent. Neurochaetae include smooth and denticulated spines, and spinulose capillaries. Free living in sediments from the coast to the deep sea.

Comments: *Litocorsa* was established by Pearson (1970) to include an undescribed species from western Scotland, *L. stremma*. The genus was revised by Pettibone (1966), and later refined by Licher and Westheide (1994) and Darbyshire and Mackie (2003), the latter describing a new species from the Seychelles, *Litocorsa seychellensis*. The genus contains many more than the seven species currently listed in Read and Fauchald (2021) (Salazar-Vallejo and Glasby in preparation).

Otopsis Ditlevsen, 1917

Type species: *Otopsis longipes* Ditlevsen, 1917: 67, by monotypy.

Diagnosis: Pilargids with body depressed, integument rugose. Antennae short, massive. Palps unfused, with small ventral palpostyle. Paired ventrolateral palpal papillae present. Pharynx distally with terminal papillae; proximally smooth. Two pairs of tentacular cirri. Dorsal cirri usually larger than ventral one. Notochaetae absent. Neurochaetae all hirsute capillaries. Free living in deep-sea sediments.

Comments: *Otopsis* and type species *O. longipes*, were originally described by Ditlevsen (1917) based on a single specimen collected by the Danish Ingolf-Expedition south of Iceland in 1587 m (Wesenberg-Lund 1951). Ditlevsen (1917) found it so strange that he placed it in its own family, Otopsidae. Hartman (1947b) and Pettibone (1966) both considered that the species belonged to family Pilargidae. To date only four species are known, all from deep water in the northern hemisphere.

Pilargis Saint-Joseph, 1899a

(Figs. 7.13.3.4.3B, 7.13.3.4.8, and 7.13.3.4.13B)

Type species: *Pilargis verrucosa* Saint-Joseph, 1899b: 176, by monotypy.

Synonyms: *Phronia* Webster, 1879: 268 (*Phronia* Webster, 1879 is a junior homonym of a dipteran genus *fide* Saint-Joseph 1899b: 179).

Diagnosis: Pilargids with body depressed, integument usually densely papillated. Lateral antennae lobate, median antenna missing; palps unfused, biarticulated, palpostyle minute. Paired ventrolateral palpal papillae present, but difficult to distinguish from abundant verrucae of same size. Pharynx surface unknown. Two pairs of tentacular cirri. Dorsal and ventral cirri lobate. Notochaetae absent. Neurochaetae smooth or limbate capillaries, tips sometimes falcate or weakly bidentate. Free living in sediments from the coast to the deep sea.

Comments: *Pilargis* was revised by Salazar-Vallejo and Harris (2006); they recognized 13 species, including four that were new, and they provided a redescription of six species based on a reexamination of type specimens and also standardized morphological concepts for members of the genus. An additional species was recently described off southeastern Brazil (Ribeiro et al. 2020).

Pseudexogone Augener, 1922

Type species: *Pseudexogone backstromi* Augener, 1922: 192, by original designation.

Diagnosis: Pilargids with body cylindrical, integument smooth. Lateral and median antennae present. Palps variably fused, palpostyles ventrolateral. Paired ventrolateral palpal papillae present. Pharynx smooth. Two pairs of tentacular cirri. Dorsal and ventral cirri cirriform. Notochaetae are falcate bidentate spines. Neurochaetae include

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pectinate and denticulate capillaries, and furcate chaetae. Free living in sediments from the shelf to the deep sea.

Comments. *Pseudoexogone* Augener, 1922 comprises five species. *Synelmis dineti* Katzmann, Laubier & Ramos, 1974 was transferred to *Pseudexogone* by Salazar-Vallejo et al. (2007).

Sigambra Müller, 1858

(Figs. 7.13.3.4.4, 7.13.3.4.7, 7.13.3.4.12, 7.13.3.4.13C, and 7.13.3.4.15A, 7.13.3.4.16A–C)

Type species: *Sigambra grubii* Müller, 1858: 214, by monotypy.

Synonyms: *Sigatargis* Misra, 1999: 142 [new synonymy].

Diagnosis: Pilargids with body depressed, integument smooth to papillated, papillae restricted to anterior segments, arranged in a single transverse row per segment. Lateral and median antennae present, cirriform. Palps unfused, biarticulated, palpostyles directed ventrally. Paired ventrolateral palpal papillae present. Pharynx distally with terminal papillae; proximally with papillae, some hardened (=denticles). Two pairs of tentacular cirri, cirriform. Dorsal and ventral cirri cirriform; ventral cirri may be absent on chaetiger 2. Notohooks present along the body, starting in anterior or median regions. Notochaetae include hooks and sometimes shorter spines or capillaries. Neurochaetae limbate capillaries of varying size. Free living in sediments mainly in estuaries and on the coast.

Comments: *Sigambra* was one of the first pilargid taxa described — based on *Sigambra grubii* Müller, 1858 — but was forgotten for more than 100 years until the genus was revised by Pettibone (1966) and Licher and Westheide (1997). The type species *S. grubii* was redescribed based on material from the type locality by Salazar-Vallejo (1990). Presently, the genus contains 25 valid species worldwide. *Sigatargis* closely resembles *Sigambra*, although no autapomorphies have been identified for the latter genus (Licher and Westheide, 1994). Features mentioned or illustrated by Misra (1999) that set his genus apart from *Sigambra* (absence of median antenna, presence of two notohooks per notopodium, and notopodial hooks with basal swellings on a single side) are features that are known already in *Sigambra*, although rare. The latter, however, could also be explained because the hooks were observed obliquely, not in lateral view; pilargid hooks usually have a swollen region just below the integument, which could help strengthen the anchoring role for hooks. Some publications indicate authorship as Grube *in* Müller, or Grube & Müller. This is incorrect. Grube's contribution consisted of a short introduction to the paper and a few interspersed notes for some species. Therefore, the authorship of *S. grubii* must be restricted to Müller.

Synelmis Chamberlin, 1919

(Figs. 7.13.3.4.14D and 7.13.3.4.18)

Type species: *Synelmis simplex* Chamberlin, 1919: 177.

Synonyms: *Kynephorus* Ehlers, 1920: 27.

Diagnosis: Pilargids with body cylindrical, integument smooth. Lateral and median antennae present. Palps unfused, biarticulated, palpostyles rounded, palpostyles ventrolateral, cirriform. Paired ventrolateral palpal papillae present. Pharynx smooth. Two pairs of tentacular cirri, cirriform. Dorsal and ventral cirri tapered, sometimes swollen basally. Notospines present along the body, starting from chaetigers 5 to 23; capillaries absent. Neurochaetae include smooth, limbate capillaries and furcate chaetae. Free living in sediments from the coast to the deep sea.

Comments: *Synelmis* was revised by Salazar-Vallejo (2003). He recognized 15 species worldwide and established that *Synelmis albini* (Langerhans, 1881), previously thought to be cosmopolitan, had a much more restricted distribution in the eastern subtropical Atlantic. In the same year, Glasby (2003) designated a neotype for *S. albini* in order to clarify the concept of the genus and compared it with a new form from New Zealand, *Synelmis knoxi* with which it had been misidentified. The genus is represented by 17 species (Glasby and Marks 2013).

Acknowledgments

The authors gratefully acknowledge the help of Yen-Ling Lee and Ang Hwee Peng (Serene), Tropical Marine Science Institute, University of Singapore, for material, specimen preparation, and use of the scanning electron microscope; Dr Tan Koh Siang kindly facilitated the visit of CJG in 2015. Julio Parapar, Markus Böggemann, and an anonymous reviewer helped us clarify our ideas by making useful recommendations.

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https://doi.org/10.1515/9783110647167-012

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7.13.4 Glyceriformia

7.13.4.1 Glyceridae Grube, 1850

Introduction

The Glyceridae Grube, 1850 and the very similar Goniadidae Kinberg, 1865 (see chapter 7.13.4.2) are treated together as Glyceriformia Fauchald, 1977, a monophyletic clade within the Phyllodocida (Rouse and Pleijel 2001). Their pointed, usually annulated prostomium with two pairs of terminal appendages (Figs. 7.13.4.1.1A–D, 7.13.4.1.2A, 7.13.4.1.3A, D, 7.13.4.1.10A, 7.13.4.1.11A, and 7.13.4.1.12A) and their long, muscular, eversible axial proboscis (Figs. 7.13.4.1.1B, D and 7.13.4.1.2A), which is densely covered with papillae (Fig. 7.13.4.1.2A) and provided with terminal jaws (Figs. 7.13.4.1.1D, E and 7.13.4.1.2A), are unique characters among the Annelida (Böggemann 2006). However, both groups can be clearly separated from each other, especially by the proboscidial armature. The four similar jaws of the glycerids are hook-shaped with an accessory lateral aileron (Figs. 7.13.4.1.1E, 7.13.4.1.2C, and 7.13.4.1.5A), whereas goniadids usually have two macrognaths and a variable number of dorsal and ventral micrognaths and sometimes additional longitudinally arranged rows of V-shaped chevrons on each side of the proboscis (Figs. 7.13.4.2.1B, C, 7.13.4.2.2E, F, 7.13.4.2.3B, C, 7.13.4.2.11D, 7.13.4.2.13B, 7.13.4.2.15B, and 7.13.4.2.16D; Böggemann 2002, 2005).

The Glyceridae have a worldwide distribution from intertidal to abyssal depths (Böggemann 2002, 2009). They are generally considered to be carnivores, capturing prey with their jaws and killing it by the injection of venom (Ockelmann and Vahl 1970, Fauchald and Jumars 1979, Manaranche et al. 1980). In most species, the animals form semipermanent burrow systems in soft-bottom sediments (Ockelmann and Vahl 1970), whereas a few occur free living under rocks or crawling on algae (Fauchald and Jumars 1979), wood and, grass substrates (Böggemann et al. 2011, 2012).

Within Glyceridae, there are currently 52 recognized nominal species, with 46 in the genus *Glycera* Lamarck, 1818; 1 in *Glycerella* Arwidsson, 1899; and 5 in *Hemipodia* Kinberg, 1865.

Morphology

External morphology

Color. The Glyceridae, commonly called bloodworms, usually appear reddish because the respiratory pigment

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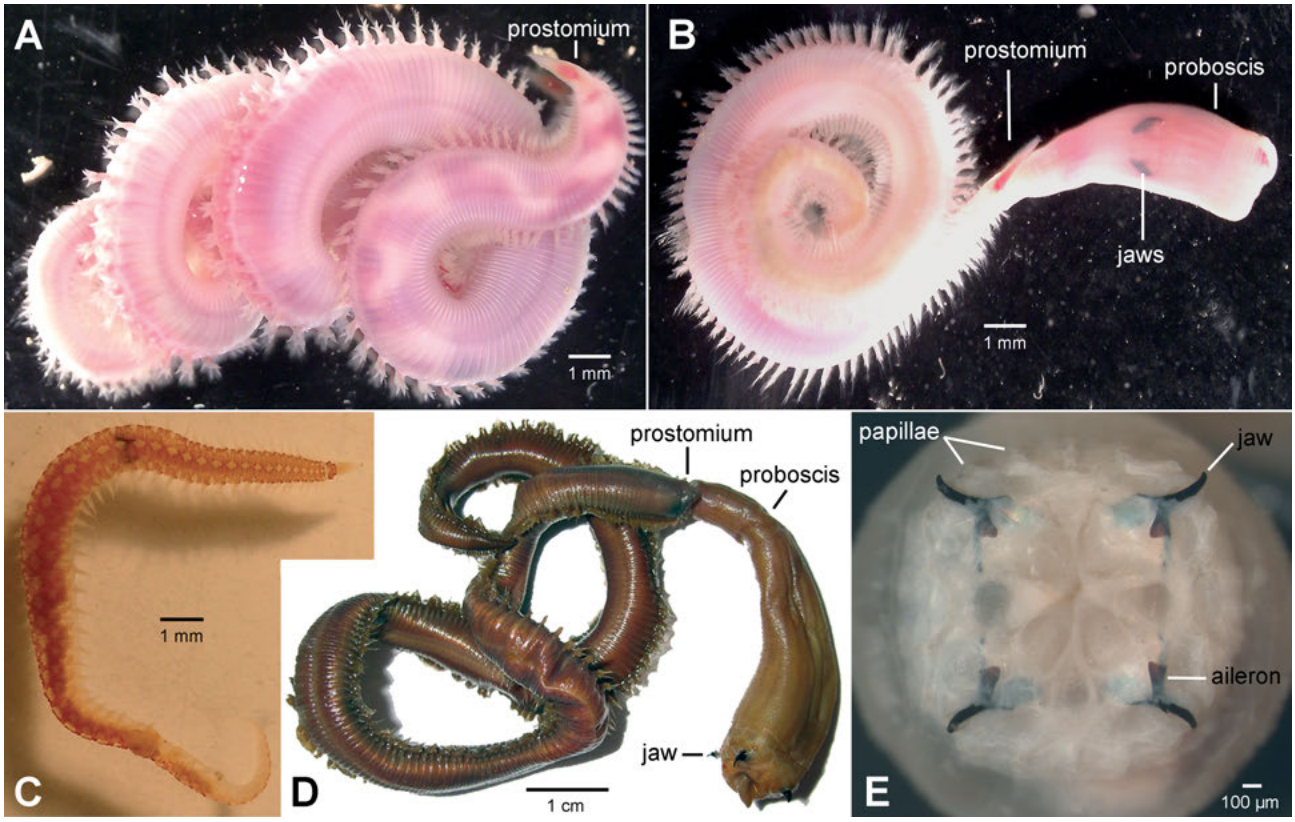


Fig. 7.13.4.1.1: *Glycera unicornis* Lamarck, 1818. A, Living specimen, dorsal view (Böggemann 2007). B, Living specimen with partly everted proboscis (Böggemann 2007); *Glycera tesselata* Grube, 1863. C, Living specimen, dorsal view (© M. Böggemann); *Glycera americana* Leidy, 1855. D, Preserved specimen with everted proboscis, dorsal view (© M. Böggemann). E, Terminal part of proboscis, frontal view (© M. Böggemann).

(hemoglobin) in the coelomic fluid is visible through the more or less transparent integument (Fig. 7.13.4.1.1A, B). Investigations on living specimens demonstrated that there are usually no species-specific color patterns (Böggemann 2002), with the exception of *Glycera tesselata* Grube, 1863 (Fig. 7.13.4.1.1C). The color of a fixed specimen (Fig. 7.13.4.1.1D) and its pigmentation are variable and seem to be dependent on the fixative and the time kept in alcohol or formalin. The original more or less uniform pigmentation is best preserved on the parapodia and the prostomium (Figs. 7.13.4.1.10–7.13.4.1.12).

Size. Glycerids are slender, cylindrical polychaetes that can reach considerable sizes (up to 1 m long). The body is elongated, tapering at both ends and consists of numerous bi- or triannulate segments (Fig. 7.13.4.1.1A–D). Tubercles on some of the anterior segments are described for a few species (Böggemann 2002).

Prostomium. The Glyceridae are easily recognized by their usually pointed, annulated prostomium (Figs. 7.13.4.1.2A, 7.13.4.1.3A, 7.13.4.1.10A, 7.13.4.1.11A, and 7.13.4.1.12A). The anteriormost annulus of the prostomium bears four appendages (Fig. 7.13.4.1.3A, D) and the posteriormost annulus one pair of nuchal organs (Fig. 7.13.4.1.3A, B). In earlier studies, different terms are used for the head appendages at the tip of the prostomium. Gravier (1898a, b) interpreted the prostomial nerves and the lateral cell clusters as the palp section of the brain and the appendages as antennae. By contrast, Hanström (1927, 1928) proposed the idea that the prostomium consists of two fused palps and the appendages might be reduced antennae. But later, he designated them as one pair of dorsal antennae and one pair of ventral palps (Hanström 1930). Orrhage (1999) strengthened Hanström's (1927) idea that the Glyceriformia prostomium represents a pair of fused palps. As a result, the appendages are interpreted as outgrowths from the prostomium and therefore as structures without direct equivalents in other polychaete families (Orrhage 1999). The nuchal organs (Fig. 7.13.4.1.3A, B) of the glycerids consist of a pair of epidermal, ciliated sensory structures located dorsally in the posterior region of the prostomium (Whittle and Zahid 1974). They are innervated by the posterior part of the brain and can be retracted by special muscles (Storch and Schlötzer-Schrehardt 1988). The investigations of Whittle and Zahid (1974) suggested that the nuchal organs are chemoreceptors. Stolte (1932a)

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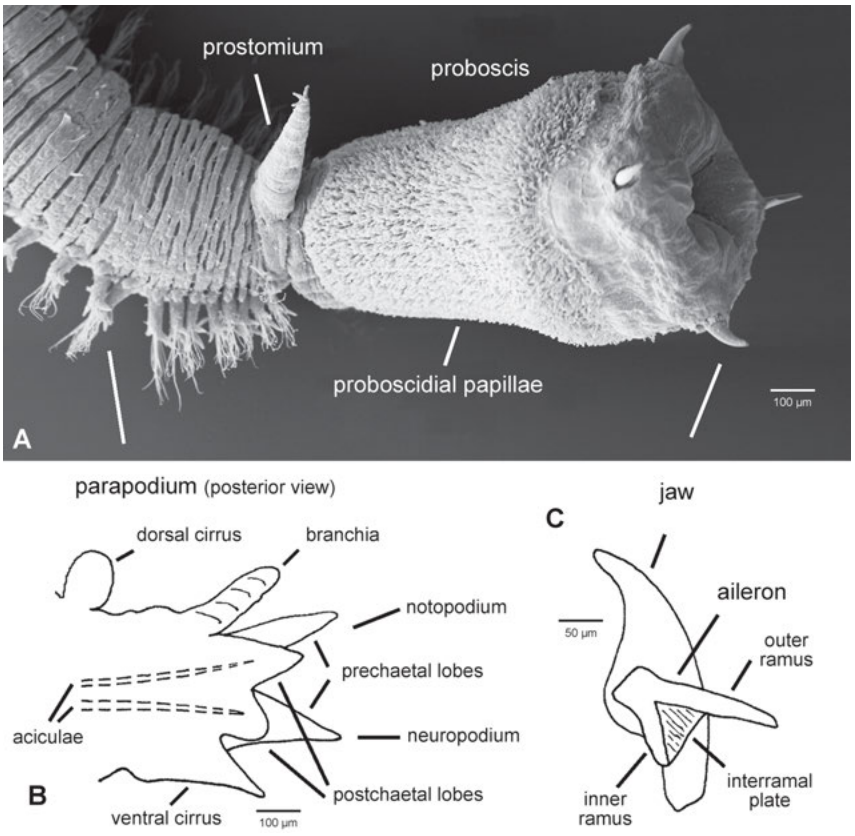


Fig. 7.13.4.1.2: *Glycera alba* (O.F. Müller, 1776). A, SEM micrograph of anterior end with everted proboscis, dorsolateral view (Böggemann 2002). B, Parapodium of midbody (Böggemann 2002). C, Jaw apparatus (Böggemann 2002).

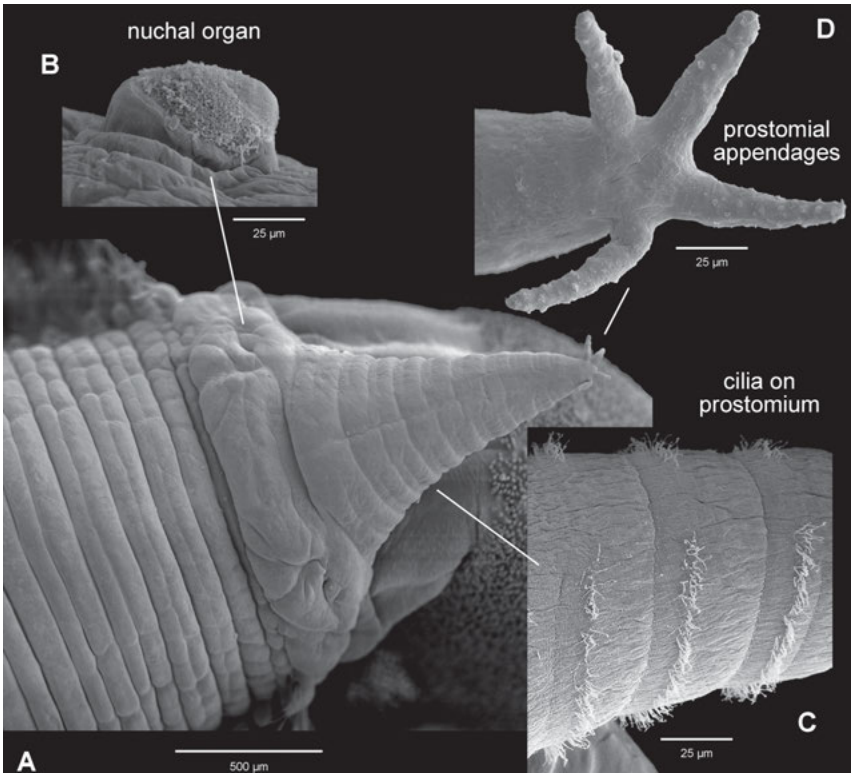


Fig. 7.13.4.1.3: SEM micrographs. A, *Glycera tridactyla* Schmarda, 1861, anterior end, dorsal view (Böggemann 2005). B, *Glycera brevicirris* Grube, 1870, nuchal organ, dorsal view (© M. Böggemann). C, Middle part of prostomium with lateral sensory cilia, dorsolateral view (© M. Böggemann). D, Prostomial appendages, dorsal view (© M. Böggemann).

supposed that the nuchal organs are used for capturing, although a direct contact with the prey only takes place with the prostomial tip and the appendages (Ockelmann and Vahl 1970). With the exception of the terminal and basal rings, each of the rings of the prostomium carries cilia (Figs. 7.13.4.1.3C and 7.13.4.1.4A–D; Stolte 1932a, Koldehoff

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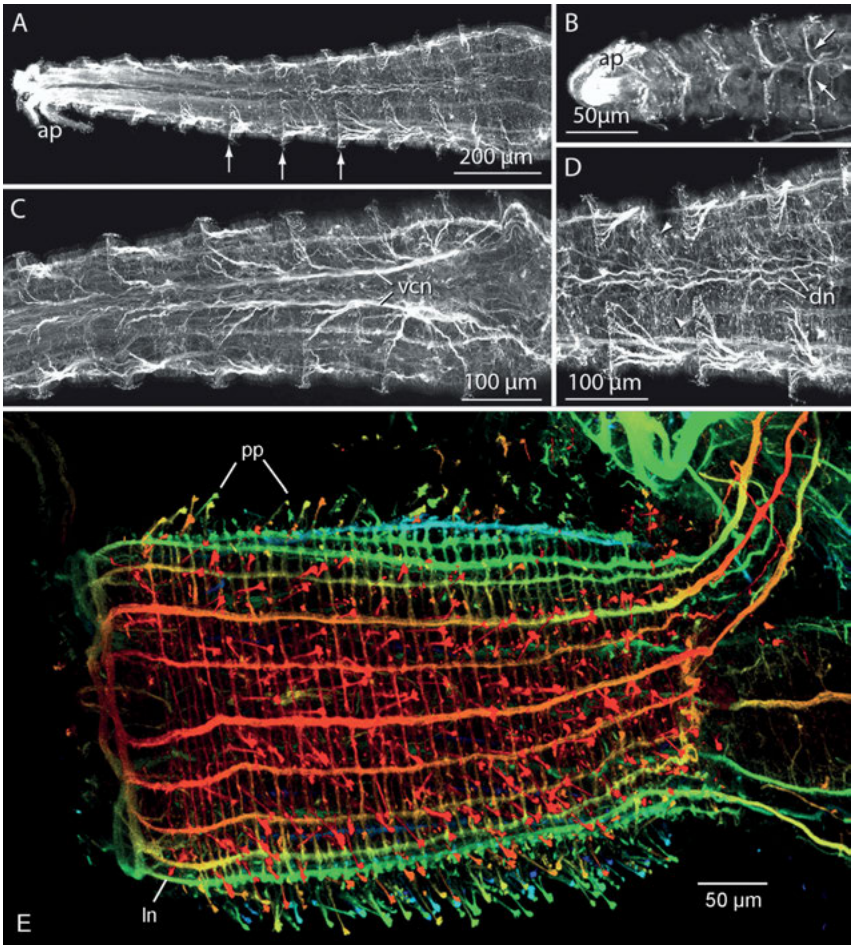


Fig. 7.13.4.1.4: CLSM micrographs. A, *Glycera* sp., prostomium with innervation of appendages (ap) and lateral sensory cilia (arrows), dorsal view (Koldehoff 1999). B, Anterior part of the same, lateral view (Koldehoff 1999). C, Posterior part, innervation of ventral sensory cilia by one pair of ventral nerves (vcn), ventral view (Koldehoff 1999). D, Middle part, innervation of dorsal sensory cilia by lateral nerves, dorsal nerves (dn) ramify into free nerve endings (arrowheads), dorsal view (Koldehoff 1999). E, *Glycera alba*, everted proboscis with longitudinal nerves (ln) and numerous proboscidial papillae (pp) (Müller 1999).

1999, Böggemann 2002). These ciliated lateral rings on the prostomium are presumed to be mechanoreceptors, which seem to be sensitive to small changes in water pressure such as may be caused by an animal moving around (Stolte 1928, 1932a, Ockelmann and Vahl 1970). By contrast, the ventral prostomial sensory cells, described by Binard and Jeener (1928), might control the eversion of the proboscis after their direct contact with the sediment (Stolte 1928). Typical eyes are absent; however, Manaranche (1966, 1968, 1971, 1975) and Simpson (1959, 1991) expected light-sensitive cell structures to be situated in the brain of the glycerids.

Pharynx. The Glyceridae have a symmetrically developed axial pharynx (Figs. 7.13.4.1.1B, D and 7.13.4.1.2A) with a strong muscular region, which is typical for the Phyllodocida (Dales 1962). This type of pharynx is often greatly protrusible in the glycerids (up to one-fourth or one-third of the whole body length) and in such cases called a proboscis (Dales 1962, Purschke 1988, Saulnier-Michel 1992), which is innervated by the stomatogastric nervous system (Michel and DeVillez 1978).

The distal armature of the proboscis consists of four jaws arranged in a cross, each with an aileron (= accessory jaw plate) and associated venom glands (Figs. 7.13.4.1.1E, 7.13.4.1.2A, C, and 7.13.4.1.5A). The jaws are brown to black, composed of tanned proteins, melanin, and embedded copper (Voss-Foucart et al. 1973, Michel et al. 1973, Michel and DeVillez 1978, Gibbs and Brian 1980, Lichtenegger et al. 2002, Moses et al. 2006). High copper levels are more dense on the distal part of the jaws near their surface (Fig. 7.13.4.1.6), in addition to sulfur and calcium, which are much more evenly distributed (Gibbs and Bryan 1980, Eriksson and Elfman 2000, Böggemann 2002, 2006). The jaws of the glycerids are always associated through special ducts with the venom glands (Fig. 7.13.4.1.5A, B; Michel 1966). Each venom duct ends at the tip of the jaw and additionally connects with a series of pores on the ventral side of the jaw (Charletta and Boyer 1974, Böggemann 2002). Wolf (1977) characterizes the resulting finer structures (Fig. 7.13.4.1.5B), and Böggemann (2002) suggests they probably show species-specific differences. Therefore, further scanning electron microscope examinations are needed to clarify the diagnostic value of glycerid jaws. This is less important to separate recent species, but it might be useful to increase the value of scolecodonts as index fossils for geology (Böggemann 2006). In addition

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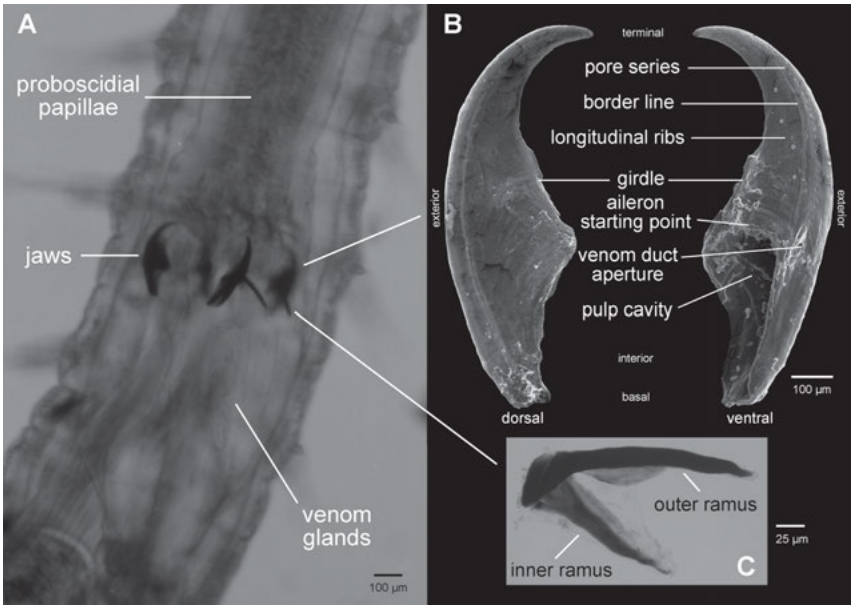


Fig. 7.13.4.1.5: A, *Glycera lapidum* Quatrefages, 1866, part of inverted proboscis (Böggemann 2007). B, *Glycera tridactyla* Schmarda, 1861, SEM micrograph of jaw (Böggemann 2002). C, *Glycera tesselata* Grube, 1863, aileron (Böggemann 2006).

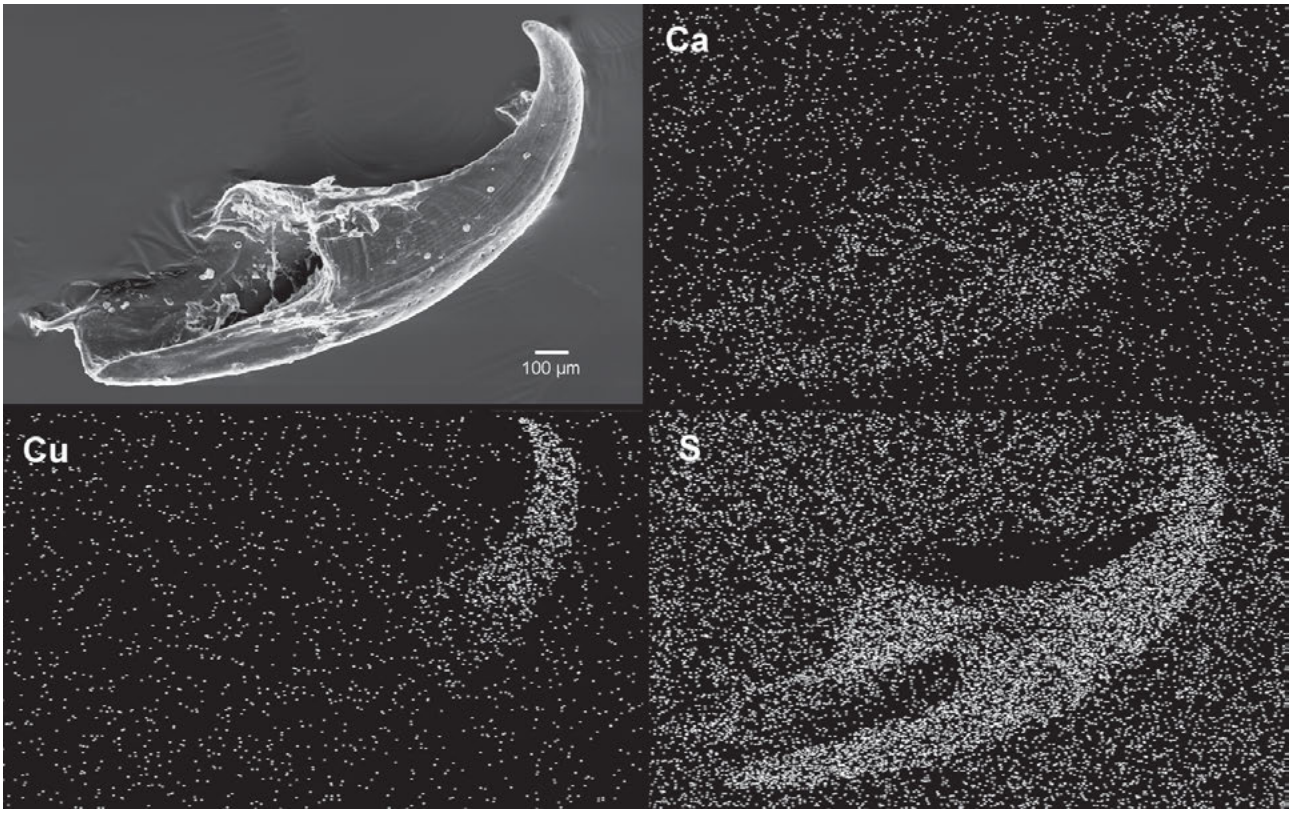


Fig. 7.13.4.1.6: *Glycera tridactyla* Schmarda, 1861, SEM micrograph of a jaw and the calcium (Ca), copper (Cu), and sulfur (S) dot maps after X-ray microanalysis (Böggemann 2002).

to phospholipases and proteases (Michel and Robin 1972, Michel and Keil 1975, Bon et al. 1985b), the glands of *Glycera convoluta* Keferstein, 1862 (syn. *Glycera tridactyla* Schmarda, 1861) secrete a biologically active venom called α-glycerotoxin (Bon et al. 1985 a, b, Michel-Saulnier 1995), which is able to upregulate presynaptic N-type Ca^{2+} channels (Meunier et al. 2002, Schenning et al. 2006), whereas *Glycera dibranchiata* Ehlers, 1868 used a different poison comprises components able to induce ion-permeable pores in lipid bilayers (Bon et al. 1985b, Kagan et al. 1980, 1982). Recently, Reumont et al. (2014) applied transcriptomic profiles to venom gland cells of three different

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species and identified coding for precursors in 20 known toxin classes that have been convergently recruited into animal venoms, as well as transcripts potentially coding for *Glycera*-specific toxins. Furthermore, as part of the nervous system or hemoglobin catabolism, the previously described pharyngeal "Lappen" (Ehlers 1868) or "languettes" (Raphaël 1933) are identified as the place of origin (Richter et al. 2017), whereas the large venom glands are only reservoirs for the toxin. Raphaël (1933) mentioned different species-specific numbers and forms of these organs, making them taxonomically interesting. In contrast to the jaws, the ailerons (Figs. 7.13.4.1.1E, 7.13.4.1.2C, 7.13.4.1.5C, 7.13.4.1.10C, 7.13.4.1.11C, and 7.13.4.1.12C) are of taxonomic use for recent species (Böggemann 2002). Either they are rodlike (Figs. 7.13.4.1.11C and 7.13.4.1.12C; *Glycerella* and all species of *Hemipodia*) or they possess a more complicated structure with outer and inner rami, and sometimes an interramal plate (Figs. 7.13.4.1.2C, 7.13.4.1.5C, and 7.13.4.1.10C; all species of *Glycera*). In addition to the jaw apparatus, the proboscis of the glycerids has terminally a ring of a few larger papillae (Fig. 7.13.4.1.1E), whereas the rest of the sheath is densely covered with numerous papillae (Fig. 7.13.4.1.2A; Böggemann 2002). These proboscidial papillae show great differences in their external morphology among species and appear in a variety of types distinguished by the shape, size, and morphology of their posterior sides: papillae with a terminal fingernail structure, digitiform papillae, conical papillae, and oval to globular papillae with or without different forms of ridges (Figs. 7.13.4.1.7A, 7.13.4.1.10B, 7.13.4.1.11B, and 7.13.4.1.12B; Fiege and Böggemann 1997, Böggemann 2002). The proboscis of each species carries one predominant type of papillae (Figs. 7.13.4.1.10B left side, 7.13.4.1.11B, and 7.13.4.1.12B left side). Besides these, usually one or two additional types are present but constitute less than 10% of the total number (Figs. 7.13.4.1.10B right side, 7.13.4.1.12B right side). These other types are more or less distinctly arranged in longitudinal rows. The proboscidial papillae appear to be one of the most reliable characters for identification (Fiege and Böggemann 1997, Böggemann 2002); however, their cellular structure seems to be quite homogeneous (Böggemann et al. 2000). The proboscidial papillae are composed of four to five cells: one anterior mucous cell, one posterior serous cell, and two to three multiciliated primary sensory cells (Fig. 7.13.4.1.7B), which are presumed to be mechanoreceptors (Bantz and Michel 1971, 1972, Böggemann et al. 2000). The intracellular ciliary rootlets of the sensory cells (Fig. 7.13.4.1.7B) are striated filamentous structures that might serve as skeletal elements, in addition to their sensory function (Böggemann et al. 2000). Each of the proboscidial papillae is correlated directly or indirectly via the nerve plexus with 1 of the 18 longitudinal nerves, which are embedded in the proboscis (Fig. 7.13.4.1.4E; Jourdan 1891, Gravier 1898b, Oppenheimer 1902).

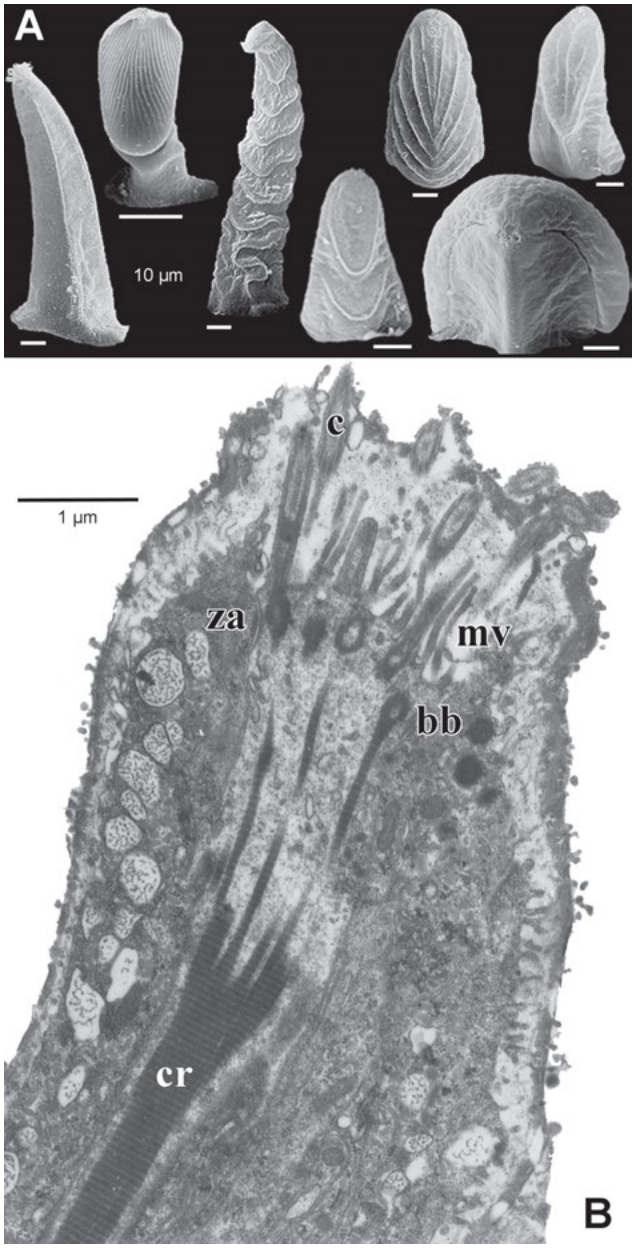


Fig. 7.13.4.1.7: A, *Glycera* spp., SEM micrographs of different proboscidial papillae, posterior view (Böggemann 2007); TEM micrograph. B, *Glycera lapidum* Quatrefages, 1866, apical part of a papilla. bb, basal body; c, cilium; cr, ciliary rootlet; mv, microvillus; za, zonula adherens (Böggemann et al. 2000).

Peristomium. Rouse and Pleijel (2001) interpret the peristomium as limited to the lips and segment one equals chaetiger one.

Parapodia and chaetae. The parapodia of the Glyceridae are either all uniramous (Fig. 7.13.4.1.12D–L), with one

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pre- and postchaetal lobe, one acicula and spinigerous compound chaetae (*Hemipodia* spp.), or biramous — usually except for the first two chaetigers — with two prechaetal and one or two postchaetal lobes, two aciculae, finely spinulose capillary notochaetae and compound neurochaetae (Figs. 7.13.4.1.2B, 7.13.4.1.10D–L, and 7.13.4.1.11D–L; *Glycerella* and all *Glycera* species; Böggemann 2002). The compound neurochaetae of the species of *Glycera* are exclusively spinigerous, whereas *Glycerella* has additional falcigers. Notopodial (if present) and neuropodial rami are indistinctly separated from each other but clearly indicated by the embedded straight and distally pointed aciculae (Fig. 7.13.4.1.2B). The prechaetal lobes are always slender triangular to digitiform in shape but sometimes differ in length (Figs. 7.13.4.1.2B, 7.13.4.1.10D–L, and 7.13.4.1.11D–L). The postchaetal lobes are short and rounded, blunt triangular or slender triangular and appear in the species of *Glycera* in different combinations and may be fused to one rounded lobe. With the exception of a few anterior chaetigers, oval to globular dorsal cirri are inserted near the parapodial base or on the body wall (Figs. 7.13.4.1.2B, 7.13.4.1.10D–L, and 7.13.4.1.11D–L). Ventral cirri of various shapes (oval, conical, slender triangular to digitiform) are situated on all parapodia (Figs. 7.13.4.1.2B, 7.13.4.1.10D–L, and 7.13.4.1.11D–L). Retractable or nonretractable branchiae are present in some *Glycera* species, and there are several types, which can be situated on different parts of the parapodia (Böggemann 2002). The branchiae are blisterlike, simple digitiform (Fig. 7.13.4.1.2B), up to six times branched, or bushlike (Fig. 7.13.4.1.10E–K) and are situated dorsally at the parapodial base, mediodorsally or terminodorsally (Fig. 7.13.4.1.2B) on the parapodia, dorsally on the posterior side of the parapodial base (Fig. 7.13.4.1.10E–K), dorsally and ventrally at the parapodial base, or medially on the anterior side of the parapodia. The parapodial lobes of juvenile specimens may be divergent from those of adult specimens. Usually, the notopodial lobes are shorter, and potential branchiae are not completely developed, whereas the parapodial lobes of very large specimens are more compact and dumpy.

Anatomy

Body wall. The body shape is cylindrical to dorsoventrally flattened in transverse section (Rouse and Pleijel 2001). Beneath the epidermis lies a simple musculature, which is composed of a layer of circular muscle and four distinct bands of longitudinal muscles (Voit 1911, Storch 1968).

Nervous system. The nervous system consists of a brain or cerebral ganglion, which resides in the prostomium, two circumesophageal connectives, a ventral nerve cord with more or less fused ganglia, and two pairs of segmental nerves of which one pair is connected with the parapodial ganglia (Gravier 1898a, Stolte 1932a, Manaranche 1966, 1975, Manaranche and L'Hermite 1973, Müller 1999, Koldehoff 1999, Orrhage 1999). Furthermore, in addition to freely terminating nerve fibers, many ciliated primary sensory cells are present and located predominantly on the prostomium, the proboscis, the dorsal and ventral cirri, and the pygidium (Figs. 7.13.4.1.3D, 7.13.4.1.4A–E, and 7.13.4.1.7B; Keferstein 1862, Ehlers 1868, Jourdan 1892, Gravier 1898a, Stolte 1932a, Manaranche 1975, Koldehoff 1999, Böggemann et al. 2000).

Blood vascular system. Most of the segmental septa and mesenteries of the glycerids are strongly reduced (Meyer 1929), and their blood vascular system is either completely absent or limited to a dorsal and a ventral longitudinal blood vessel (Müller 1858, Quatrefages 1866, Ehlers 1868, Arwidsson 1897, Voit 1911, Stolte 1932b, Smith and Ruppert 1988, Smith 1992). Nevertheless, a distinct circulation system can be found in the parapodial structures (Grube 1855, Meyer 1929, Böggemann 2002). The common name "bloodworm" is attributed to the reddish color of living specimens, which is caused by their high content of hemoglobin (Fig. 7.13.4.1.1A, B). The hemoglobin of the glycerids is associated with erythrocytes floating in the coelom, and their structure is well known (Imamura et al. 1972, Padlan and Love 1974, Cooke and Wright 1985a, b, Simons and Satterlee 1989). In addition to the hemoglobin, a monomeric myoglobin is present in the muscles of the body wall and especially in the proboscis muscles (Hoffmann and Mangum 1970, Terwilliger et al. 1976, Terwilliger and Garlick 1978, Terwilliger and Terwilliger 1981). Anderson (1980) reported the presence of hemolysins and hemagglutinins in the coelomic fluid of *Glycera dibranchiata*. It is probable that these factors participate in immune mechanisms. Furthermore, Anderson and Chain (1982) and Chain and Anderson (1983a, b, c) found an antibacterial factor (*Glycera* antibacterial factor), which was active against several Gram-negative bacteria.

Digestive system. The excretory system is a nephridial complex that is composed of a protonephridium with solenocytes, a nephridial or phagocytal sac, and a ciliated organ (Goodrich 1898, 1945, Fage 1906, Brandenburg and Kümmel 1961, Smith and Ruppert 1985). This nephridial complex occurs on almost all segments, attached to the ventral body wall near the parapodial bases, and it is used for filtration and reabsorption (Goodrich 1898, 1945, Smith and Ruppert 1985). Glycerids are euryhaline osmoconformers tolerating a wide range of salinities (Machin

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1975, Costa et al. 1980). The digestive tract is a straight tube, which begins with a ventral mouth opening and ends with a dorsal anus on the pygidium. It is separated into three sections: foregut, midgut, and hindgut. The gut lies more or less free in the body cavity attached only by the dorsal mesentery (Stolte 1928).

Pygidium. The pygidium ends with a single pair of elongated anal cirri (Fig. 7.13.4.1.8A, C).

Biology and ecology

Glyceridae are widely distributed benthic organisms and occur from intertidal to abyssal depths (Böggemann 2002, 2009). They are common burrowers in endopsammal sediments but usually found in low abundance. Some species form complex semipermanent burrow systems with a series of openings (Ockelmann and Vahl 1970), whereas other taxa appear to be motile (Klawe and Dickie 1957,

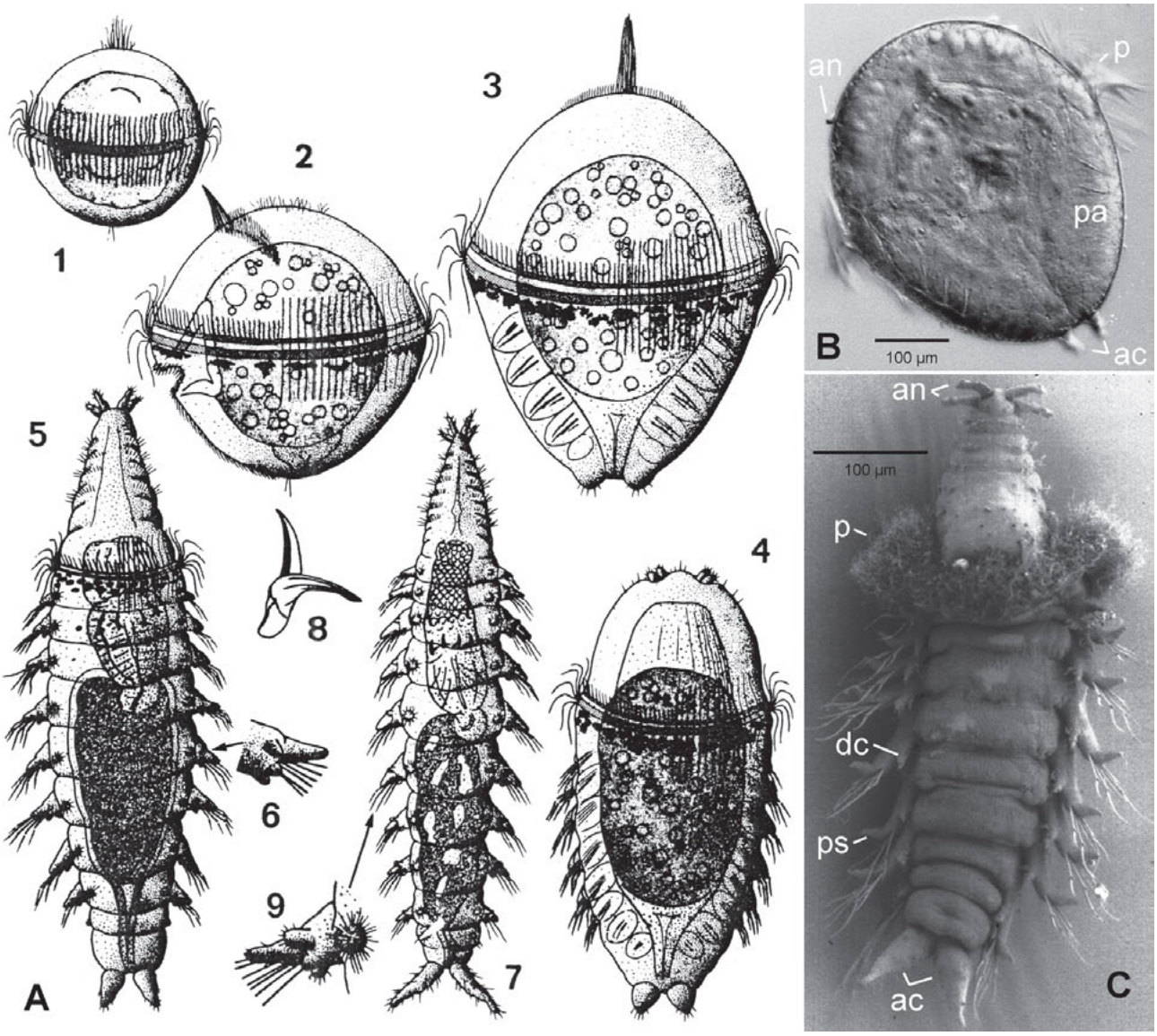


Fig. 7.13.4.1.8: A, Several developmental stages of *Glycera convoluta* Keferstein, 1862 (= *Glycera tridactyla* Schmarda, 1861). (1) Trochophore 36 hours old. d = 140 µm. (2) Trochophore 10 days old (left side). L = 240 µm. Note the presence of a crescent-shaped ciliated area (meniscotroch or acrotroch) bearing a tapered falciform brush with long flagella. (3) Metatrochophore 4 weeks old (dorsal side). L = 400 µm. (4) Metatrochophore 7 weeks old with six chaetigerous segments. The four anterior buds announce the prostomial antennae. (5) Erpochaete 8 weeks old (dorsal side). L = 1 mm, 8 chaetigers. (6) Right parapodium of the middle segment. (7) Young worm 2 months old (dorsal side). L = 1.2 mm. (8) Jaw at the same stage. (9) Left middle parapodium of a young 2 months old worm (Bhaud and Cazaux 1987). B, *Glycera capitata* Ørsted, 1842 (= *Glycera lapidum* Quatrefages, 1866), metatrochophore. ac, anal cirri; an, prostomial appendage; p, prototroch; pa, parapodia under construction (Husemann 1992). C, *Glycera capitata* Ørsted, 1842 (= *Glycera lapidum* Quatrefages, 1866), Erpochaeta with nine segments. ac, anal cirri; an, prostomial appendages; dc, dorsal cirrus; p, prototroch; ps, prechaetal lobe (Husemann 1992).

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Böggemann et al. 2011, 2012). It might be possible that the same species can change between the semisessile and the motile way of life. Gardiner (1976) mentioned that the hesionid *Gyptis brevipalpa* live commensal in the burrows of *Glycera robusta*. Studies on feeding and examination of stomach contents suggested that the majority are predators, which prefer moving prey, such as small polychaetes and crustaceans (Blegvad 1914, Hunt 1925, Mare 1942, Yonge 1954, Retière 1967, MacGinitie and MacGinitie 1968, Michel 1970, Ockelmann and Vahl 1970, Evans 1971, Pearson 1971, Ronan 1977, Fauchald and Jumars 1979, Ambrose 1984a, b, Gambi and Giangrande 1985, Jumars et al. 2015). However, some taxa might be detritivorous (Stolte 1932a, Klawe and Dickie 1957, Sanders et al. 1962, Banse and Hobson 1968), being capable of feeding on fecal pellets (Frankenberg and Smith 1967) or absorb dissolved organic matter (Preston and Stephens 1969, Chien et al. 1972, Southward and Southward 1972, Stephens 1972, Van Pilsum et al. 1975, Stevens and Preston 1976, 1977, 1980a, b, c, Chien and Rice 1985, Qafaiti and Stephens 1988). The prey is grasped by a rapid eversion of the proboscis, killed by the venom, and swallowed whole. The proboscidial papillae, which are presumed to be mechanoreceptors, might be used for the location of the prey just before their capture and their mucous cells supporting the transfer to the digestive tract and protecting the proboscis from damage (Böggemann et al. 2000). Some authors (e.g., Stolte 1932a, Klawe and Dickie 1957, Ockelmann and Vahl, 1970, Vahl 1976) described the anus of the glycerids as nonfunctional because the proboscis regurgitates the undigested remains of the food. However, this feature cannot be verified by personal observations.

Glycerids themselves are predated by some birds (Brown 1993) as well as benthic fishes and crustaceans (Treadwell 1937). Stolte (1928) observed the regenerative capacity of glycerids as very low because the specimens die after losing body fragments. However, often individuals after loss of posterior segments subsequently regenerate a new tail (Böggemann 2002). Spawning specimens of *Glycera dibranchiata* are preyed upon by herring gulls and striped bass, whereas mud shrimps (Creaser 1973) consume spent epitokous stages. Furthermore, atoke stages are used as fish bait for sport and commercial fisheries (Klawe and Dickie 1957, Dow 1964, 1973, Taylor and Saloman 1968, Creaser et al. 1983, Wilson and Ruff 1988, Brown 1992, 1993, Olive 1994, Watson et al. 2016).

In addition to capturing prey, the proboscis also represents an efficient organ during the initial stage of burrowing (Stolte 1928, 1932b, Böggemann 2002, Murphy and Dorgan 2011). The worm projects its proboscis almost instantaneously into the sediment, when the prostomium encounters the natural habitat. The proboscis retracts and simultaneously the front part of the body is drawn into the emerging burrow. In contrast to the feeding behavior, the jaws were not exposed during the burrowing process (Böggemann 2002). Once in the sediment, the animal moves slowly through it by crawling and peristaltic/antiperistaltic movements of the body, the parapodia, and the retractable chaetae. Støp-Bowitz (1941) considered the fast burrowing as an escape response. This might be the same for the forward swimming described by Storch (1968). However, the epitokous stages of *Glycera dibranchiata* and *Glycera nicobarica* Grube, 1866 usually swim head first, propelled by lateral sinusoidal undulations of the body (Simpson 1962a, Ibrahim and Sato 2013). During backward swimming, the tail is first and uppermost and the head lowermost, and the individuals swim in an open "figure 8" (Stolte 1932a, b, Storch 1968, Röder and Röder 1974, 1975). Dean (1978) suggested that this migratory ability is a general phenomenon, and one that is not related to spawning. In contrast to the crawling and swimming movements, breathing is not correlated with locomotion. Stolte (1928, 1932b) distinguished between a slow and a fast breathing movement. He mentioned that the glycerids appear to be insensitive to H_2S and oxygen absence, but they are very sensitive to CO_2. In the presence of CO_2, the branchiae, if present, are extended and breathing begins.

Parasites. Endoparasitic gregarines (Protozoa: Sporozoa) are often found in the glycerids (Pixell-Goodrich 1916, Gunderson 1984) and sometimes also ectoparasitic nematodes (Fig. 7.13.4.1.9C, D; Fauvel 1936, McIntosh 1885, Böggemann 2002, Ibrahim and Sato 2013) and copepods (Ibrahim and Sato 2013) as well as probable commensal epibionts like Ciliophora and Cycliophora (Fig. 7.13.4.1.9A–C; Böggemann 2002). MacGinitie and MacGinitie (1968) reported that *Glycera robusta* Ehlers, 1868, common in regions of *Zostera*, often plays host to a species of a stalked, colonial protozoan of the genus *Zoothamnium*, which grows attached between the parapodia. These organisms are typically situated on the parapodia, and they partially resemble branchiae, which have lead to descriptions of new species (*Glycera manorae* Fauvel, 1932; *Glycera dentribranchia* Lee, 1984; *Glycera amadaiba* Imajima, 2003).

Reproduction and development

The sexes of glycerid species are separated, and they possess segmentally paired gonads (Simpson 1962b). Gametogenesis occurs in the coelom and requires about 1 year (Klawe and Dickie 1957). At the end of this stage, the bodies undergo varying degrees of alteration, and pelagic

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individuals develop from the previous atoke, benthic specimens. Metamorphosis is associated with more or less distinct morphological changes. The body become flattened, and the parapodia are partially enlarged and equipped with numerous elongated natatory chaetae, which obviously facilitate the swimming (Arwidsson 1899, McIntosh 1910, Augener 1928, Støp-Bowitz 1941, Simpson 1962a, Ockelmann and Vahl 1970, Ibrahim and Sato 2013). Sometimes simple capillary chaetae appear in the neuropodia (Arwidsson 1899, Augener 1925, Fage and Legendre 1927, Gravier and Dantan 1928, Støp-Bowitz 1941, Simpson 1962a, Ibrahim and Sato 2013). In most of the species, the morphological changes occur on almost all parapodia, whereas the epitokous stages of *Glycera brevicirris* Grube, 1870 have enlarged parapodia only in the posterior part of the body (Chamberlin 1919) or *Glycera tesselata* only in the midbody region (Gravier and Dantan 1928). Furthermore, an atrophy of the body musculature and the digestive tube often occurs, which makes the absorption of food impossible (Ehlers 1868, Arwidsson 1899, Augener 1928, Gravier and Dantan 1928, Simpson 1962a, Ockelmann and Vahl 1970, Ibrahim and Sato 2013). The bodies of sexually mature worms become distended by the fully developed gametes, which fill the body cavity and are visible through the thin body wall. These gametes are responsible for the characteristic colors of mature animals (females pale brown, males creamy) in contrast to the reddish color of immature specimens (Klawe and Dickie 1957). The males emitted streams of sperm while swimming slowly at the surface, whereas the females swam very rapidly at the surface and then suddenly shed up to 10 million eggs through the mouth or through ruptures in the body wall (Simpson 1962a). However, some epitokes of *Glycera nicobarica* shed their gametes through ventral pores at the parapodial base of the midbody (Ibrahim and Sato 2013). The release of male and female gametes happens at the same time, and the specimens typically die shortly thereafter (Klawe and Dickie 1957, "ghost worms"), although Creaser (1973) observed that some males dig themselves into the sediment after spawning. Most of the intertidal populations of *Glycera dibranchiata* spawn when 3 years old, but a small fraction spawn when 4 or 5 years old (Klawe and Dickie 1957, Creaser 1973). The spawning of *G. dibranchiata* occurs in the afternoon, between 2 hours before and 1 hour after high water (Creaser 1973). However, *G. nicobarica* was mostly collected in the evening within 2 hours after sunset, but without relation to tidal conditions or moon phases (Ibrahim and Sato 2013). The breeding period of species in a specific geographic area seems to be very constant (Arwidsson 1899, Chamberlin 1919, Augener 1928, Støp-Bowitz 1941, Allen 1957, Klawe and Dickie 1957, Simpson 1962a, Pettibone 1963, Lebskii 1970, Creaser 1973, Husemann 1992, Ibrahim and Sato 2013). Simpson (1962a) suggested that the water temperature is the decisive stimulus for spawning. The glycerid specimens spawn many small sperms (head diameter about 3 µm) or larger eggs (diameter about 140–160 µm), which are freely fertilized in the water column (external fertilization) (Simpson 1962a, Creaser 1973, Ibrahim and Sato 2013).

Only a few papers deal with the larval development of glycerids (Fuchs 1911, Thorson 1946, Klawe and Dickie 1957, Simpson 1962b, Cazaux 1967, Lebskii 1970, Blake 1975, Husemann 1992). Simpson (1962b), Cazaux (1967), and Rouse (2000) believe that the larvae are planktotrophic, whereas Lebskii (1970) suspected that they are lecithotrophic. The spherical trochophore larvae (Fig. 7.13.4.1.8A; length 115–450 µm) possess a prototroch with long cilia (Husemann 1992) and usually an additional acrotroch. In the early metatrochophora stages, segments become visible (Fig. 7.13.4.1.8A, B). On the episphere four appendages and on the pygidium two anal cirri appear. The parapodia first consist only of the neuropodia and a few compound chaetae. The erpochaeta (Fig. 7.13.4.1.8A, C; length 550–1100 µm), composed of seven to nine segments, has the typical annulated prostomium and pre- and postchaetal lobes together with ventral cirri on most of the parapodia. In the juvenile benthic stages, the prototroch is completely reduced, and most of the morphological changes are complete (Fig. 7.13.4.1.8A). At this developmental stage, feeding is possible (Husemann 1992). The trochophora develops about 1 day after fertilization, and the development to the erpochaeta requires a further 2 (Lebskii 1970) or 3 weeks (Husemann 1992). It is suspected that the larvae of *Glycera dibranchiata* either have a short planktonic existence or live close to the bottom, because they are never found in the water column (Klawe and Dickie 1957, Vadas and Bristow 1985).

Phylogeny and taxonomy

Glycera unicornis Lamarck, 1818 was the first described species of the genus *Glycera*. Assuming that this taxon now has jaws, it was placed by Savigny (1822, 1826) in the "Néréides Glycériennes," which also included the genera *Aricia* (= *Orbinia), Hesione, Myriana* (= Phyllodocidae), *Ophelia*, and *Phyllodoce*. Based on the same interpretation, Blainville (1825) placed *Glycera* and *Proboscidea* Lesueur in the "Néréides Proboscidées ou non dentées." Audouin and Milne Edwards (1833) combined *Glycera* with *Goniada* and *Nephtys* in the "Néréidiens non tentaculés." Örsted (1843) followed this scheme, but he created the "Division Glycereæ" for these three genera. Grube (1850, 1851) formally established the family Glyceridae as

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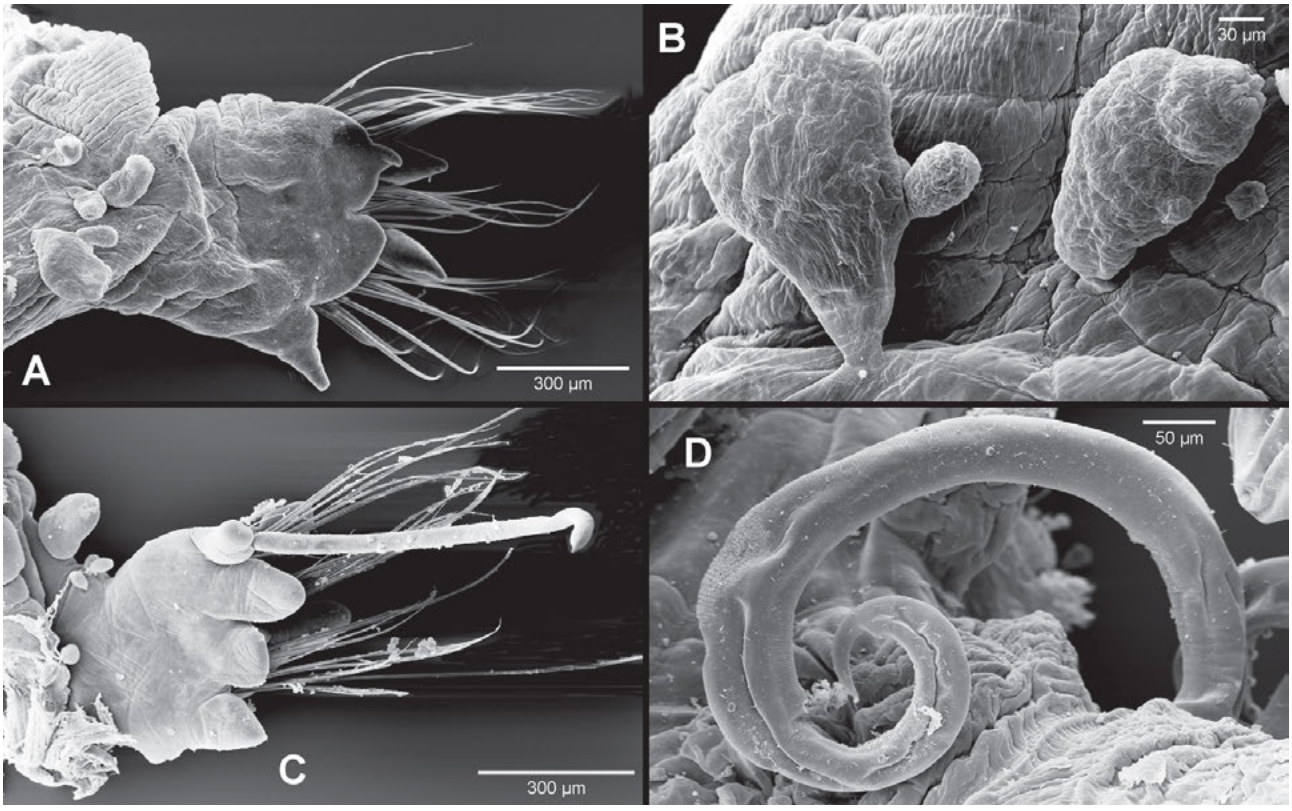


Fig. 7.13.4.1.9: SEM micrographs. A, *Glycera pseudorobusta* Böggemann and Fiege, 2001, parapodium with Cycliophora, posterior view (Böggemann 2002). B, Cycliophora (Böggemann 2002). C, *Glycera tridactyla* Schmarda, 1861, parapodium with ciliates and nematode, posterior view (Böggemann 2002). D, Nematode on *Glycera lamelliformis* McIntosh, 1885 (Böggemann 2002).

"Glycerea," including the two genera *Glycera* and *Goniada*. Kinberg (1865) pointed out the distinguishing characters between glycerids and goniadids and established the separate family Goniadidae (as Goniadea). The independence of these two families was controversial for a long time (Ehlers 1868, Fauvel 1923), until Hartman (1950) described their clear differences. Nevertheless, some subsequent authors (e.g., Day 1967, Rullier 1972) chose to align with Fauvel (1923) and resurrected the subfamilies Glycerinae and Goniadinae. Today, the independent nature of the two families is not really in doubt, but they are grouped together by Rouse and Pleijel (2001) to the monophyletic group Glyceriformia Fauchald, 1977, because of their uniqueness and great morphological similarity. This taxon name was established by Fauchald (1977) but originally included also the family Lacydoniidae (Rouse and Pleijel 2001).

The results of cladistic analyses based on morphological data (Böggemann 2006) confirmed the sister-group relationship of Glyceridae and Goniadidae, as proposed by Böggemann (2002, 2005). The monophyly of the sister groups is well supported by autapomorphies in the structure of the jaws (see above), the proboscidial papillae, and the ciliation pattern on the prostomium (Böggemann 2002, 2005). Glyceridae bear soft, partly keratinized proboscidial papillae with prominent intracellular ciliary rootlets (Fig. 7.13.4.1.7A, B; Böggemann et al. 2000), and Goniadidae usually sclerotized papillae without rootlets (Fig. 7.13.4.2.5A, B; Böggemann and Purschke 2006). Additionally, glycerids carry more or less distinct dorsal and ventral ciliated rings on the prostomium (Fig. 7.13.4.1.3C), in contrast to goniadids, where the cilia are concentrated in laterodorsal and lateroventral depressions (Fig. 7.13.4.2.2D; Böggemann 2005, 2006). However, in analyses using morphological and molecular data (Worsaae et al. 2005) or exclusively molecular data (Rousset et al. 2007, Struck et al. 2007, Böggemann 2009, Ravara et al. 2016), glycerids and goniadids alternatively resulted as distinctly separated, as monophyletic clades with a sister-group relationship, or with a monophyletic Glyceridae nested within a paraphyletic Goniadidae. Nevertheless, the great morphological similarities suggested a close relationship and might not be the result of a convergent evolution. A recent study using Illumina sequencing technology highly supported the previously postulated sister-group relationship and the monophyletic status of Glyceriformia (Richter et al. 2015).

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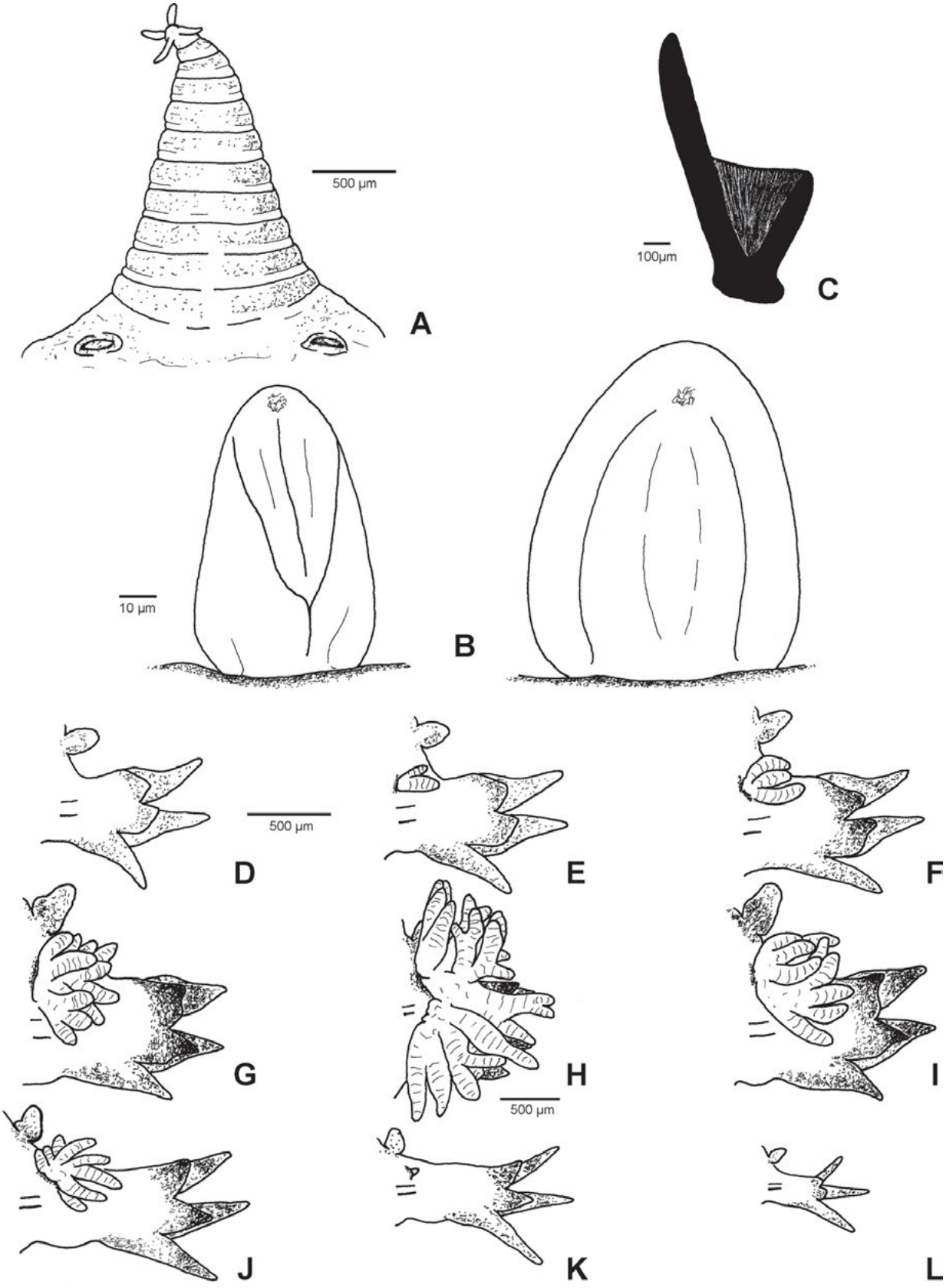


Fig. 7.13.4.1.10: *Glycera ovigera* Schmarda, 1861. A, Prostomium, dorsal view. B, Proboscidial papillae, posterior view. C, Aileron. D–L. Anterior to posterior parapodia, posterior view (Böggemann 2002).

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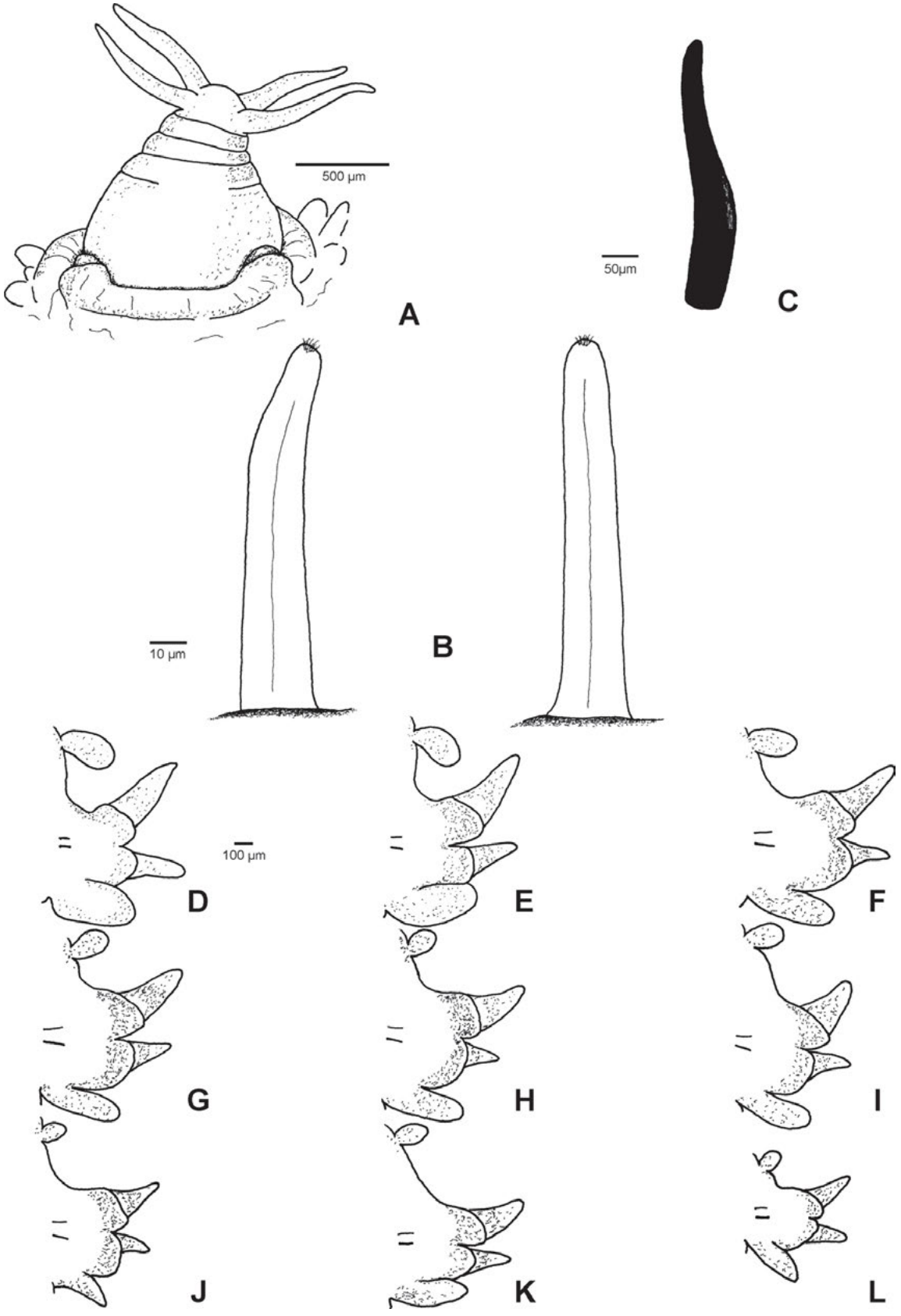


Fig. 7.13.4.1.11: *Glycerella magellanica* (McIntosh, 1885). A, Prostomium, dorsal view. B, Proboscidial papillae, posterior view. C, Aileron. D–L, Anterior to posterior parapodia, posterior view (Böggemann 2002).

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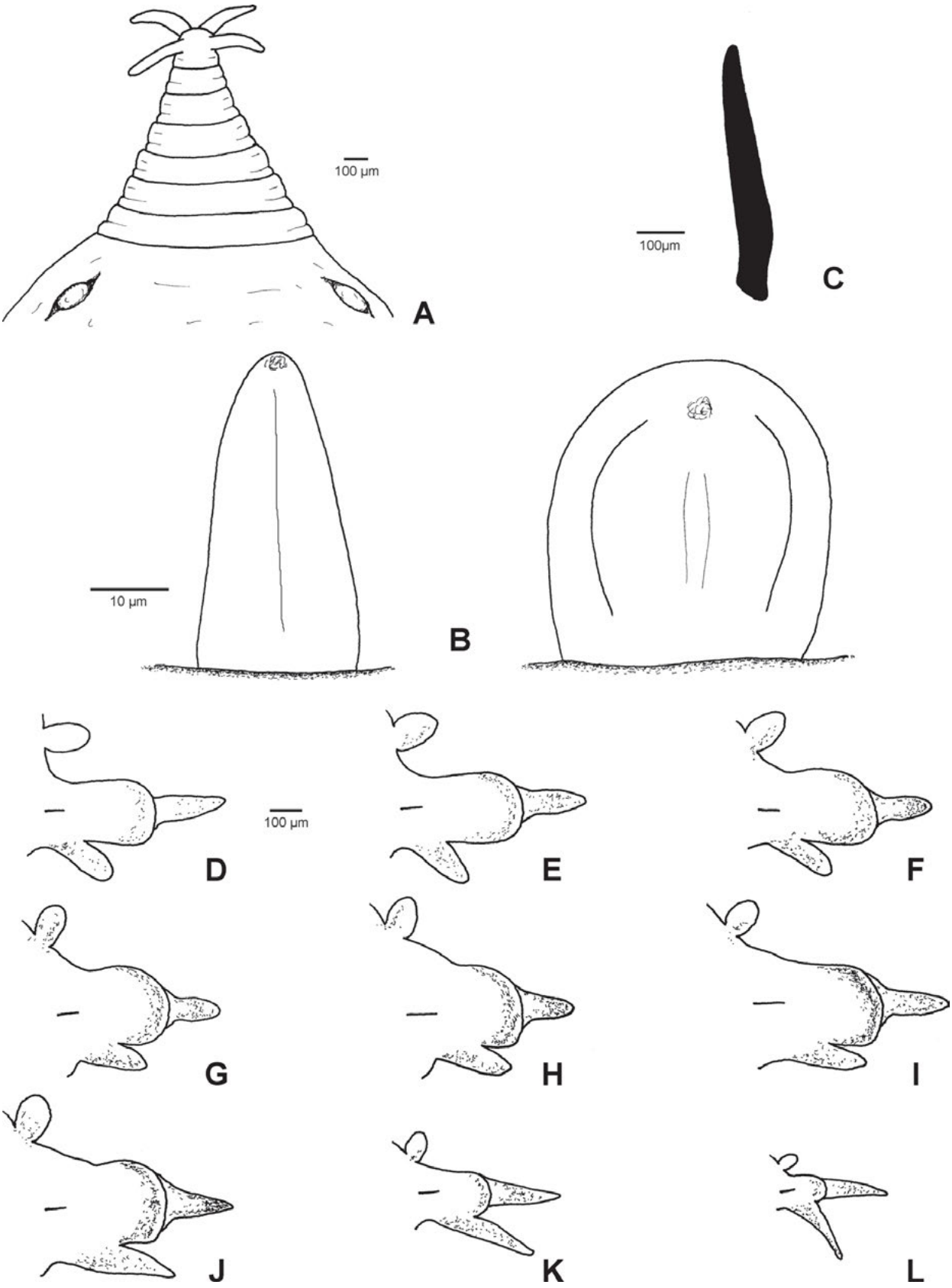


Fig. 7.13.4.1.12: *Hemipodia simplex* (Grube, 1857). A, Prostomium, dorsal view. B, Proboscidial papillae, posterior view. C, Aileron. D–L, Anterior to posterior parapodia, posterior view (Böggemann 2002).

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A few genera have been attributed to the Glyceridae during the taxonomic history (*Proboscidea* Blainville, 1825; *Hemipodia* Kinberg, 1865; *Hemipodus* Quatrefages, 1866; *Rhynchobolus* Claparede, 1868; *Euglycera* Verrill, 1881; *Glycera* Lamarck, 1818; *Glycerella* Arwidsson, 1899; *Hamiglycera* Ehlers, 1908; *Telake* Chamberlin, 1919; †*Paranereites* Eisenack, 1939). Today the family only consists of the genera *Glycera, Glycerella*, and *Hemipodia*, which show clear differences in several diagnostic characters: *Glycerella* has an autapomorphic short prostomium consisting of four rings (Fig. 7.13.4.1.11A), one type of proboscidial papillae (Fig. 7.13.4.1.11B), and spinigerous as well as falcigerous compound chaetae, which is a plesiomorphic character also present in some goniadids. *Glycera* and *Hemipodia* are sister groups, based on the different types of proboscidial papillae (Figs. 7.13.4.1.10B and 7.13.4.1.12B), a prostomium with more than five rings (Figs. 7.13.4.1.10A and 7.13.4.1.12A) and only neuropodial spinigers. Notopodia and their capillary chaetae have been lost in *Hemipodia* (Fig. 7.13.4.1.12D–L), and rodlike ailerons are present (Fig. 7.13.4.1.12C), as in *Glycerella* (Fig. 7.13.4.1.11C), but a defining morphological apomorphy is not known, whereas more complicated ailerons, with outer and inner ramus and sometimes an interramal plate (Figs. 7.13.4.1.1E, 7.13.4.1.2C, 7.13.4.1.5C, and 7.13.4.1.10C), are an autapomorphic character developed within the genus *Glycera* (Böggemann 2002, 2006).

A worldwide revision of the family Glyceridae is provided by Böggemann (2002), which recognize 42 nominal species as valid (36 in *Glycera*, 1 in *Glycerella*, and 5 in *Hemipodia*). Recent regional studies described 10 additional species of the genus *Glycera* (*Glycera amadaiba* Imajima, 2003 from Japan; *Glycera boeggemanni* Rizzo, Steiner & Amaral, 2007 from Brazil; *Glycera diva* Böggemann, 2009 from Angola and Guinea Basins; *Glycera juliae* Magalhães & Rizzo, 2012 from Mariana Islands; *Glycera neorobusta* Imajima, 2009 from Japan; *Glycera noelae* Böggemann, Bienhold & Gaudron, 2011 from eastern Mediterranean Sea; *Glycera okai* Imajima, 2009 from Japan; *Glycera semibranchiopoda* Imajima, 2009 from Japan; *Glycera sheikhmujibi* Hossain & Hutchings, 2020 from Bangladesh; and *Glycera southeastatlantica* Böggemann, 2009 from Angola, Cape, and Guinea Basins). However, *G. amadaiba* seems to be a synonym of *Glycera brevicirris*, with epibionts believed by Imajima (2003) to be branchiae. *Glycera juliae* might be a synonym of *Glycera nicobarica* because some of the SEM pictures supposed that the conical papillae have three not well-preserved U-shaped ridges on their posterior surface and not a straight, median, longitudinal ridge as described by Magalhães and Rizzo (2012). *Glycera sheikhmujibi* also seems to be a synonym of *G. nicobarica*, but the original description by Hossain and Hutchings (2020) is unfortunately too imprecise on some points (e.g., shape and position of branchiae). The parapodial shapes differ during developmental age, and therefore the mammiform pre- and postchaetal lobes mentioned by Imajima (2009) for *G. neorobusta* do not separate this taxon from *G. robusta*. *Glycera okai* might be a synonym of *Glycera knoxi* Kirkegaard, 1995, in which the oval to globular papillae without ridges has been possibly overlooked. Imajima (2009) distinguished *G. semibranchiopoda* from *Glycera branchiopoda* Moore, 1911 because of the shorter notopodial prechaetal lobes. However, as noted, some specimens of the later taxon do not always have these structures distinctly elongated (Böggemann 2002). Therefore, these six species are presumed to be not valid and so only 40 recent nominal species of the genus *Glycera* appear to be present; however, for a final assessment, the type material is needed to clarify their status.

In addition to the recent taxa, three fossil species are described for the glycerids: †*Paranereites balticus* Eisenack, 1939; †*Glycera glaucopsammensis* Charletta & Boyer, 1974; and †*Glycera pilicae* Szaniawski, 1974, which are only known from their scolecodonts. These are fossilized elements of the proboscidial armatures of polychaetes (Jansonius and Craig 1971, Szaniawski 1996). The oldest ones exist from the Late Permian-Triassic (around 270–250 million years ago), and their general structure is exactly the same as in jaws of recent taxa (Kozur 1971, Charletta and Boyer 1974, Szaniawski 1974, Mierzejewska and Mierzejewski 1977, Szaniawski and Wrona 1987, Nakrem et al. 2001, Bergman and Eriksson 2003). Typical ailerons were first reported from the Jurassic age, but they are smaller and more fragile than the jaws and have probably been previously overlooked (Szaniawski 1974).

Glyceridae Grube, 1850

Type genus: *Glycera* Lamarck, 1818: 314

Synonyms: Glycerea Grube, 1850: 309 [partim]
Glyceraceæ — Johnston 1865: 184 [partim]
Glycerea — Kinberg 1865: 244
Glyceridæ — Malmgren 1867: 183

Diagnosis: Body with numerous segments (up to 548), elongated, tapering at both ends (Fig. 7.13.4.1.1A–D). Segments bi- or triannulate (Figs. 7.13.4.1.2A and 7.13.4.1.3A). Prostomium conical, mostly pointed, distinctly annulated; anteriormost annulus with four appendages, anterior pair situated terminolaterally and posterior pair more dorsolaterally; posteriormost annulus with one pair of nuchal organs; most remaining annuli with more or less distinct dorsal and ventral ciliated rings on each side of prostomium; eyes absent (Figs. 7.13.4.1.2A, 7.13.4.1.3A, B, C, D, 7.13.4.1.10A, 7.13.4.1.11A, and 7.13.4.1.12A). Proboscis long,

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cylindrical to club shaped, muscular (Figs. 7.13.4.1.1B, D and 7.13.4.1.2A), densely covered with numerous papillae bearing specialized structures on their posterior sides (Figs. 7.13.4.1.2A, 7.13.4.1.7A, 7.13.4.1.10B, 7.13.4.1.11B, and 7.13.4.1.12B); tip of fully everted proboscis with terminal soft papillae and four dark, hooklike curved jaws, each with a rodlike, more or less triangular or deeply incised aileron (Figs. 7.13.4.1.1E, 7.13.4.1.2A, C, 7.13.4.1.5A–C, 7.13.4.1.10C, 7.13.4.1.11C, and 7.13.4.1.12C). Usually, the first two parapodia uniramous, consisting of neuropodia, ventral cirri, and compound chaetae only; following parapodia, uni- or biramous with dorsal and ventral cirri; largest parapodia in midbody region; in biramous parapodia, notopodia and neuropodia indistinctly separated from each other; each biramous parapodium with two prechaetal and one or two postchaetal lobes (Figs. 7.13.4.1.2B, 7.13.4.1.10D–L, 7.13.4.1.11D–L, and 7.13.4.1.12D–L). Branchiae present or absent, blisterlike to simple digitiform or branched, retractile in some species; located on different parts of parapodia (Figs. 7.13.4.1.2B and 7.13.4.1.10E–K). Noto- and neuropodia each with a single acicula (Fig. 7.13.4.1.2B); notopodia with simple capillaries, neuropodia usually with spinigerous compound chaetae only. Pygidium with a dorsal anus and a terminal pair of slender elongated anal cirri (Figs. 7.13.4.1.8A, C).

Glycera Lamarck, 1818

Type species: *Glycera unicornis* Lamarck, 1818: 315
Synonyms: *Glyceres* Peters in Bianconi, 1862: 477
Rhynchobolus Claparède, 1868: 492
Euglycera Verrill, 1881: 296
Hamiglycera Ehlers, 1908: 105
Telake Chamberlin, 1919: 345
†*Paranereites* Eisenack, 1939: 169
Diagnosis: Segments bi- or triannulate. Prostomium consisting of more than five rings, appendages relatively short (Figs. 7.13.4.1.2A, 7.13.4.1.3A, D, and 7.13.4.1.10A). Each aileron with a more or less triangular or deeply incised base (Figs. 7.13.4.1.1E, 7.13.4.1.2C, 7.13.4.1.5C, and 7.13.4.1.10C). Usually, the first two parapodia uniramous, consisting of neuropodia, ventral cirri, and compound chaetae only; following parapodia biramous with dorsal and ventral cirri; notopodia and neuropodia indistinctly separated from each other; each parapodium with two prechaetal and one or two postchaetal lobes (Figs. 7.13.4.1.2B and 7.13.4.1.10D–L). Branchiae present or absent, blisterlike to simple digitiform or branched, retractile in some species; located on different parts of parapodia (Figs. 7.13.4.1.2B and 7.13.4.1.10E–K). Notopodia with simple capillaries, neuropodia usually with spinigerous compound chaetae only.

Glycerella Arwidsson, 1899

Type species: *Glycerella magellanica* (McIntosh, 1885): 349
Synonym: *Pseudolacydonia* Rullier, 1964: 150
Diagnosis: Segments triannulate. Prostomium consisting of four rings, appendages relatively long (Fig. 7.13.4.1.11A). Ailerons rodlike (Fig. 7.13.4.1.11C). First two parapodia uniramous, consisting of neuropodia, ventral cirri and compound chaetae, dorsal cirrus from the second parapodium; following parapodia biramous with dorsal and ventral cirri; notopodia and neuropodia indistinctly separated from each other; each parapodium with two prechaetal and two postchaetal lobes (Fig. 7.13.4.1.11D–L). Branchiae absent. Notopodia with simple capillaries, neuropodia in the upper part with spinigerous and in the lower part with falcigerous compound chaetae.

Hemipodia Kinberg, 1865

Type species: *Hemipodia simplex* (Grube, 1857): 177
Synonyms: *Hemipodus* Quatrefages, 1866: 194
Diagnosis: Segments more or less distinctly triannulate. Prostomium consisting of more than five rings, appendages relatively short (Fig. 7.13.4.1.12A). Ailerons rodlike (Fig. 7.13.4.1.12C). All parapodia uniramous, with one prechaetal and one postchaetal lobe; ventral cirri from first, dorsal cirri from third parapodium (Fig. 7.13.4.1.12D–L). Branchiae absent. Notopodia absent, neuropodia with spinigerous compound chaetae.

Acknowledgments

The author thanks Eginhard Husemann, Jens Koldehoff, and Monika C.M. Müller for the use of some figures from their publications.

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Markus Böggemann

7.13.4.2 Goniadidae Kinberg, 1865

Introduction

The Goniadidae Kinberg, 1865 and the very similar Glyceridae Grube, 1850 (see chapter 7.13.4.1) are treated together as Glyceriformia Fauchald, 1977, a monophyletic clade within the Phyllodocida (Rouse and Pleijel 2001). The pointed, usually annulated prostomium with two pairs of terminal appendages (Figs. 7.13.4.2.1A, 7.13.4.2.2A, B, D, 7.13.4.2.3A, 7.13.4.2.7A, 7.13.4.2.9A, 7.13.4.2.10A, 7.13.4.2.11A, 7.13.4.2.12A, 7.13.4.2.13A, 7.13.4.2.14A, 7.13.4.2.15A, and 7.13.4.2.16A), and long, muscular, eversible axial proboscis (Figs. 7.13.4.2.1B and 7.13.4.2.2A, B), which is densely covered with papillae (Fig. 7.13.4.2.2A, B) and provided with terminal jaws (Figs. 7.13.4.2.1B, C, 7.13.4.2.2F, and 7.13.4.2.3C), are unique characters among the Annelida (Böggemann 2006). However, both groups can be clearly separated from each other, especially by the proboscidial armature. Goniadids usually have two macrognaths and a variable number of dorsal and ventral micrognaths and sometimes additional longitudinally arranged rows of V-shaped chevrons on each side of the proboscis (Figs. 7.13.4.2.1C, 7.13.4.2.2E, F, 7.13.4.2.3B, C, 7.13.4.2.11D, and 7.13.4.2.16D), whereas the four similar jaws of the glycerids are hook-shaped with an accessory lateral aileron (Figs. 7.13.4.1.1E, 7.13.4.2.2C, and 7.13.4.2.5A; Böggemann 2002, 2005).

The Goniadidae have a worldwide distribution from intertidal to abyssal depths (Böggemann 2005, 2009). They are generally considered to be motile endopsammal benthic predators, which construct nonpermanent burrows and capture prey with their jaws (Fauchald and Jumars 1979, Mattson 1981). Even when they constitute a significant component of soft bottom benthic communities worldwide, their diversity and distribution are still poorly documented in many regions (Böggemann 2009).

Within Goniadidae, there are currently 65 recognized nominal species, with 5 in the genus *Bathyglycinde* Fauchald, 1972; 12 in *Glycinde* F. Müller, 1858; 31 in *Goniada* Audouin & Milne Edwards, 1833; 6 in *Goniadella* Hartman, 1950; 5 in *Goniadides* Hartmann-Schröder, 1960; 3 in *Goniadopsis* Fauvel, 1928; 1 in *Ophiogoniada* Böggemann, 2005; and 2 in *Progoniada* Hartman, 1965.

Morphology

External morphology

Size. The Goniadidae are slender, cylindrical polychaetes that can reach considerable sizes (up to 80 cm long). The body is elongate, tapering at both ends and consists of numerous uni-, bi-, or triannulate segments (Fig. 7.13.4.2.1A, B). Species of the genus *Goniadopsis* are described with tubercles on some of their anterior segments (Böggemann 2005).

Color. The integument is slightly transparent and has a thick whitish, yellowish, brownish, or blackish cuticle usually with a distinctly iridescent sheen (Fig. 7.13.4.2.1A, B; Böggemann 2005). After Böggemann (2005), fixed specimens usually have a more or less conspicuous uniform pigmentation: the dorsum of anterior segments has two lateral and one median dark spot, which might be further

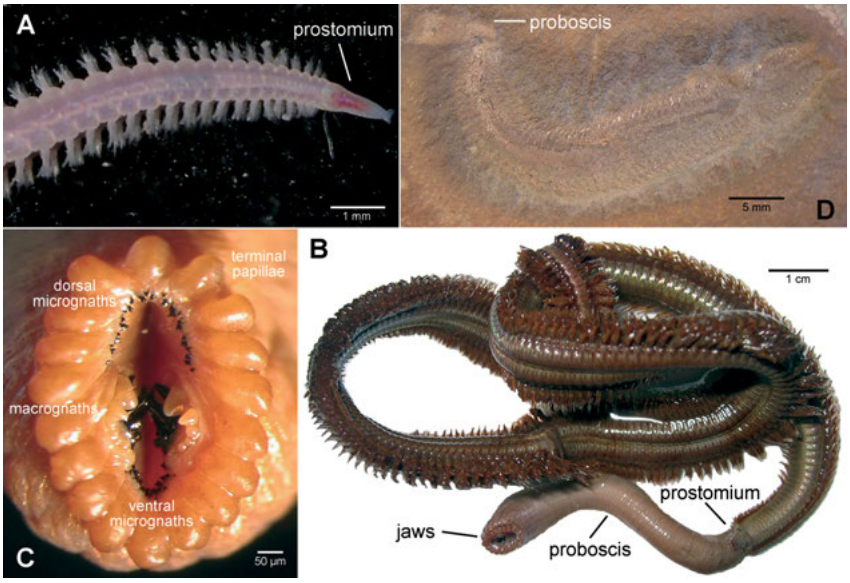


Fig. 7.13.4.2.1: A, *Goniada vorax* (Kinberg, 1865), anterior end of living specimen, dorsal view (Böggemann 2007). B, *Goniada gigantea* (Verrill, 1885), preserved specimen with everted proboscis (© M. Böggemann). C, Terminal part of proboscis, frontal view (© M. Böggemann). D, Whole body fossil of †*Pieckonia helenae* Thompson, 1979 with partly everted proboscis (Böggemann 2006, 2007).

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separated, whereas the ventral surface is more or less completely dark pigmented. Posterior segments have two more transverse curved bands on the dorsum, whereas on the ventral surface additional small dark dots or lines are present which are located intersegmentally in the median groove. The ventral pigmented dots of posterior segments are sometimes erroneously misinterpreted as neural eyespots (Moore 1911, Southern 1921). Dorsal cirri, ventral cirri, notopodial lobes, and neuropodial lobes have dark pigmentation, especially on the tips of the lobes. The rings of the prostomium and the pygidium with anal cirri also have darker pigmentation compared to the rest of the body. This pattern is often not well preserved, and therefore the specimens appear to be mottled or even pale. However, some species (e.g., *Goniada brunnea* Treadwell, 1906) are more or less completely dark brown to black with larger specimens the darkest. The segments of *Goniada echinulata* Grube, 1870 usually have an unique pattern of three longitudinal rows of large ovoid to rounded spots on the dorsal and ventral sides of the body, and especially in some smaller species (e.g., *Goniadella*, *Goniadides*, *Progoniada*) only the dorsal cirri, ventral cirri, and prechaetal lobes have pigmentation (Böggemann 2005).

Prostomium. The Goniadidae are easily recognized by their pointed, usually annulated prostomium (Figs. 7.13.4.2.1A, 7.13.4.2.2A, 7.13.4.2.3A, 7.13.4.2.10A, 7.13.4.2.11A, 7.13.4.2.12A, 7.13.4.2.13A, 7.13.4.2.14A, 7.13.4.2.15A, and 7.13.4.2.16A). Only

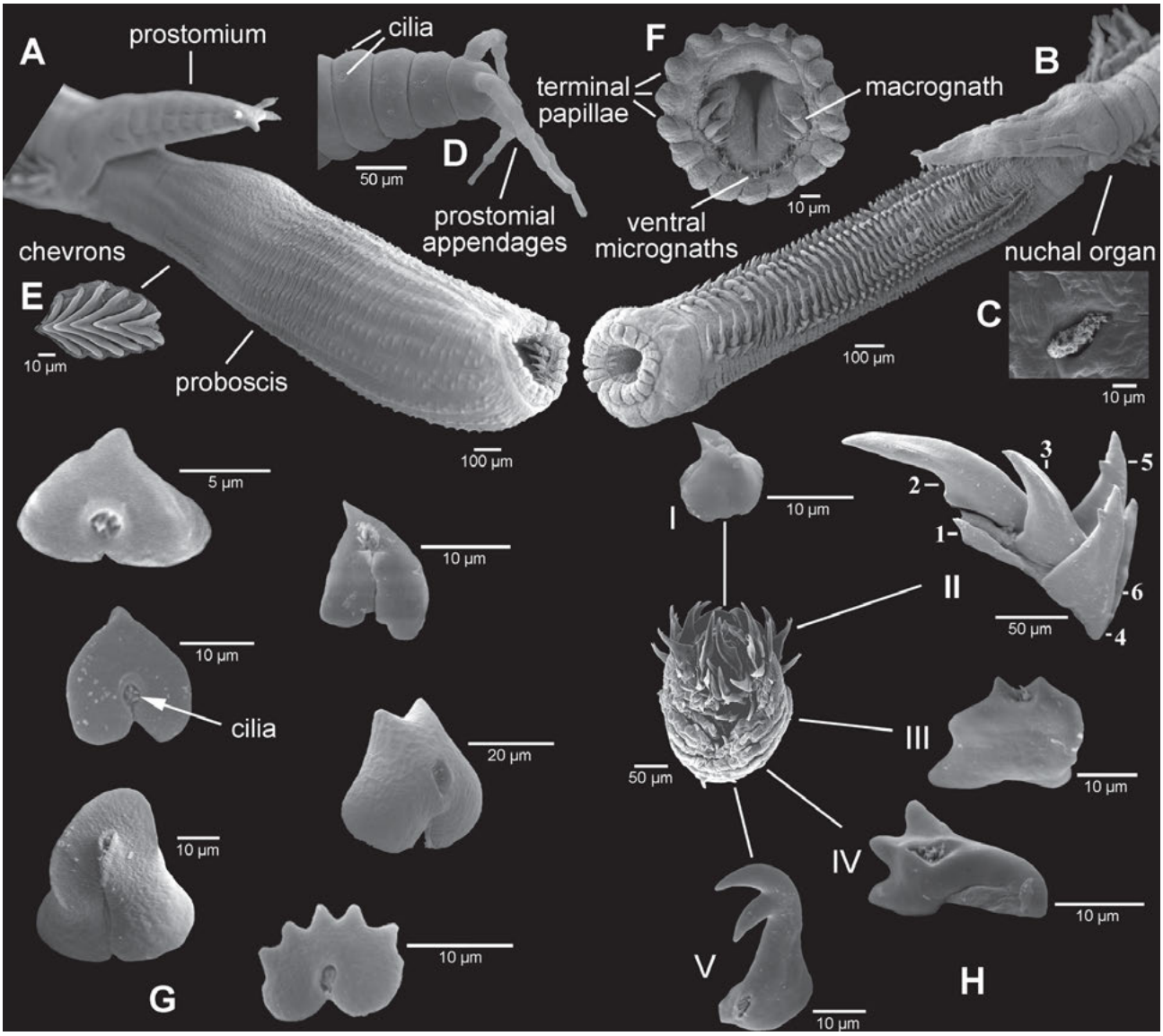


Fig. 7.13.4.2.2: SEM micrographs. A, *Goniada maculata* Örsted, 1843, anterior end, lateral view. B, *Glycinde multidens* F. Müller, 1858, anterior end, dorsal view. C, Nuchal organ. D, *Goniadides falcigera* Hartmann-Schröder, 1962, terminal part of prostomium, lateroventral view. E, *Goniada hexadentes* Böggemann & Eibye-Jacobsen, 2002, chevrons. F, *Goniada antipoda* Augener, 1927, terminal part of proboscis, frontal view. G, *Goniada* sp., different types of proboscidial papillae. H, *Glycinde* sp., different types of proboscidial papillae (Böggemann 2005).

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Goniada congoensis Grube, 1877; *Goniada foliacea* Moore, 1903; and the species of the genus *Bathyglycinde* have secondarily a smooth or indistinctly annulated prostomium (Figs. 7.13.4.2.2B and 7.13.4.2.9A; Böggemann 2005). According to Orrhage (1999), most of the prostomial rings are equivalent to fused palps and the two pairs of terminal appendages are outgrowths from the prostomium and therefore structures without direct equivalents in other polychaete families. These four appendages are usually articulated (Fig. 7.13.4.2.2D, 3A), except for the species of *Goniadopsis*, which only have simple appendages (Fig. 7.13.4.2.14A). The posterior part of the prostomium bears one pair of nuchal organs (Fig. 7.13.4.2.2C), which can be retracted by special muscles (Storch and Schlötzer-Schrehardt 1988) and seem to be chemoreceptors (Whittle and Zahid 1974). Most of the prostomial rings between the basal and the terminal part are provided with a pair of ciliated laterodorsal and lateroventral depressions on each side of the prostomium (Fig. 7.13.4.2.2D), which are even present in taxa without distinct annulation (Böggemann 2005). Ehlers (1901) and Perkins (1980) suggested that these organs are sensory in function. In some species of goniadids, a subdistal and/or basal pair of subdermal eyes may be present (Figs. 7.13.4.2.12A, 7.13.4.2.13A, and 7.13.4.2.14A), which may be hidden by the integument, lost in adult specimens or sometimes disappear during fixation (Böggemann 2005).

Pharynx. The Goniadidae have a symmetrically developed axial pharynx (Figs. 7.13.4.2.1B and 7.13.4.2.2A, B) with a strong muscular region, which is typical for the Phyllodocida (Dales 1962). This type of pharynx is often greatly protrusible in the goniadids (up to one-fourth or one-third of the whole body length) and in such cases called a proboscis (Dales 1962, Purschke 1988, Saulnier-Michel 1992), which is innervated by the stomatogastric nervous system (Michel and DeVillez 1978).

The distal armature of the proboscis consists of a circlet composed of two macrognaths and/or a different number of ventral and/or dorsal micrognaths (Figs. 7.13.4.2.1B, C, 7.13.4.2.2F, 7.13.4.2.3C, 7.13.4.2.9C, 7.13.4.2.10C, 7.13.4.2.11C, 7.13.4.2.13B, 7.13.4.2.15B, C, and 7.13.4.2.16C; Böggemann 2005). Species-specific differences in the finer structures of the jaws are not significant and therefore not of use in the separation of species or even genera (Böggemann 2005). These solid elements of the jaws are mostly brown to black and composed of tanned proteins (Gibbs and Bryan 1980a) and embedded calcium and magnesium (Gibbs and Bryan 1980b) together with low levels of aluminum (Böggemann 2005). The additional lateral rows of V-shaped chevrons (Figs. 7.13.4.2.2E, 7.13.4.2.3B, 7.13.4.2.11D, and 7.13.4.2.16D), which are present on almost all species of the genera *Goniada*, *Goniadella*, and *Progoniada*, contained large concentrations of iron (Fig. 7.13.4.2.4; Böggemann 2002, 2005).

In addition to the jaw apparatus, the proboscis of the goniadids has terminally a ring of larger soft papillae (Figs. 7.13.4.2.1B, C and 7.13.4.2.2A, B, F) and each one containing either a row of sensory cells (Retzius 1902) or freely terminating nerve fibers (Wallengren 1901). Stolte (1932) suggested that these papillae in the similar glycerids are mechanoreceptors, which are responsible for raising the

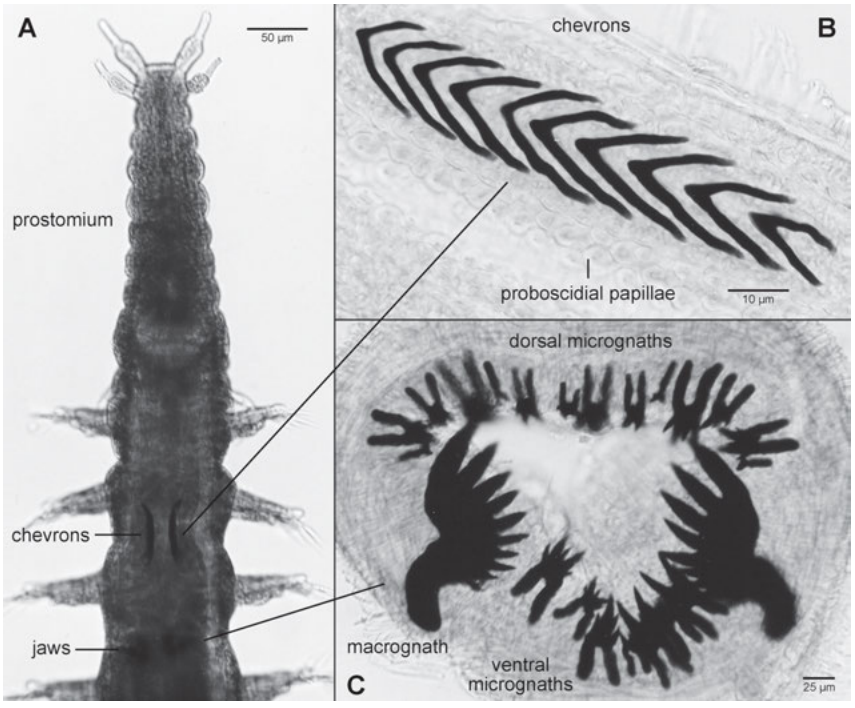


Fig. 7.13.4.2.3: A, *Goniada* sp., anterior end, dorsal view (Böggemann 2005). B, *Goniada* sp., chevrons (Böggemann 2007). C, *Goniada multidentata* Arwidsson, 1899, ring of macro- and micrognaths (Böggemann 2005).

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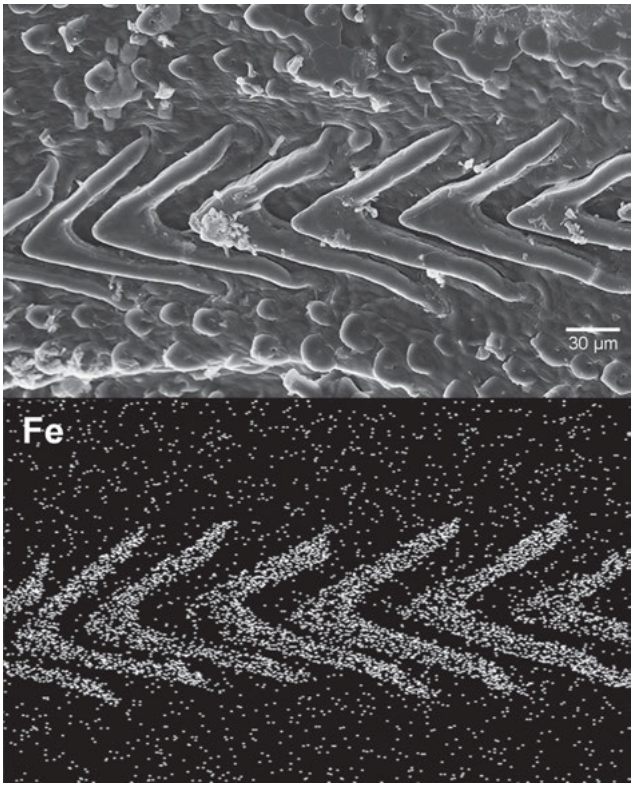


Fig. 7.13.4.2.4: *Goniada maculata* Örsted, 1843, SEM micrograph of chevrons and the iron (Fe) dot map after X-ray microanalysis (Böggemann 2006).

jaws during prey capture. Usually, 18 terminal papillae are present, which correspond to the 18 longitudinal nerves found in the proboscis (Hartman 1950). From the longitudinal nerves, fibers spread outward to form the peripheral nerve plexus that is correlated with the proboscidial papillae (Wallengren 1901). These papillae are numerous and densely cover the sheath of the proboscis (Figs. 7.13.4.2.2A, B, G, H and 7.13.4.2.3B; Böggemann 2005). They are usually hard and thickened sclerotized structures that reveal subapical, cuplike depressions containing tufts of short cilia (Figs. 7.13.4.2.2G, H and 7.13.4.2.5A, Smith et al. 1995). However, a few papillae are without cilia and some species of the genus *Bathyglycinde* carry additional soft papillae with hardened terminal fingernail-like structures, which are also present in some glycerids (Böggemann 2005). The proboscis of *Goniada*, *Goniadella*, *Goniadopsis*, *Ophiogoniada*, and *Progoniada* species is usually densely covered with a few different types of papillae of small size, which are arranged irregularly or in more or less regular longitudinal rows (Figs. 7.13.4.2.2A, 7.13.4.2.11B, and 7.13.4.2.16B; Böggemann 2005). By contrast, the species of *Bathyglycinde*, *Glycinde*, and *Goniadides* are provided with several different types of papillae (Hartman 1950, Hubendick 1952, Smith et al. 1995, Böggemann 2005, Böggemann and Purschke 2006), which are arranged in distinct longitudinal rows and grouped into well-defined areas (Figs. 7.13.4.2.2B, H, 7.13.4.2.9B, and 7.13.4.2.10B). The external appearance of the sclerotized proboscidial papillae is quite different, but their cellular structure is more or less homogeneous and composed of three or four cells: two secretory supporting cells and one or two multiciliated primary sensory cells, which are presumed to be mechanoreceptors (Fig. 7.13.4.2.5B; Böggemann 2005, Böggemann and Purschke 2006).

Peristomium. The peristomium is interpreted as being limited to the lips and segment one equals chaetiger one (Rouse and Pleijel 2001).

Parapodia and chaetae. The body of the Goniadidae is usually divided into an anterior region with uniramous parapodia and a following region with biramous or subbiramous parapodia (Figs. 7.13.4.2.1B, 7.13.4.2.9D–K, 7.13.4.2.10D–K, 7.13.4.2.11E–L, 7.13.4.2.12B–I, 7.13.4.2.13C–D, 7.13.4.2.14B–I, and 7.13.4.2.15D–J), except for *Progoniada*, which has uniramous parapodia along the entire body (Fig. 7.13.4.2.16E–L; Böggemann 2005). The change may be abrupt or a transitional middle region with gradually changing parapodia is present. In numerous species or some juvenile specimens, the first segment is apodous and achaetous, with only a pair of small lateral cirri (Figs. 7.13.4.2.3A, 7.13.4.2.9A, 7.13.4.2.11A, 7.13.4.2.12A, 7.13.4.2.13A, 7.13.4.2.15A, and 7.13.4.2.16A). Uniramous parapodia consist of a neuropodium with one or two prechaetal lobes and one postchaetal lobe, one acicula, and falcigerous and/or spinigerous compound chaetae (Fig. 7.13.4.2.6A). Biramous parapodia have an additional acicula bearing the well-separated notopodial ramus, which has a single lobe or is subdivided into one prechaetal and one postchaetal lobe and carry numerous finely spinulose capillaries, a few acicular chaetae, or in species of *Glycinde* stout and hooked chaetae with a terminal pointed hood (Figs. 7.13.4.2.6C, D and 7.13.4.2.10L). In the subbiramous parapodia, the notopodial lobes are absent and the notopodium is represented only by an acicula and a few acicular chaetae (Figs. 7.13.4.2.6B, 7.13.4.2.12D–H, and 7.13.4.2.13D, E). Furthermore, *Ophiogoniada lyra* (Granados-Barba & Solís-Weiss, 1997) has additional lyrate chaetae in a superior position on biramous chaetigers (Fig. 7.13.4.2.15L). Noto- and neuropodial prechaetal lobes are conical, triangular, or digitiform in shape and sometimes differ in length, whereas the postchaetal lobes are usually shorter and rounded, conical, triangular, or digitiform (Figs. 7.13.4.2.6A–D, 7.13.4.2.9D–K, 7.13.4.2.10D–K, 7.13.4.2.11E–L, 7.13.4.2.12B–I, 7.13.4.2.13C–D, 7.13.4.2.14B–I, 7.13.4.2.15D–J, and 7.13.4.2.16E–L). All parapodia have basally inserted dorsal and ventral cirri of mostly conical, triangular to digitiform shape (Figs. 7.13.4.2.6A–D, 7.13.4.2.9D–K, 7.13.4.2.10D–K,

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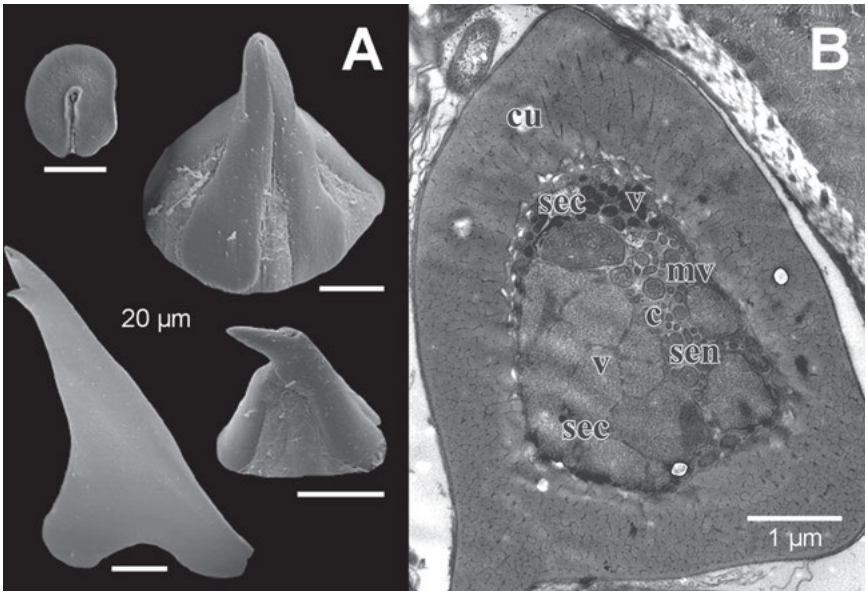


Fig. 7.13.4.2.5: A, SEM micrographs of different proboscidial papillae (Böggemann 2005); TEM micrograph. **B**, *Goniadides falcigera* Hartmann-Schröder, 1962, cross section through the subapical part of a papilla in area II. c, cilium; cu, cuticle; mv, microvilli; sec, secretory cell; sen, sensory cell; v, vesicles (Böggemann and Purschke 2006).

7.13.4.2.11E–L, 7.13.4.2.12B–I, 7.13.4.2.13C–D, 7.13.4.2.14B–I, 7.13.4.2.15D–J, and 7.13.4.2.16E–L). However, in a few *Goniada* species, foliaceous dorsal cirri are present (Fig. 7.13.4.2.6C), and in the species of *Goniadopsis*, some anterior chaetigers have elongated ventral cirri (Fig. 7.13.4.2.14C, D). Branchiae are absent in the Goniadidae, but the very long, more tongue-shaped notopodial lobes of large specimens of *Goniada vorax* (Kinberg, 1865) could be interpreted as such structures. The parapodial lobes of juveniles may be divergent from those of adult specimens. Usually, the notopodia are absent or incompletely developed and their lobes are shorter. Furthermore, the shape and size of the neuropodial lobes may be also different, but very large specimens have sometimes misshapen parapodia with additional or notched lobes.

Anatomy

Body wall. The body shape is cylindrical to dorsoventrally flattened in transverse section (Rouse and Pleijel 2001). Beneath the epidermis lies a simple musculature, which is composed of a layer of circular muscle and four distinct bands of longitudinal muscles (Storch 1968).

Nervous system. The nervous system consists of a brain or cerebral ganglion, which resides in the prostomium, two circumesophageal connectives, a ventral nerve cord with more or less fused ganglia, and segmental nerves (Ehlers 1868, Orrhage 1999). Furthermore, in addition to freely terminating nerve fibers, many ciliated primary sensory cells are present and located predominantly on the prostomium, the proboscis, the dorsal and ventral cirri, and the pygidium (Wallengren 1901, Retzius 1902, Böggemann 2005).

Blood vascular system. Most of the segmental septa and mesenteries of the goniadids are strongly reduced in the anterior part of the body, and their blood vascular system is either completely absent or limited to a dorsal and a ventral longitudinal blood vessel (Müller 1858, Quatrefages 1866, Ehlers 1868, Arwidsson 1897, Voit 1911, Smith and Ruppert 1988). Hemoglobin is the respiratory pigment, and it is associated with erythrocytes floating freely in the coelom (Dales and Dixon 1981). The segmental organs of the goniadids are classified as protonephromixia that are present in most of the segments; the anterior organs presumably have an excretory function and the posterior organs are gonoducts (Goodrich 1898, 1945, Fage 1906, Fauchald and Rouse 1997, Rouse and Pleijel 2001). Goodrich (1945) reported that the funnels (coelomostome) of the coelomoducts developed later and the posterior fertile region of the trunk greatly enlarged at maturity. The posterior end (gonoduct) then fuses with and opens into the nephridial canal. Little is known about the osmoregulation of the goniadids, but they seem to be very similar to the glycerids, which are euryhaline osmoconformers tolerating a wide range of salinities (Machin 1975, Costa et al. 1980).

Digestive System. The digestive tract is a straight tube, which begins with a ventral mouth opening and ends with a dorsal anus on the pygidium. It is separated into three sections: foregut, midgut, and hindgut. The foregut consists of the muscular eversible proboscis and lies more or less freely in the body cavity, whereas the rest seems to be well fixed by mesenteries (Ehlers 1868).

Pygidium. The pygidium ends with a single pair of elongated anal cirri (Fig. 7.13.4.2.7A, C).

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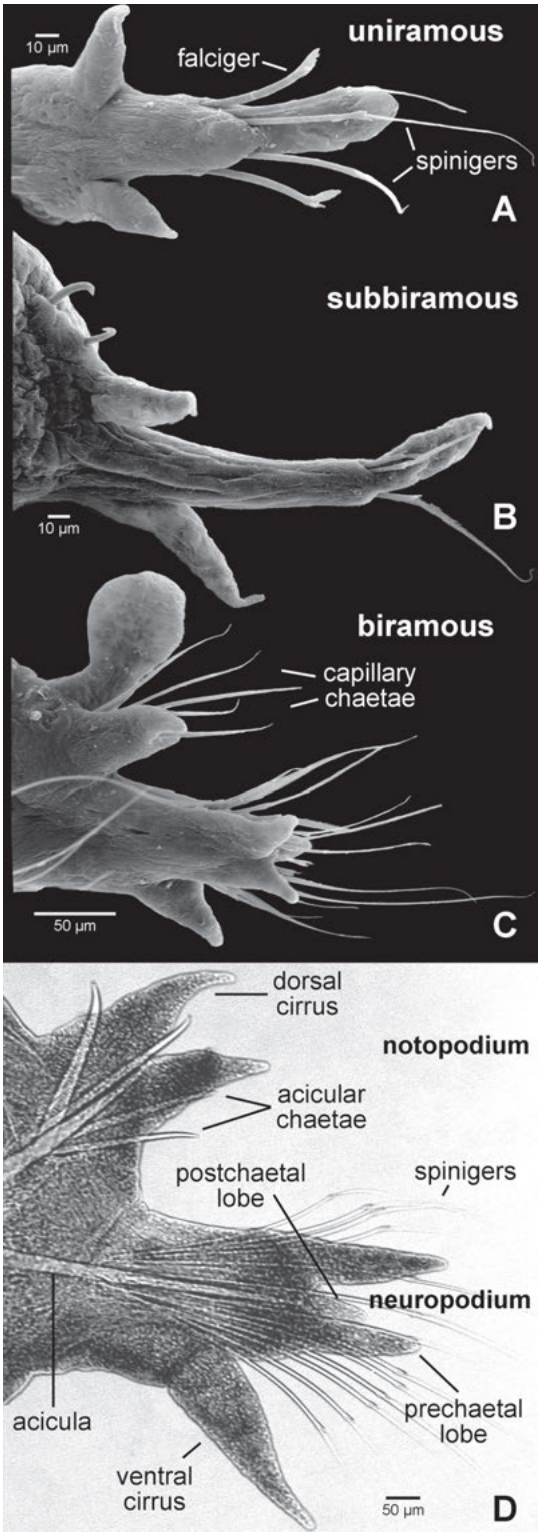


Fig. 7.13.4.2.6: SEM micrographs. A, *Progoniada regularis* Hartman, 1965, uniramous parapodia, posterior view (Böggemann 2005). B, *Goniadides carolinae* Day, 1973, subbiramous parapodia, posterior view (Böggemann 2005). C, *Goniada foliacea* Moore, 1903, biramous parapodia, posterior view (Böggemann 2005); LM micrograph. D, *Goniada acicula* Hartman, 1940, biramous parapodia, posterior view (Böggemann 2005).

Biology and ecology

Goniadidae are widely distributed endobenthic organisms and occur in sandy substrates from intertidal to abyssal depths, although they are rarely found in high densities (Böggemann 2005). Southward and Southward (1972) reported that *Goniada* specimens are able to absorb dissolved organic matter, usually all species are considered to be carnivorous (Blegvad 1914, Hunt 1925, Fauchald and Jumars 1979, Mattson 1981, Jumars et al. 2015). They are motile, construct nonpermanent burrows, and prefer burrowing, deposit-feeding prey like spionids, orbiniids, cirratulids, and other "sedentary" polychaetes (Mattson 1981), which were consumed head first (Silberstein 1987). By contrast, *Glycinde picta* Berkeley, 1927 specimens live in solidified burrows, and their juveniles prefer motile polychaetes like small *Nephtys* (Silberstein 1987). Benthic fishes, especially cod, haddock, plaice, flounder, squirrelfish, and red mullet, are predators on goniadids (McIntosh 1905, 1910, Benham 1932, Pettibone 1963, Ben-Eliahu et al. 1983, Ben-Eliahu and Golani 1990).

The prey is grasped by a rapid eversion of the proboscis, killed by the jaw apparatus, and swallowed completely. The proboscidial papillae probably aid in grasping and holding the prey during swallowing (Smith et al. 1995). The dorsal radula-like papillae of area II in the *Bathyglycinde*, *Glycinde*, and *Goniadides* species (Figs. 7.13.4.2.2B, 7.13.4.2.9B, and 7.13.4.2.10B) appear to be adapted for this task and might act as grappling hooks for the retracting proboscis (Böggemann and Purschke 2006). However, Silberstein (1987) suggested that these papillae anchor the proboscis within the prey tube during eversion. The ciliated sensory cells of the proboscidial papillae (Figs. 7.13.4.2.2G, H and 7.13.4.2.5A), which are presumed to bear mechanoreceptors, might be used to locate the prey just before capture. The serous cells (Fig. 7.13.4.2.5B) presumably develop into the external sclerotized cuticle, and the mucus cells might envelope the prey with a secretion to protect the proboscis and the digestive tract from damage and stabilize the burrow system with mucus (Böggemann and Purschke 2006). However, exact compositions of the secretions and their toxic, lubricating, adhesive, or hydrolytic activities are unknown (Jumars et al. 2015). Analogous to the glycerids (see chapter 7.13.4.1), the proboscis of the goniadids is not only involved in prey capture but also represents an efficient organ during the initial stage of burrowing (Böggemann 2005). All movement and behavior of the Glyceriformia are very similar. However, if goniadid specimens are placed in an aquarium containing only sea water, the animals coil up in an irregular fashion or into a spiral and produce mucus. During this time, the

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anterior part of the body, including the prostomium, is usually highly active and sometimes the specimens try to escape by swimming (Böggemann 2005). The latter usually atypical movement is especially used by epitokous stages for spawning (Verrill 1885), but it might also be used for migration because some specimens (e.g., *Goniada maculata* Örsted, 1843) are observed as having long natatory chaetae before reaching maturity (Böggemann 2005).

Parasites. Symbiotic organisms are often found on the goniadids, located usually on or between the parapodia (Böggemann 2005). The nematodes are ectoparasitic, whereas the protozoa and entoprocts seem to be commensals. Furthermore, two specimens of *Goniada asiatica* Hartman, 1974 are reported as having a parasitic copepod on the ventral surface of the body (Böggemann and Eibye-Jacobsen 2002).

Reproduction and development

The goniadid species are monotelic with separate sexes (Hartman 1950), and gametogenesis occurs in the coelom, but only in the posterior part of the body (Moore 1905, 1911), which becomes distended by the fully developed gametes. These sometimes brownish sperm and greenish eggs (McIntosh 1905, 1910, Mohammad 1973) are visible through the thin body wall and are responsible for the color of mature animals. The pelagic epigamous epitokes of the goniadids show only slight morphological modifications compared to the preceding benthic atoke specimens (Böggemann 2005). Anterior parapodia remain unchanged, and posterior parapodia when filled with gametes might be enlarged and equipped with numerous elongate natatory neurochaetae in the middle of each fascicle, which obviously facilitate swimming. Natatory chaetae have been described several times and can be found in numerous species and genera of the Goniadidae, but they do not always seem to be present in pelagic epitokes (Hartman 1940). Atrophy of the body musculature and the digestive tract, which often occurs in the glycerids, has not been observed in goniadids (Böggemann 2005). The fertilization success of the goniadid species seems to be increased by temporal synchrony. The gametes are simultaneously expelled from the body through ventral pores, which are associated with the gonoducts and the nephridial system (Goodrich 1898, 1945). The ventral pores on the posterior segments are observed in different genera of the Goniadidae (Ehlers 1868, Augener 1918, Benham 1932, Böggemann 2005). Functional gonoducts perhaps indicate that spawning is not associated with rupture of the body and death as described for the glycerid species (Wilson 2000). Therefore, the life cycles of the Goniadidae seem to be iteroparous, but only little is known about the breeding periods (Cazaux 1972, Blake 1975, Silberstein 1987, Husemann 1992, Hilbig 1994, Plate and Husemann 1994). The goniadid specimens spawn many small sperms or larger eggs, which are freely fertilized in the water column (external fertilization) and develop into larvae that can remain in the plankton for weeks or months before settling and metamorphosing into a juvenile (Rouse and Pleijel 2001). However, Thorson (1946) suggested that *Goniada maculata* reproduces by nonpelagic larvae in the Øresund (Sound).

The few studied larvae of the Goniadidae show only slight differences in their morphology and are described as lecithotrophic and not very mobile (Cazaux 1972, Blake 1975, Bhaud and Cazaux 1987, Husemann 1992, Plate and Husemann 1994, Rouse 2000, Rouse and Pleijel 2001). The spherical trochophore larvae (diameter of 200–400 mm; Fig. 7.13.4.2.7A) have a well-developed prototroch and a gut with yolk granules (Husemann 1992, Plate and Husemann 1994). Eyes and an additional acrotroch are present in *Glycinde armigera* Moore, 1911 (Blake 1975) and *Goniadella bobrezkii* (Annenkova, 1929) (Husemann 1992, Plate and Husemann 1994). Metatrochophora and nectochaeta (length of 480–1200 mm; Fig. 7.13.4.2.7A, B) are composed of 4 to 14 segments. In the early stages, the segments become visible, and the four prostomial appendages on the episphere and the two anal cirri on the pygidium appear. The parapodia first consist of only the neuropodia and a few compound chaetae. Older stages have the typical annulated prostomium and uniramous parapodia with pre- and postchaetal lobes together with dorsal and ventral cirri. Plate and Husemann (1994) reported interpodial ciliary bands (Fig. 7.13.4.2.7C), which are present in the posterior segments of *Goniada maculata* and *Goniadella bobrezkii*, together with an additional ventral gastro- and a pygidial telotroch for *Goniada maculata*. Proboscis with papillae, two macro- and a few micrognaths, and chevrons are visible in the late erpochaeta stages (Fig. 7.13.4.2.7A; Bhaud and Cazaux 1987, Husemann 1992, Plate and Husemann 1994). In the juvenile benthic stages, the prototroch is completely reduced, and from this stage, feeding is possible (Fig. 7.13.4.2.7A, C; Husemann 1992). The development from the trochophore larvae to the nectochaeta takes 3 weeks in *Goniadella bobrezkii* and 5 to 6 weeks in *Goniada maculata* (Husemann 1992), whereas the development to the erpochaeta requires approximately 7 weeks in *Goniada emerita* Audouin & Milne Edwards, 1833 (Bhaud and Cazaux 1987).

Phylogeny and taxonomy

Goniada emerita Audouin & Milne Edwards, 1833 was the first described species of the genus *Goniada* and was

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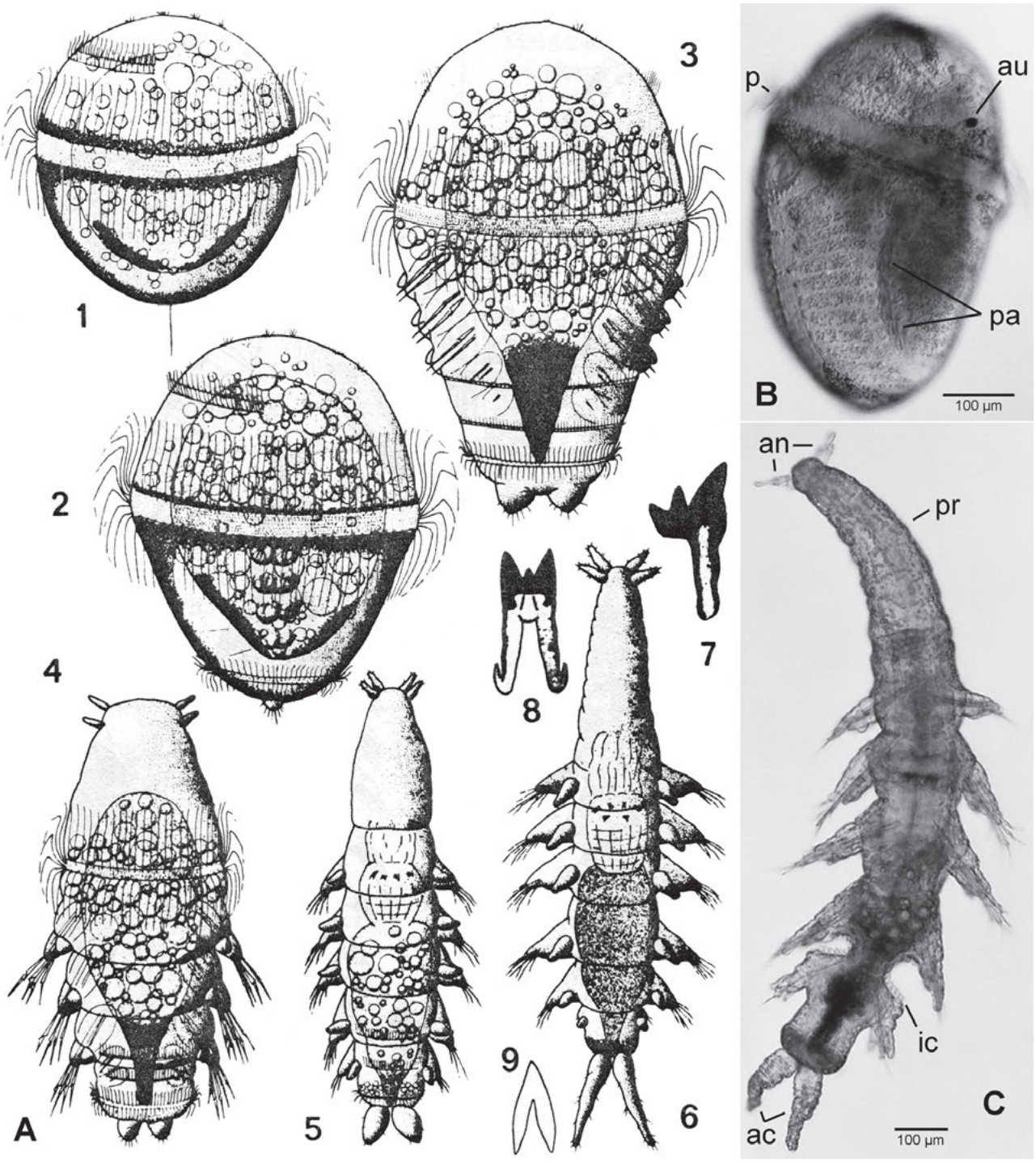


Fig. 7.13.4.2.7: A, Several developmental stages of *Goniada emerita* Audouin & Milne Edwards, 1833. (1) Trochophore (left side) L = 300 µm. (2) Old trochophore (left side). L = 350 µm. Note the presence of a simple crescent-shaped ciliated area without a falciform bundle. (3) Metatrochophore (dorsal side). L = 390 µm. (4) Metatrochophore (dorsal side). L = 540 µm. Note the presence, from this stage, of four antennae on the anterior edge of the prostomium, already prolonged. (5) Erpochaete (dorsal side). L = 1.16 mm, 5 chaetigers. (6) Young worm. L = 1.4 mm, 6 chaetigers. (7) Jaw of the above young worm. (8) X-shaped paragnath. (9) Chevron (Bhaud and Cazaux 1987). B, *Goniadella bobrezkii* (Annenkova, 1929), metatrochophore, dorsal view; au, eye; p, prototroch; pa, parapodia under construction (Husemann 1992). C, *Goniada maculata* Örsted, 1843, juvenile benthic stage with five segments, dorsal view; ac, anal cirri; an, prostomial appendages; ic, interpodial ciliary band; pr, prostomium (Husemann 1992).

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placed by Audouin and Milne Edwards (1833) together with *Glycera* and *Nephtys* in the "Néréidiens non tentaculés." Örsted (1843) followed this scheme and created the "Division Glycereæ" for them. Kinberg (1865) pointed out distinguishing characters between *Glycera* and *Goniada* and established the family Goniadidae (as Goniadea). The independence of these two groups was controversial for a long time (e.g., Ehlers 1868, Fauvel 1923, Hartman 1950, Day 1967, Rullier 1972), but today their family status is not really in doubt (Böggemann 2005). However, because of their uniqueness and great morphological similarity, Rouse and Pleijel (2001) grouped both together to the monophyletic clade Glyceriformia Fauchald, 1977.

The results of cladistic analyses based on morphological data (Fig. 7.13.4.2.8; Böggemann 2006) confirmed the sister-group relationship of Goniadidae and Glyceridae, as proposed by Böggemann (2002, 2005). The monophyly of the sister groups is well supported by autapomorphies in the structure of the jaws (see above), the proboscidial papillae, and the ciliation pattern on the prostomium (Böggemann 2002, 2005). Goniadidae usually bear sclerotized papillae without rootlets (Fig. 7.13.4.2.5A, B; Böggemann and Purschke 2006), and Glyceridae bear soft, partly keratinized proboscidial papillae with prominent intracellular ciliary rootlets (Fig. 7.13.4.1.7A, B; Böggemann et al. 2000). Additionally, goniadids carry laterodorsal and lateroventral depressions with cilia on the prostomium (Fig. 7.13.4.2.2D; Böggemann 2005, 2006), in contrast to glycerids that have more or less distinct dorsal and ventral ciliated rings (Fig. 7.13.4.1.3C). However, in analyses using morphological and molecular data (Worsaae et al. 2005) or exclusively molecular data (Rousset et al. 2007, Struck et al. 2007, Böggemann 2009, Ravara et al. 2016), goniadids and glycerids alternatively resulted as distinctly separated, as monophyletic clades with a sister-group relationship, or with a monophyletic Glyceridae nested within a paraphyletic Goniadidae. Nevertheless, the great morphological similarities suggested a close relationship and might not be the result of convergent evolution. A recent study using Illumina sequencing technology highly supported the previously postulated sister-group relationship and the monophyletic status of Glyceriformia (Richter et al. 2015).

Nineteen genera have been attributed to the Goniadidae during the taxonomic history (†*Alienites* Kozur, 1967; *Bathyglycinde* Fauchald, 1972; *Bookhoutia* Mohammad, 1973; †*Carbosesostris* Schram, 1979; *Eone* Malmgren, 1866; *Epicaste* Kinberg, 1865; †*Ferragutia* Bracchi & Alessandrello, 2005; *Glycinde* F. Müller, 1858; *Goniada* Audouin & Milne Edwards, 1833; *Goniadella* Hartman, 1950; *Goniadides* Hartmann-Schröder, 1960; *Goniadopsis* Fauvel, 1928; *Lacharis* Kinberg, 1865; *Leonnatus* Kinberg, 1865; *Ophioglycera* Verrill, 1885; *Ophiogoniada* Böggemann, 2005; †*Pieckonia* Thompson, 1979; *Progoniada* Hartman, 1965; and *Progoniadides* Hartmann-Schröder, 1974). Today the family only consists of the eight recent genera *Bathyglycinde*, *Glycinde*, *Goniada*, *Goniadella*, *Goniadides*, *Goniadopsis*, *Ophiogoniada*, and *Progoniada*, which show clear differences in several diagnostic characters (Böggemann 2005, 2006): *Goniadopsis* has plesiomorphic simple prostomial appendages (Fig. 7.13.4.2.14A), autapomorphic Y-shaped ventral simple micrognaths and tubercles on some of the anterior segments, whereas all other genera have articulated prostomial appendages and usually compound ventral micrognaths. An autapomorphy for *Ophiogoniada* is the presence of additional lyrate neurochaetae in the superior position of biramous parapodia (Fig. 7.13.4.2.15L). The autapomorphic character for the clade *Goniada*, *Goniadella*, and *Progoniada* are chevrons (Figs. 7.13.4.2.2E, 7.13.4.2.3B, 7.13.4.2.11D, and 7.13.4.2.16D), whereas the radula-like proboscidial papillae are an autapomorphy for the clade *Bathyglycinde*, *Glycinde*, and *Goniadides* (Figs. 7.13.4.2.2B, 7.13.4.2.9B, and 7.13.4.2.10B). In *Goniada*, the posterior parapodia are biramous with usually only spinigerous neurochaetae (Fig. 7.13.4.2.11G–L), in contrast to *Goniadella* and *Progoniada*, which have bi-/subbi- or uniramous parapodia with spinigerous and falcigerous neurochaetae (Figs. 7.13.4.2.12D–I and

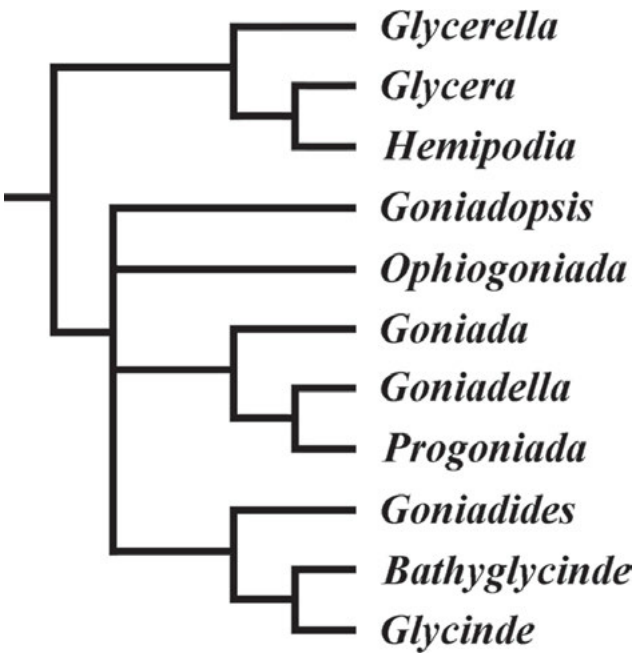


Fig. 7.13.4.2.8: Systematic arrangement of the Glyceriformia. Parsimonious tree from the analysis of morphological characters (Böggemann 2006).

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7.13.4.2.16E–L). Species of *Goniadides* share some of these latter features (Fig. 7.13.4.2.13D, subbiramous parapodia; Fig. 7.13.4.2.13F, spinigerous and/or falcigerous neurochaetae), but the three dorsal longitudinal double rows of radula-like papillae are an autapomorphic character of this group because *Bathyglycinde* and *Glycinde* have five or six double rows of radula-like papillae (Figs. 7.13.4.2.9B and 7.13.4.2.10B). An autapomorphy of *Glycinde* are hooked notochaetae, each with a terminal pointed hood (Fig. 7.13.4.2.10L), whereas only capillary notochaetae and a smooth or only indistinctly annulated prostomium (Fig. 7.13.4.2.9A) are present in *Bathyglycinde*. Most of the goniadid species are larger forms with posterior biramous parapodia. However, specimens of *Goniadella*, *Goniadides*, and *Progoniada* are small and usually have reduced subbiramous or uniramous parapodia with falcigerous and/or spinigerous chaetae, which are juvenile characters as described, for example, for tiny *Goniada* specimens (Gilbert 1984) and might be specific adaptations to a meiofaunal environment. This supports the hypothesis that they possibly evolved by progenesis (Westheide 1987) from larger forms.

A worldwide revision of the family Goniadidae is provided by Böggemann (2005), which recognize 63 nominal species as valid (5 in *Bathyglycinde*, 11 in *Glycinde*, 31 in *Goniada*, 6 in *Goniadella*, 5 in *Goniadides*, 3 in *Goniadopsis*, 1 in *Ophiogoniada*, and 1 in *Progoniada*). Recent regional studies described two additional species of the genera *Glycinde* (*Glycinde henningi* Böggemann & Orensanz, 2007 from South America) and *Progoniada* (*Progoniada oahuensis* Barrett & Bailey-Brock, 2005 from Hawaii). However, *Progoniada oahuensis* seems to be a synonym of *Progoniada regularis* Hartman, 1965, because the supposed difference in the length of the falcigerous blades only depending on the size of the specimens.

In addition to the recent taxa, six fossil species are described for the goniadids by their fossilized jaws (scolecodonts): †*Alienites cuneatus* Kozur, 1967; †*Alienites longidentatus* Kozur, 1967; †*Goniada bakeri* Charletta & Boyer, 1974; †*Goniada constricta* Kozur, 1971; †*Goniada diversidentata* Szaniawski, 1974; †*Goniada szaniawskii* Kozur in Szaniawski, 1974. The oldest are from the Triassic (around 250 million years ago), and their general structure is very similar to the jaws of recent taxa (Kozur 1967, 1971, Charletta and Boyer 1974, Szaniawski 1974, 1996). Furthermore, well-preserved whole body fossils of the putative goniadids †*Pieckonia helenae* Thompson, 1979 (Fig. 7.13.4.2.1D) (with micrognaths) and †*Carbosesostris megaliphagon* Schram, 1979 (with micro- and macrognaths) have been reported from the Carboniferous (around 320–300 million years ago) and appear to be the oldest records of this group (Thompson 1979, Schram 1979, Böggemann 2005, 2006). Both taxa lack chevrons, which are present in *Ferragutia cenomaniana* Bracchi & Alessandrello, 2005 from the Upper Cretaceous. However, this species is equipped with micrognaths only (Bracchi and Alessandrello 2005) and therefore resemble the recent taxon *Goniada amacrognatha* Böggemann & Eibye-Jacobsen, 2002.

Goniadidae Kinberg, 1865

Type genus: *Goniada* Audouin & Milne Edwards, 1833: 266

Synonyms: Goniadea Kinberg, 1865: 246
Goniadeorum Malmgren, 1866: 409
Glycerea polygnatha Ehlers, 1868: 702

Diagnosis: Body with numerous segments (up to 427), elongated, tapering at both ends (Fig. 7.13.4.2.1A, B). Segments uni-, bi-, or triannulate (Figs. 7.13.4.2.1A, B and 7.13.4.2.3A). Prostomium conical, pointed, usually annulated; anteriormost annulus with four usually articulated appendages, anterior pair situated terminolaterally and posterior pair more dorsolaterally; posteriormost annulus with one pair of nuchal organs; most remaining annuli with one laterodorsal and one lateroventral ciliated depression on each side of prostomium; pair of subdistal and/or basal subdermal eyes may be present (Figs. 7.13.4.2.1A, B, 7.13.4.2.2A–D, 7.13.4.2.3A, 7.13.4.2.9A, 7.13.4.2.10A, 7.13.4.2.11A, 7.13.4.2.12A, 7.13.4.2.13A, 7.13.4.2.14A, 7.13.4.2.15A, and 7.13.4.2.16A). Proboscis long, cylindrical to club shaped, muscular (Figs. 7.13.4.2.1B and 7.13.4.2.2A, B), densely covered with numerous, usually sclerotized papillae (Figs. 7.13.4.2.2G, H, 7.13.4.2.5A, B, 7.13.4.2.9B, 7.13.4.2.10B, 7.13.4.2.11B, and 7.13.4.2.16B); tip of fully everted proboscis with terminal soft papillae and usually with two macrognaths (except for *Goniada amacrognatha*) and a number of ventral and/or dorsal micrognaths, arranged in a more or less complete circlet (Figs. 7.13.4.2.1B, C, 7.13.4.2.2A, B, F, 7.13.4.2.3C, 7.13.4.2.9C, 7.13.4.2.10C, 7.13.4.2.11C, 7.13.4.2.13B, 7.13.4.2.15B, C, and 7.13.4.2.16C); lateral rows of V-shaped chevrons may be present (Figs. 7.13.4.2.2E, 7.13.4.2.3B, 7.13.4.2.11D, and 7.13.4.2.16D). First segment sometimes with only a pair of small lateral cirri and without parapodia or chaetae (Figs. 7.13.4.2.3A, 7.13.4.2.9A, 7.13.4.2.11A, 7.13.4.2.12A, 7.13.4.2.13A, 7.13.4.2.15A, and 7.13.4.2.16A). Body usually divided into anterior region with uniramous parapodia and following region with biramous (Fig. 7.13.4.2.1B) or subbiramous parapodia (except for *Progoniada*, which has uniramous parapodia along the entire body); a transitional middle region with gradually changing parapodia may be present; notopodia with single lobe or

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subdivided into pre- and postchaetal lobes (biramous), limited to aciculae and chaetae (subbiramous), or absent (uniramous); neuropodia with one or two prechaetal and one postchaetal lobe; all parapodia with basally inserted dorsal and ventral cirri (Figs. 7.13.4.2.6A–C, 7.13.4.2.9D–K, 7.13.4.2.10D–K, 7.13.4.2.11E–L, 7.13.4.2.12B–I, 7.13.4.2.13C–D, 7.13.4.2.14B–I, 7.13.4.2.15D–J, and 7.13.4.2.16E–L). Branchiae absent. Noto- and neuropodia each with a single acicula (Fig. 7.13.4.2.6D); notochaetae capillaries (Fig. 7.13.4.2.6C), acicular (Figs. 7.13.4.2.6B, D, 7.13.4.2.13E, and 7.13.4.2.15K) or basally stout, hooked at tip and with terminal pointed hood (Fig. 7.13.4.2.10L); neurochaetae usually with only compound falcigers and/or spinigers (Figs. 7.13.4.2.6A–D, 7.13.4.2.13F, and 7.13.4.2.15M), in one case with additional lyrate chaetae (Fig. 7.13.4.2.15L). Pygidium with a dorsal anus and a terminal pair of slender elongated anal cirri (Fig. 7.13.4.2.7A, C).

Bathyglycinde Fauchald, 1972

Type species: *Bathyglycinde mexicana* Fauchald, 1972: 108

Diagnosis: Segments uni- or biannulate. Prostomium smooth or indistinctly annulated; terminal annulus with biarticulate appendages (Fig. 7.13.4.2.9A). Proboscis with several different types of papillae, arranged in distinct longitudinal rows (Fig. 7.13.4.2.9B); with macrognaths and dorsal micrognaths (Fig. 7.13.4.2.9C); chevrons absent. First segment sometimes with only a pair of small lateral cirri and without parapodia or chaetae (Fig. 7.13.4.2.9A). Anterior part of body with uniramous parapodia, following region with biramous parapodia (Fig. 7.13.4.2.9D–K). Notochaetae capillary; neurochaetae compound spinigers.

Glycinde F. Müller, 1858

Type species: *Glycinde multidens* F. Müller, 1858: 214

Synonyms: *Epicaste* Kinberg, 1865: 247
Eone Malmgren, 1866: 409

Diagnosis: Segments uni- or biannulate. Prostomium annulated; terminal annulus with biarticulate appendages (Fig. 7.13.4.2.10A). Proboscis with several different types of papillae, arranged in distinct longitudinal rows (Figs. 7.13.4.2.2B, H and 7.13.4.2.10B); with macrognaths and dorsal and sometimes ventral micrognaths (Fig. 7.13.4.2.10C); chevrons absent. Anterior part of body with uniramous parapodia, following region with biramous parapodia (Fig. 7.13.4.2.10D–K). Notochaetae stout, hooked at tip, and with terminal pointed hood (Fig. 7.13.4.2.10L); neurochaetae compound spinigers.

Goniada Audouin& Milne Edwards, 1833

Type species: *Goniada emerita* Audouin & Milne Edwards, 1833: 268

Synonyms: *Lacharis* Kinberg, 1865: 247
Leonnatus Kinberg, 1865: 247
Ophioglycera Verrill, 1885: 436

Diagnosis: Segments uni- or biannulate. Prostomium annulated, sometimes with only indistinct rings; terminal annulus with biarticulate appendages (Figs. 7.13.4.2.1A, 7.13.4.2.2A, 7.13.4.2.3A, and 7.13.4.2.11A). Proboscis with a few different types of papillae (Figs. 7.13.4.2.2G and 7.13.4.2.11B); usually with macrognaths (except for *Goniada amacrognatha*) and dorsal and ventral micrognaths (Figs. 7.13.4.2.1C, 7.13.4.2.2F, 7.13.4.2.3C, and 7.13.4.2.11C); chevrons usually present (might be lost in larger specimens of *Goniada gigantea* (Verrill, 1885)) (Figs. 7.13.4.2.2E, 7.13.4.2.3B, and 7.13.4.2.11D). Anterior part of body with uniramous parapodia, following region with biramous parapodia, transitional region may be present (Fig. 7.13.4.2.11E–L). Notochaetae capillary (Fig. 7.13.4.2.6C) or acicular (Fig. 7.13.4.2.6D); neurochaetae usually compound spinigers (Fig. 7.13.4.2.6C, D), additional falcigers might be present on anterior few chaetigers of smaller specimens.

Goniadella Hartman, 1950

Type species: *Eone gracilis* Verrill, 1873: 596

Diagnosis: Segments bi- or triannulate. Prostomium annulated, consisting of eight rings; terminal annulus with biarticulate appendages, which may appear to be tri- or quadriarticulated due to constrictions of the basal article (Fig. 7.13.4.2.12A). Proboscis with a few different types of papillae; with macrognaths and dorsal and ventral micrognaths; chevrons present. First segment with only a pair of small lateral cirri and without parapodia or chaetae (Fig. 7.13.4.2.12A). Anterior part of body with uniramous parapodia, following region with biramous or subbiramous parapodia (Fig. 7.13.4.2.12B–I). Notochaetae acicular; neurochaetae compound falcigers and spinigers in all parapodia.

Goniadides Hartmann-Schröder, 1960

Type species: *Goniadides aciculata* Hartmann-Schröder, 1960: 116

Diagnosis: Segments bi- or triannulate. Prostomium annulated, consisting of eight rings; terminal annulus with biarticulate appendages, which may be appear to be tri- or quadriarticulated due to constrictions of the basal article (Figs. 7.13.4.2.2D and 7.13.4.2.13A). Proboscis with several different types of papillae, arranged in distinct longitudinal rows; with macrognaths and dorsal and sometimes ventral micrognaths (Fig. 7.13.4.2.13B); chevrons absent. First segment sometimes with only a pair of small lateral cirri and without parapodia or chaetae (Fig. 7.13.4.2.13A).

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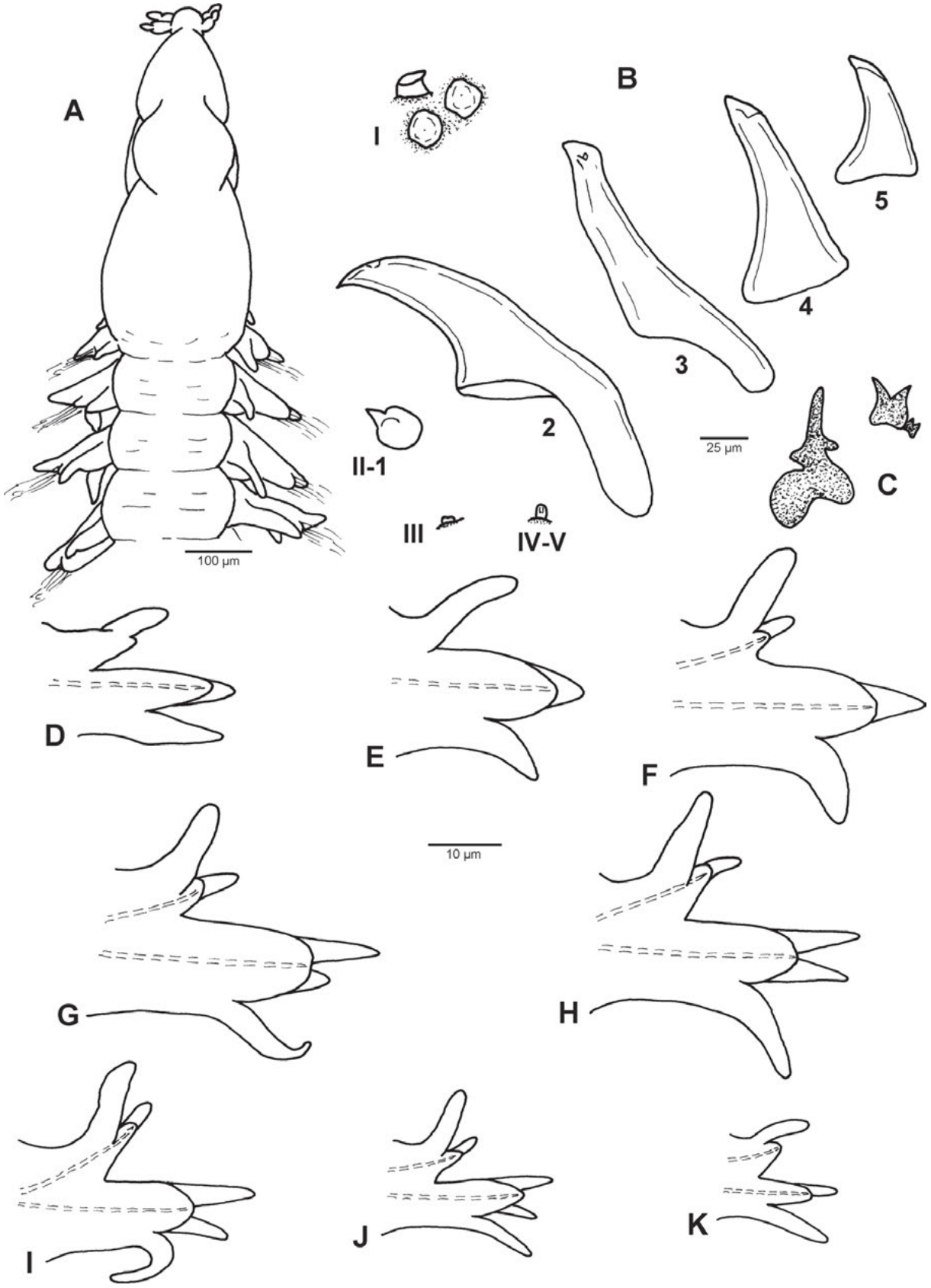


Fig. 7.13.4.2.9: *Bathyglycinde sibogana* (Augener & Pettibone in Pettibone, 1970). A, Anterior end, dorsal view. B, Proboscidial papillae. C, Macro- and micrognath. D–K, Anterior to posterior parapodia, posterior view (Böggemann 2009).

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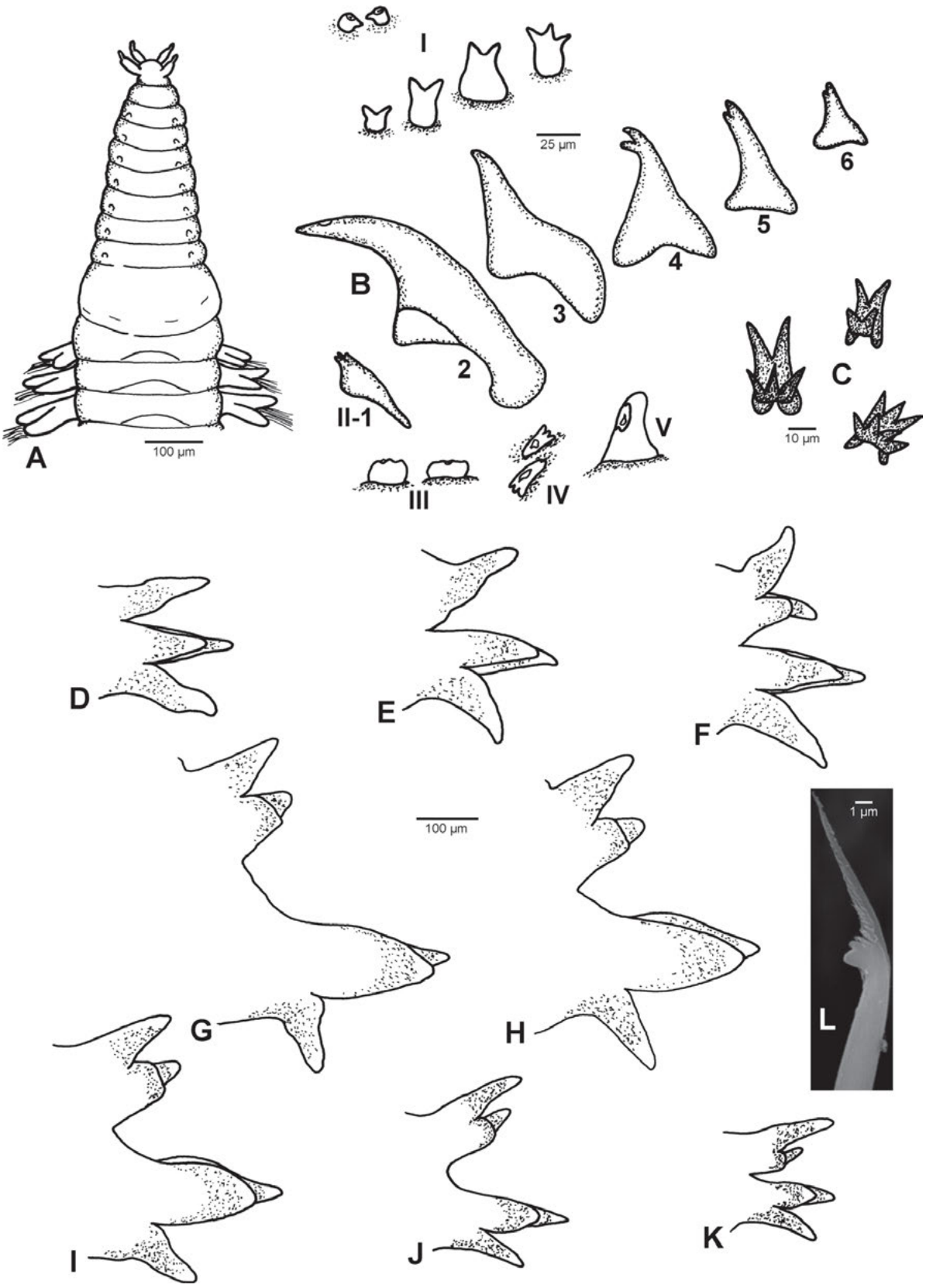


Fig. 7.13.4.2.10: *Glycinde henningi* Böggemann & Orensanz, 2007. A, Anterior end, dorsal view. B, Proboscidial papillae. C, Micrognaths. D–K, Anterior to posterior parapodia, posterior view (Böggemann and Orensanz 2007). *Glycinde kameruniana* Augener, 1918. L, SEM micrograph of a notochaetae (Böggemann and Eibye-Jacobsen 2002).

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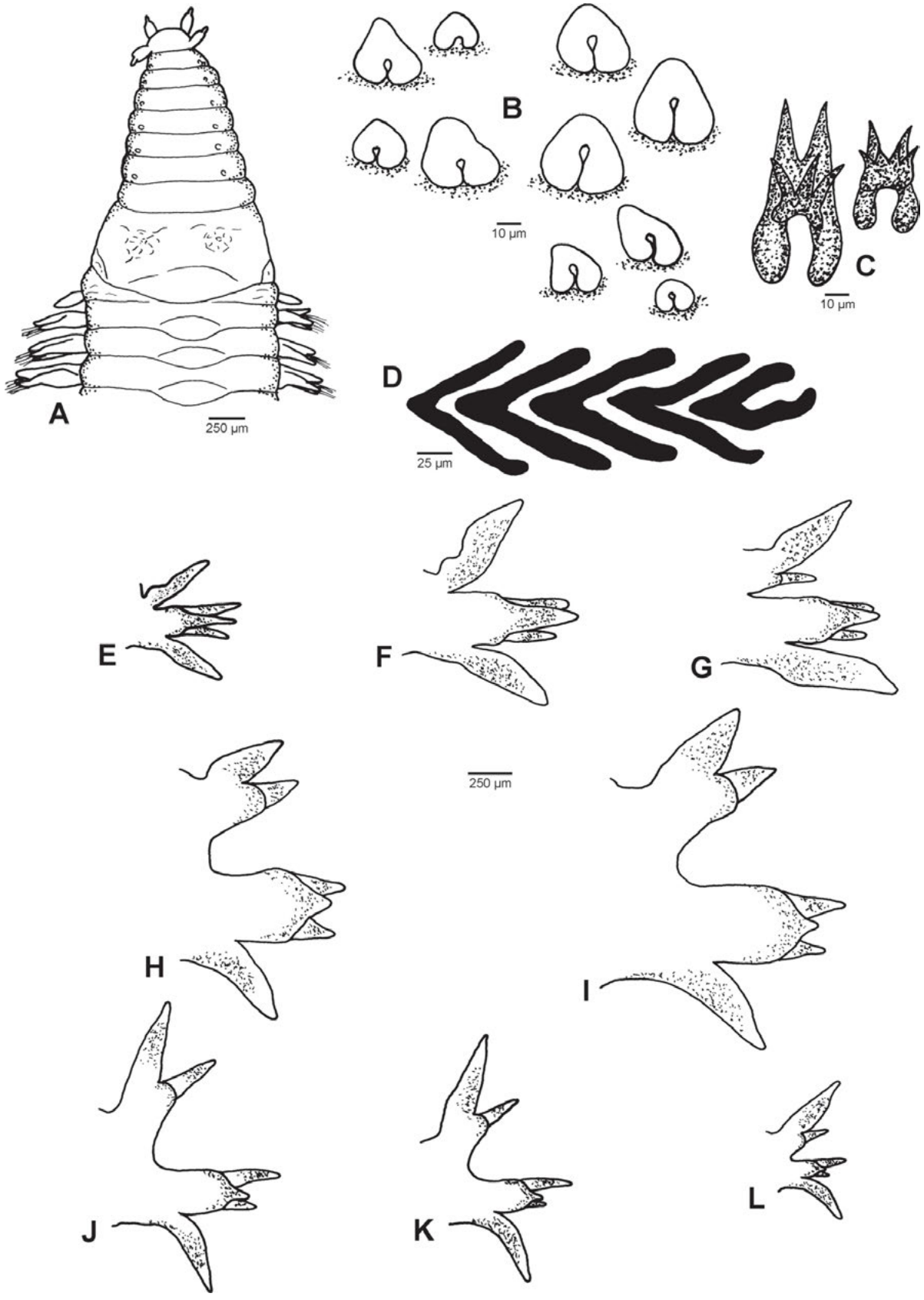


Fig. 7.13.4.2.11: *Goniada gigantea* (Verrill, 1885). A, Anterior end, dorsal view. B, Proboscidial papillae. C, Micrognaths. D, Chevrons. E–L, Anterior to posterior parapodia, posterior view (Böggemann and Orensanz 2007).

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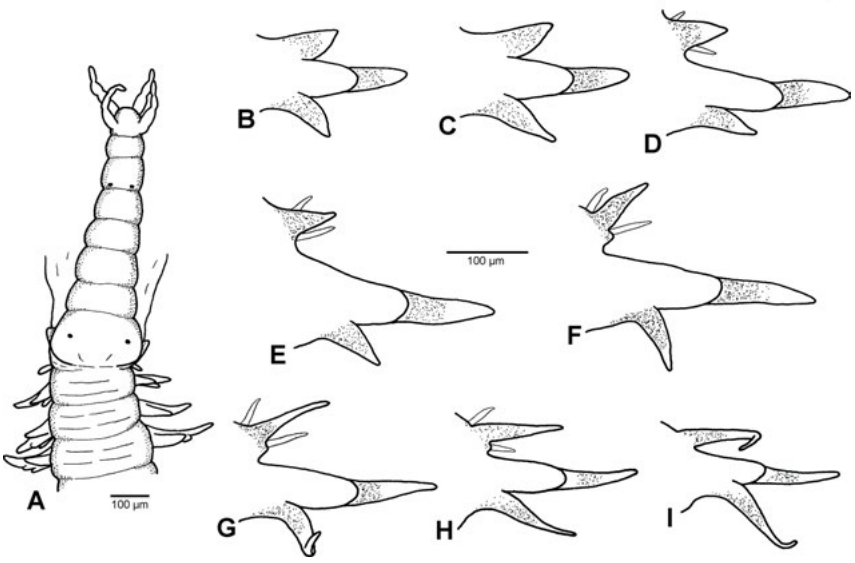


Fig. 7.13.4.2.12: *Goniadella gracilis* (Verrill, 1873). A, Anterior end, dorsal view. B–I, Anterior to posterior parapodia, posterior view (Böggemann 2005).

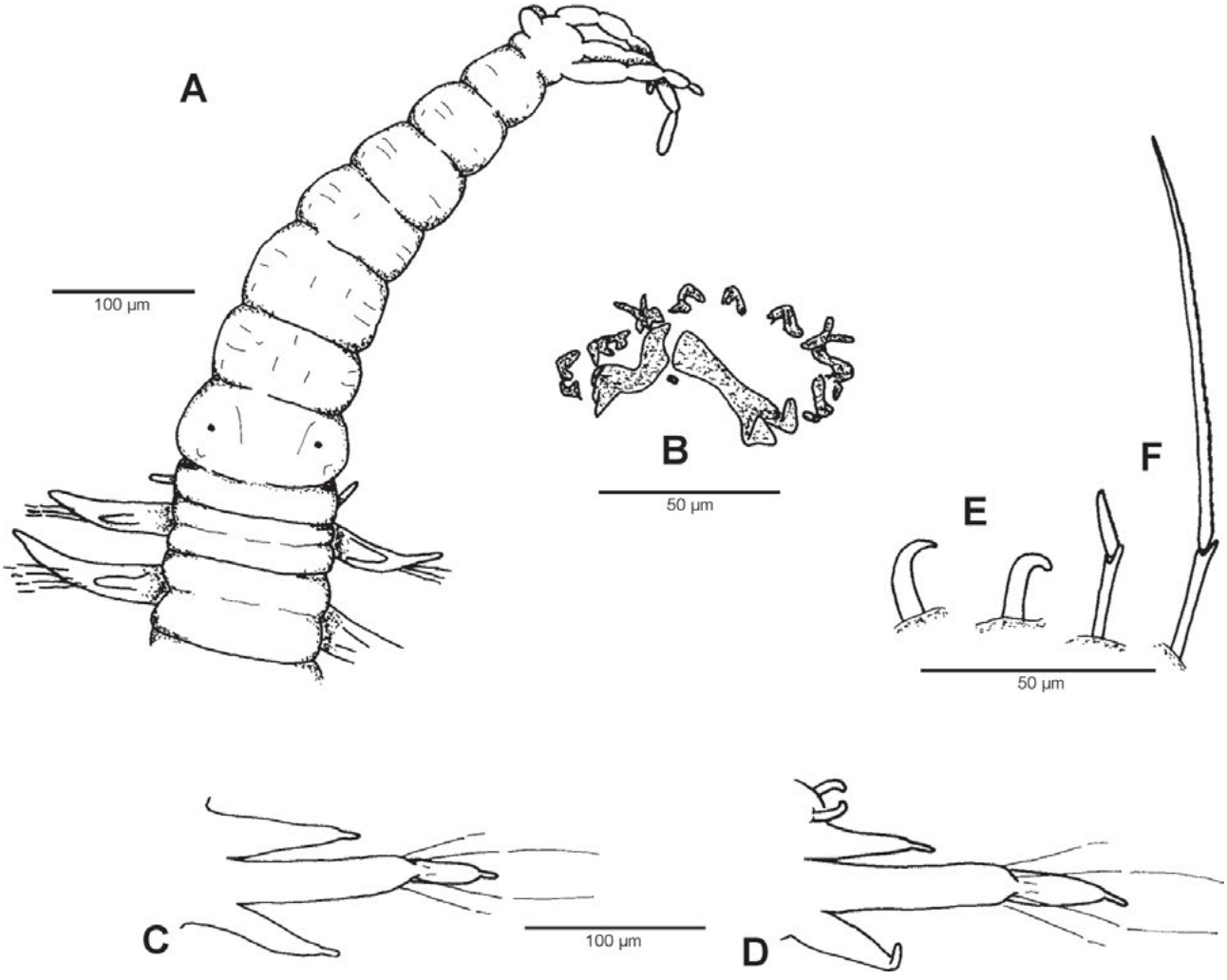


Fig. 7.13.4.2.13: *Goniadides carolinae* Day, 1973. A, Anterior end, dorsal view. B, Macro- and micrognaths. C, Parapodium of chaetiger 8, posterior view. D, Parapodium of chaetiger 35, posterior view. E, Two acicular notochaetae. F, Neurochaetae: compound falciger (left) and compound spiniger (right) (Böggemann and Eibye-Jacobsen 2002).

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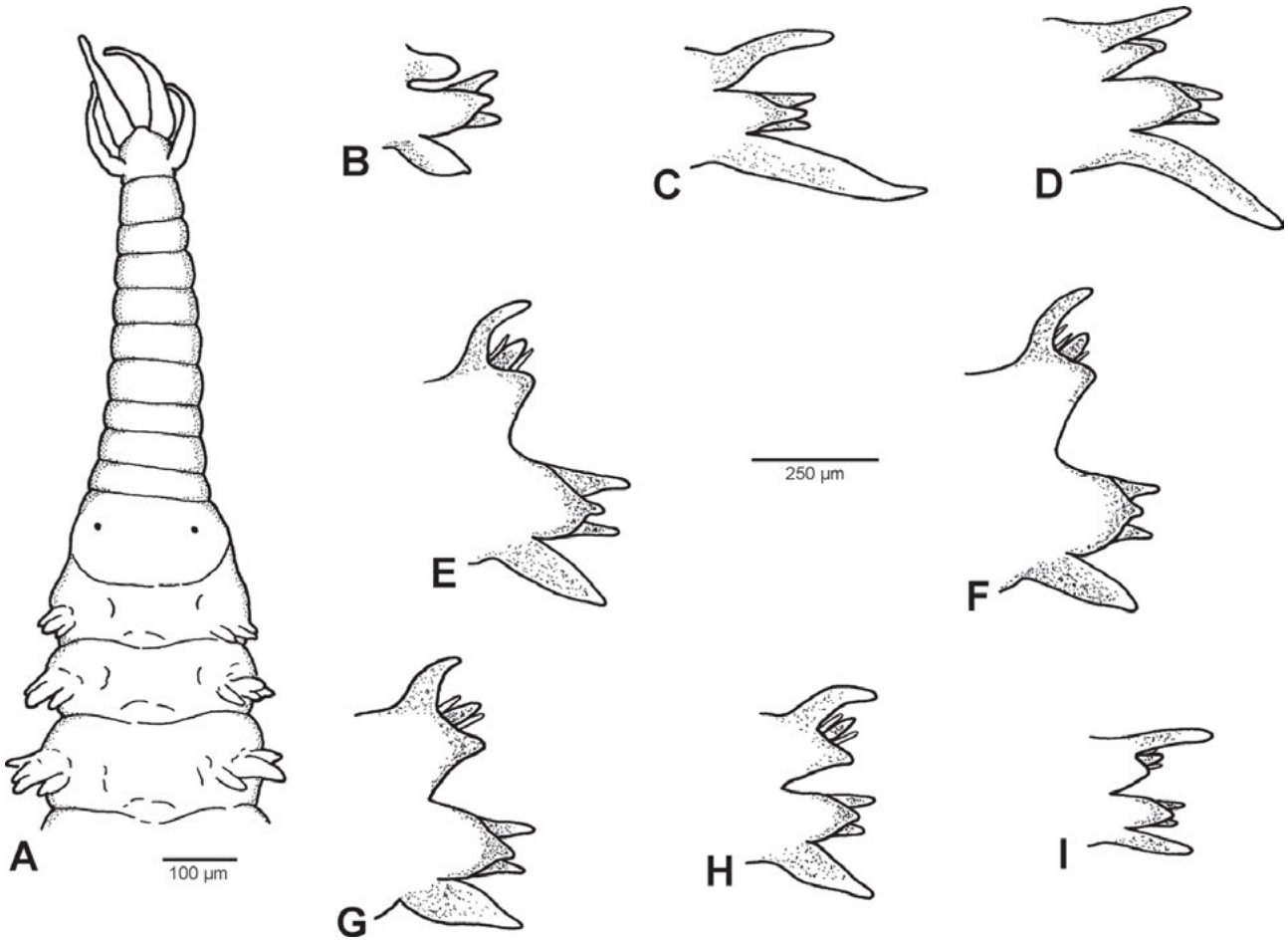


Fig. 7.13.4.2.14: *Goniadopsis longicirrata* (Arwidsson, 1899). A, Anterior end, dorsal view. B–I, Anterior to posterior parapodia, posterior view (Böggemann 2005).

Anterior part of body with uniramous parapodia, following region with subbiramous parapodia (Figs. 7.13.4.2.6B and 7.13.4.2.13C, D). Notochaetae acicular with more or less straight or distinctly curved tips (Fig. 7.13.4.2.6B and 7.13.4.2.13D, E), arising from body wall dorsal to dorsal cirri or at level of dorsal cirri; neurochaetae compound spinigers and/or falcigers (Fig. 7.13.4.2.13F).

***Goniadopsis* Fauvel, 1928**

Type species: *Goniada* (*Goniadopsis*) *agnesiae* Fauvel, 1928: 92

Synonyms: *Bookhoutia* Mohammad, 1973: 29
Progoniadides Hartmann-Schröder, 1974: 60

Diagnosis: Segments uni- or biannulate. Prostomium annulated; terminal annulus with simple or only indistinctly articulated appendages (Fig. 7.13.4.2.14A). Proboscis with slightly different types of papillae; with macrognaths and dorsal and ventral simple micrognaths; chevrons absent. Body divided into three regions: anterior with uniramous parapodia provided with short cirri and falcigerous compound chaetae; intermediate with uniramous parapodia, elongated ventral cirri and falcigerous and/or spinigerous compound chaetae; and a posterior region with biramous parapodia, acicular notochaetae sometimes with terminal guarded hooks, and falcigerous and/or spinigerous compound neurochaetae (Fig. 7.13.4.2.14B–I). A few segments between the anterior and the intermediate region with more or less distinct tubercles.

***Ophiogoniada* Böggemann, 2005**

Type species: *Ophioglycera lyra* Granados-Barba & Solís-Weiss, 1997: 462

Diagnosis: Segments uni- or biannulate. Prostomium annulated; terminal annulus with biarticulate appendages (Fig. 7.13.4.2.15A). Proboscis with slightly different types of papillae; with macrognaths and dorsal and ventral micrognaths (Fig. 7.13.4.2.15B, C); chevrons absent. First segment with only a pair of small lateral cirri and without parapodia or chaetae (Fig. 7.13.4.2.15A). Anterior part of body with uniramous parapodia, following region with biramous parapodia (Fig. 7.13.4.2.15D–J). Notochaetae acicular (Fig.

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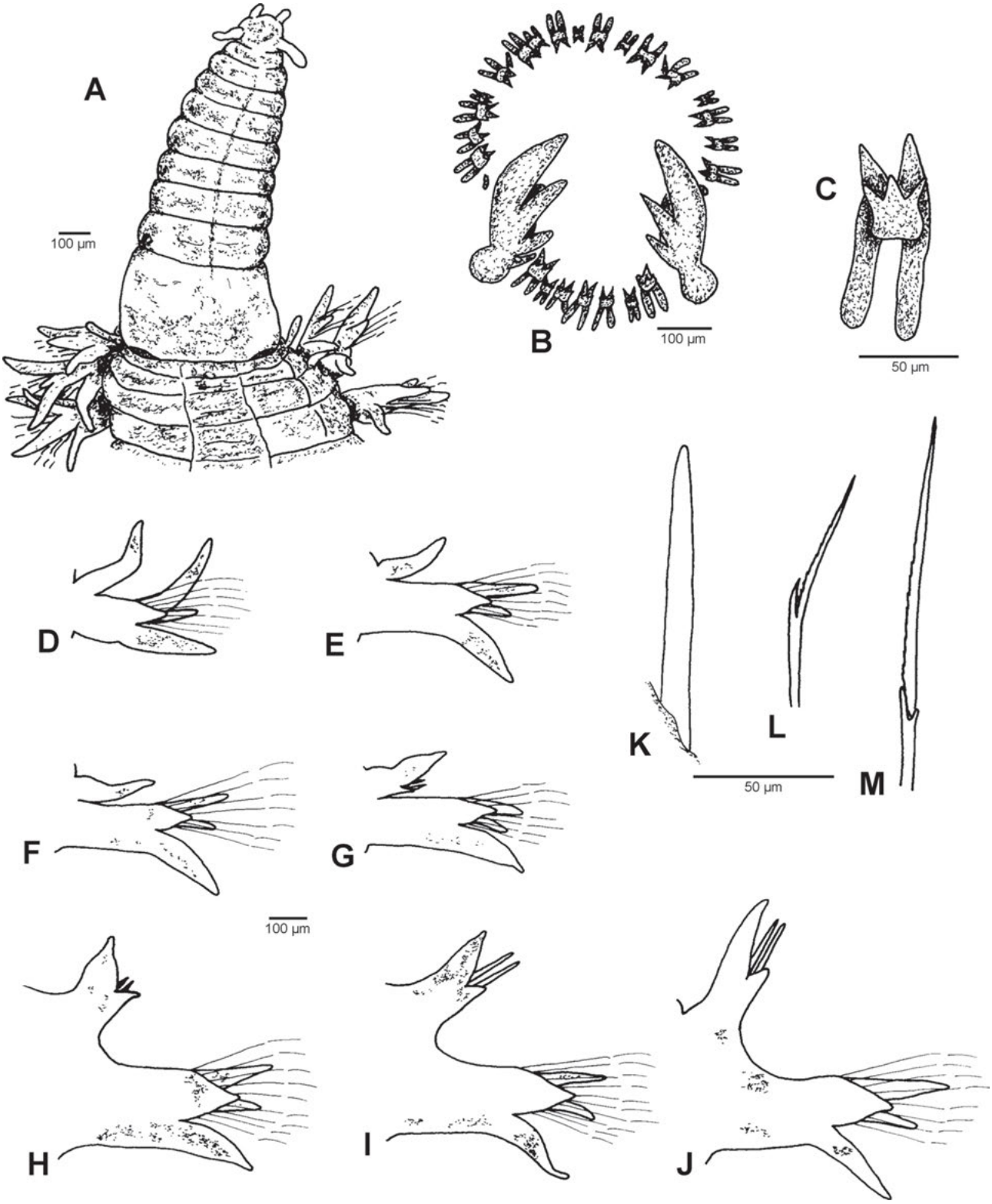


Fig. 7.13.4.2.15: *Ophiogoniada lyra* (Granados-Barba & Solís-Weiss, 1997). A, Anterior end, dorsal view. B, Macro- and micrognaths. C, Detail of compound micrognath. D–J, Anterior to posterior parapodia, posterior view. K, Notochaeta. L, Lyrate neurochaeta. M, Compound neuropodial spiniger (Böggemann and Eibye-Jacobsen 2002).

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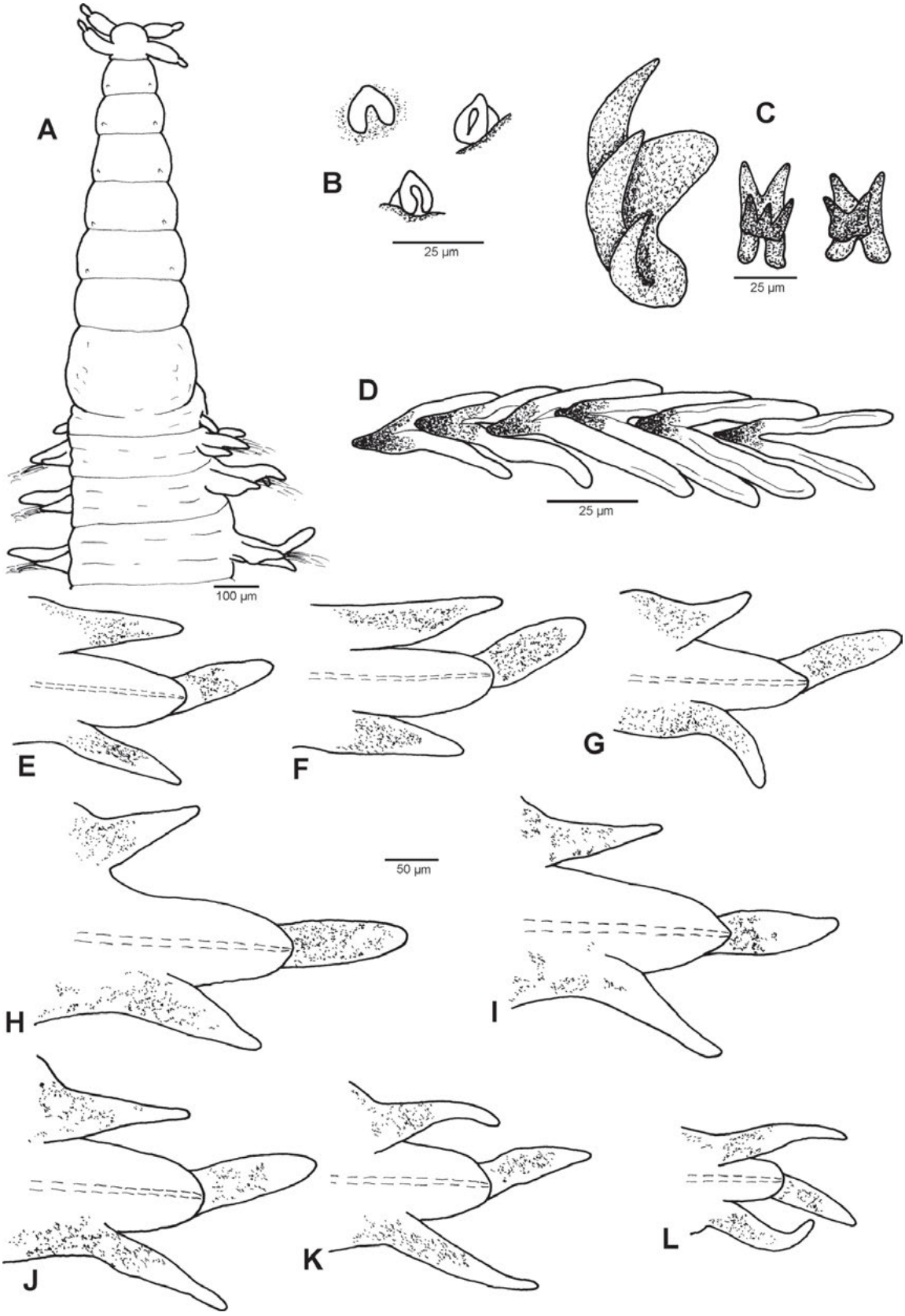


Fig. 7.13.4.2.16: *Progoniada regularis* Hartman, 1965. A, Anterior end, dorsal view. B, Proboscidial papillae. C, Macro- and micrognaths. D, Chevrons. E–L, Anterior to posterior parapodia, posterior view (Böggemann 2009).

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7.13.4.2.15K); neurochaetae compound spinigers (Fig. 7.13.4.2.15M), biramous parapodia with a few additional lyrate chaetae in superior position (Fig. 7.13.4.2.15L).

***Progoniada* Hartman, 1965**

Type species: *Progoniada regularis* Hartman, 1965: 100

Diagnosis: Segments bi- or triannulate. Prostomium annulated, consisting of eight rings; terminal annulus with biarticulate appendages (Fig. 7.13.4.2.16A). Proboscis with a few different types of papillae (Fig. 7.13.4.2.16B); with macrognaths and dorsal and ventral microgna ths (Fig. 7.13.4.2.16C); chevrons present (Fig. 7.13.4.2.16D). First segment with only a pair of small lateral cirri and without parapodia or chaetae (Fig. 7.13.4.2.16A). All parapodia uniramous (Figs. 7.13.4.2.6A and 7.13.4.2.16E–L). Notochaetae absent; neurochaetae compound falcigers and/or spinigers in all parapodia (Fig. 7.13.4.2.6A).

Acknowledgments

The author thanks Eginhard Husemann for the use of some figures from his PhD thesis.

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Alexandra Elaine Rizzo and Wagner F. Magalhães

7.13.5 Ichthyotomidae Eisig, 1906

Introduction

This family is represented by a single species, *Ichthyotomus sanguinarius* Eisig, 1906 from the Gulf of Naples (Fig. 7.13.5.1A–F). The species is a parasite of eel fishes, specially *Conger conger* (Culurgioni et al. 2006), *Conger vulgaris*, *Myrus vulgaris* and *Sphagebranchus vulgaris* (Rouse & Pleijel 2001), and *Echelus myrus* (Martin & Britayev 2018). The specimens are usually found attached to the dorsal and ventral fins of the eels. Since the original description of *Ichthyotomus*, they were not rediscovered until Stoch (2003) and Culurgioni et al. (2006) recorded *I. sanguinarius* parasitizing conger eels from the Sardinian coast. As reported by Martin and Britayev (1998), this species is a parasite specific for Congridae.

Morphology

Size. Ichthyotomids when adult can reach a length of 1 cm.

Prostomium. They have a rounded prostomium (Fig. 7.13.5.1A, B) with a rudimentary median antenna inserted anteriorly, a pair of small dorsolateral antennae, and a pair of ventral palps; antennae and palps are not articulated. Ontogenetic studies are necessary to understand the phylogenetic significance of these appendages (Rouse and Pleijel 2001). A pair of lenticulate eyespots is present, and also a pair of nuchal organs.

Pharynx. An axial pharynx similar to a pair of scissors was described in detail by Eisig (1906); in its anterior part, there is a pair of prominent jaws or stylets (Fig. 7.13.5.1D) attached to a strong musculature functioning as a sucker.

Parapodia and chaetae. The first segment has dorsal cirri, parapodial lobes, chaetae, and ventral cirri. Following chaetigers are similar to the first but larger in size. Median segments have subbiramous parapodia with notoaciculae and distally inserted dorsal cirri. Neuropodia have rounded parapodial lobes, neuroaciculae, and a ventral cirrus with distal gland openings. Neurochaetae are supra-acicular spinigers and subacicular falcigers more numerous than the supra-acicular ones (Fig. 7.13.5.1F).

Pygidium. Culurgioni *et al.* (2006) provided photographs of the posterior end of an individual showing a rounded pygidium with a pair of elongate anal cirri (Culurgioni *et al.* 2006, fig. 4).

Reproduction and development

Small round eggs were also shown laterally, between two parapodia (Culurgioni *et al.* 2006, fig. 5).

Biology and ecology

Eisig (1906) provided a detailed account of the morphology and internal anatomy, including the feeding apparatus of *Ichthyotomus sanguinarius*. This species is a parasite specific for the fish family Congridae (Martin and Britayev 1998). The specimens are usually found attached to the dorsal and ventral fins of the eels (Fig. 7.13.5.1C). Culurgioni et al. (2006) listed several eel parasites but *I. sanguinarius* was the only species found attached to the fins and skin of 11.5% of the conger eels collected. The mean infestation of worms per eel was 17.3, but one individual was heavily infested by 50 individuals. According to these authors, the infection is due to a paired male and female living attached to the fins; in that study, a very heavy infection was caused by 25 couples also attached to the skin of the eel. Details on how these ectoparasites find their hosts are unknown. *Ichthyotomus sanguinarius* is believed to be a blood-feeding parasite attaching to the fins of its hosts; it is a discretely motile carnivore using jaws to pierce and attach to its host's fins (Jumars et al. 2015).

Phylogeny and taxonomy

"Polychaetes" are usually considered as a paraphyletic grouping of more than 70 families, and the relationships among these taxa are poorly understood (Rouse and Pleijel 2001, Aguado et al. 2013). This is particularly true for several taxa, including Ichthyotomidae and other symbiotic polychaetes. Symbionts and/or parasites often have simple external morphology, and consequently, the position of these groups may be unreliable in phylogenetic analyses that are based only on morphological data (Aguado et al. 2013).

It is thought, based on jaw structure and ventral palps, that ichthyotomids could belong to Eunicida (Fauchald 1977, Glasby 1993). Nowadays, this monotypic family is placed within Palpata, Aciculata, Phyllodocida unplaced (Rouse and Fauchald 1997, Rouse and Pleijel 2001). Rouse and Pleijel (2001, p. 116) did not encourage the use of the family name Ichthyotomidae, pointing out that Eisig himself did not use the family name in his original description (Eisig referred to the taxon as "Ich.," an abbreviation for *Ichthyotomus*), only once mentioning it. However, pending further studies, placement of the genus elsewhere is uncertain (Read & Fauchald 2021).

https://doi.org/10.1515/9783110647167-014

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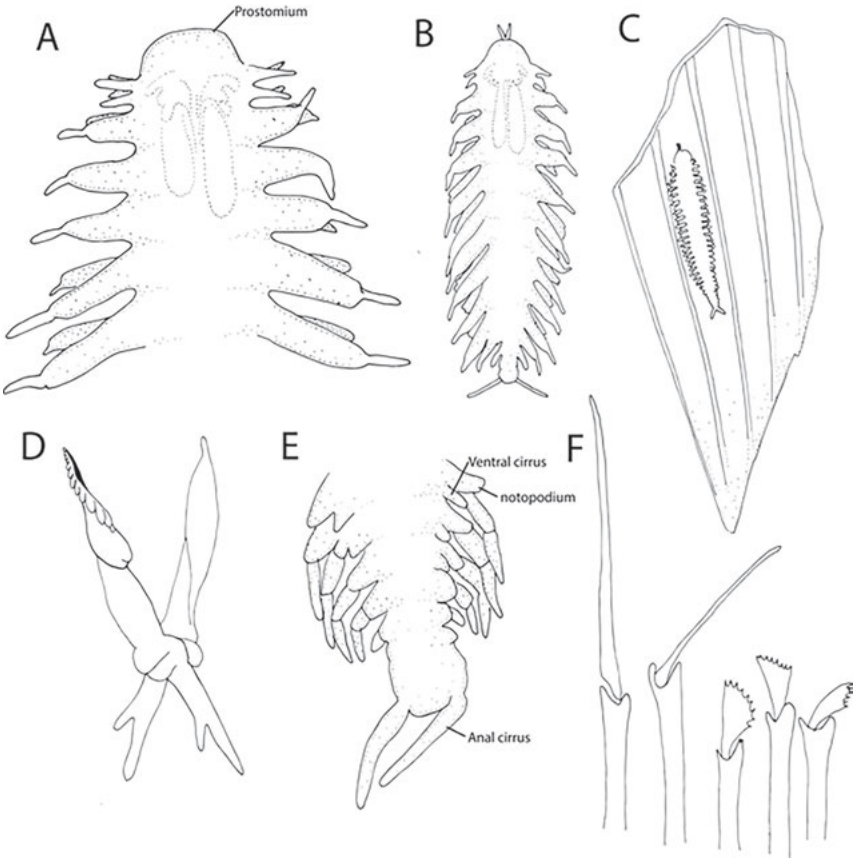


Fig. 7.13.5.1: *Ichthyotomus sanguinarius* (redrawn from Eisig 1906). A, Anterior end, dorsal view. B, Complete juvenile individual with 1 mm long and 12 segments. C, Juvenile individual with 2.8 mm long and 26 segments attached to an unpaired fin of a living eel. D, Jaw apparatus in a locking position. E, Posterior end with pygidium, ventral view. F, Neuropodial spinigers and falcigers.

Ichthyotomidae Eisig, 1906

***Ichthyotomus* Eisig, 1906**

Type species: *Ichthyotomus sanguinarius* Eisig, 1906; by monotypy.

Diagnosis (after Fauchald & Rouse 1997): Prostomium and peristomium fused, forming a single frontally rounded structure. Paired frontal antennae and a median antenna present. A pair of rudimentary palps present. First segment on median chaetigers similar to following segments with subbiramous parapodia; neuropodia slightly longer than notopodia. Dorsal and ventral cirri present. A single pair of anal cirri present. An axial pharynx with paired lateral jaws crossing in a scissor-like arrangement.

A single species is known:

1. *Ichthyotomus sanguinarius* Eisig, 1906, Gulf of Naples, Italy, attached to the fins of eels.

Acknowledgments

The authors thank Dr. Chris Glasby for providing relevant references.

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7.13.6 Lacydoniidae Bergström, 1914

Introduction

The Lacydoniidae Bergström, 1914 are free-living benthic polychaetes that inhabit sandy and muddy sediments mixed with shell debris and gravel. They can be found over a wide bathymetric range, from shallow subtidal to deeper continental shelf areas and even at abyssal zones (Rouse and Pleijel 2001).

Lacydoniids are small-sized polychaetes with few body segments. The prostomium is rounded and usually wider than long (Fig. 7.13.6.1A–D). A pair of dorsolateral antennae and ventrolateral palps are present on the prostomium (Fig. 7.13.6.1D); a dorsal median antenna has been recorded in most species and might be present in all (Rouse and Pleijel 2001). However, this fragile and minute structure can be easily lost or overlooked (Blake 1994). Eyes may be present and have been used as important characters to separate groups of species (Fig. 7.13.6.1C–E). Ciliated nuchal organs are present laterally on the posterior margin of the prostomium and may be well developed. The pharynx is strongly muscular, eversible, and has a pair of lateral glands. The tentacular segment is achaetous with a pair of ventrolateral cirri. The first three parapodia are uniramous, with neuropodial lobes, dorsal and ventral cirri, and spinigerous neurochaetae. The subsequent parapodia are biramous, with notopodia and neuropodia, dorsal and ventral cirri (Fig. 7.13.6.2C), capillary notochaetae, and spinigerous neurochaetae (Fig. 7.13.6.2D–E, respectively). Aciculae are present in both noto- and neuropodia. The pygidium has a terminal anus with two anal cirri and one or more papillae (Fig. 7.13.6.2 F).

Lacydonia Marion & Bobretzky in Marion, 1874 includes 16 nominal species, which in chronological order are as follows: (1) *Lacydonia miranda* Marion & Bobretzky *in* Marion, 1874; (2) *Lacydonia mikrops* Ehlers, 1913; (3) *Lacydonia papillata* Uschakov, 1958; (4) *Lacydonia incognita* Rullier, 1965; (5) *Lacydonia oculata* (Hartman, 1967); (6) *Lacydonia cirrata* (Hartman & Fauchald, 1971); (7) *Lacydonia laureci* Laubier, 1975; (8) *Lacydonia antarctica* Hartmann-Schröder & Rosenfeldt, 1988; (9) *Lacydonia elongata* Hartmann-Schröder & Rosenfeldt, 1992; (10) *Lacydonia gorda* Hartmann-Schröder, 1993; (11) *Lacydonia hampsoni* Blake, 1994; (12) *Lacydonia eliasoni* Hartmann-Schröder, 1996; (13) *Lacydonia quadrioculata* Magalhães, Bailey-Brock & Rizzo, 2012; (14) *Lacydonia anapaulae* Rizzo, Magalhães & Santos (2015), (15) *Lacydonia braziliensis* Rizzo, Magalhães & Santos (2015); and (16) *Lacydonia jacki* Rizzo, Magalhães & Santos (2015). Four out of these 16 species were synonymized with others or invalidated; *L. antarctica* was considered a junior synonym of *L. oculata* by Pleijel & Fauchald (1993); *L. incognita* is considered a questionable species because its description was based on an incomplete specimen, and the parapodia did not correspond to lacydoniids (Blake 1994). This species was later considered to belong to a known species of Goniadidae (Böggemann 2005). Further, *L. elongata* was synonymized with *L. papillata* (Böggemann 2009), although they were considered as distinct in Rizzo et al. (2015). *Lacydonia eliasoni* may be considered a *nomen nudum* because it was named based on a previous description and with no deposition of type material (Magalhães et al. 2012). Therefore, only 12 species of *Lacydonia* are valid. An identification key for all *Lacydonia* species was proposed by Uschakov (1972), including the four valid species described at that time. Recently, Rizzo et al. (2015) presented a key for all valid species of *Lacydonia*.

Species of *Lacydonia* have been reported in the Mediterranean, North Atlantic, Gulf of Mexico, Northeastern Pacific, and Antarctica (Blake 1994). Böggemann (2009) recorded two species from abyssal depths off the West coast of Africa. The record of this family in the South Atlantic Ocean (Campos Basin, Brazil) by Rizzo et al. (2015) expanded its distributional range and added to the diversity of lacydoniids for that region.

Morphology

Size. The body of lacydoniids is dorsoventrally flattened, widest in the anterior chaetigers (pharynx region), and slightly tapered in the posterior end. The body length can

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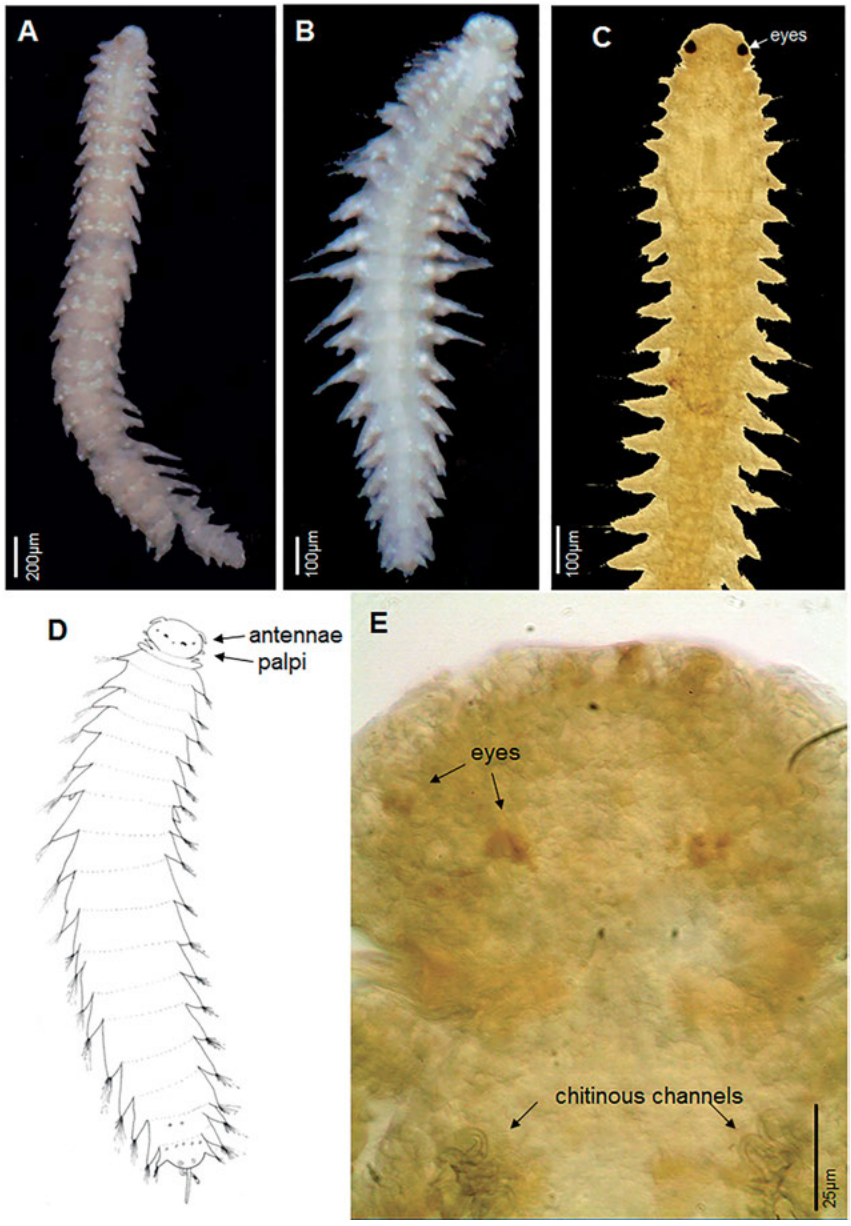


Fig. 7.13.6.1: Species of *Lacydonia* in dorsal view. A, *Lacydonia cirrata*. B, *Lacydonia mikrops*. C, *Lacydonia miranda*. D, *Lacydonia braziliensis*. E, Prostomium and first segment of *L. braziliensis*.

be less than 2 mm and usually with short parapodial lobes (i.e., *Lacydonia mikrops* and *Lacydonia braziliensis*), or longer with more than 4 mm with longer parapodial lobes (i.e., *Lacydonia gorda, Lacydonia jacki*, and *Lacydonia oculata*). The number of chaetigers may be proportional to the body length; species with longer bodies have about 40–45 chaetigers as adults, whereas shorter species have about 20 chaetigers. Transverse ciliated bands, better seen with SEM, are present dorsally and ventrally throughout the body. Segments are anteriorly as a single annulus and posteriorly indistinctly biannulated.

Prostomium. The prostomium is rounded with three dorsal antennae and two ventral palps; eyes are present or absent. Prostomium can be as wide as long (e.g., *Lacydonia cirrata*), or 1.5–3.0 times wider than long (as seen in *Lacydonia anapaulae*, *Lacydonia braziliensis*, and *Lacydonia jacki*). Some variation in the shape of prostomia has been observed by Magalhães et al. (2012). The authors noted that for 31 specimens, including the holotype of *Lacydonia quadrioculata*, the prostomium width was usually twice the length, but three specimens had a prostomium only 1.5 times wider than long, and one having the prostomium as long as wide. The anterior edge of the prostomium may have one or two frontolateral incisions (as seen in *L. anapaulae* and *L. jacki*, respectively; Fig. 7.13.6.2A). The prostomium can also have two lateral lobes on the posterior edge, as in *Lacydonia laureci* (Fig. 7.13.6.2B).

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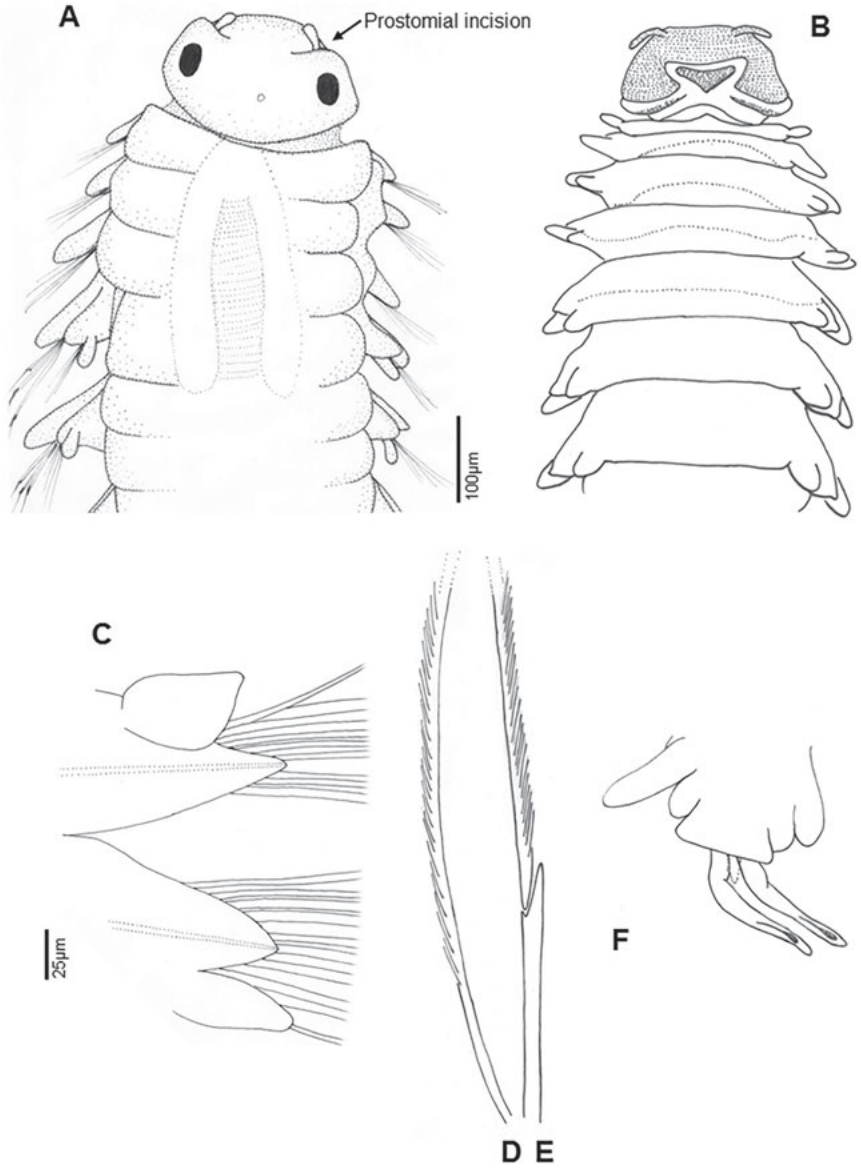


Fig. 7.13.6.2: Species of *Lacydonia* in dorsal view. A, *Lacydonia jacki*. B, *Lacydonia laureci*. C, Biramous parapodium of *Lacydonia miranda*. D, Capillary chaeta of *Lacydonia laureci*. E, Spinigerous chaeta of *Lacydonia laureci*. F, Pygidium of *Lacydonia anapaulae*.

Eyes, when present, are large, black or brownish taking up almost one third of prostomial length (as in *Lacydonia miranda, Lacydonia oculata*, and *Lacydonia jacki*), or eyes are small, punctiform brownish (as in *Lacydonia mikrops, Lacydonia quadrioculata*, and *Lacydonia braziliensis*). When large, eyes are positioned laterally, sometimes in the same level as the median antenna, or slightly in front of or behind it (*L. oculata* and *L. miranda*, respectively). On the other hand, one or two pairs of punctiform eyes may be present on the lateral and central areas of the prostomium, sometimes with only one of the two pairs well-defined and the other present as scattered dark brown spots. *Lacydonia mikrops* has only one pair of lateral eyes, near the prostomial margin, whereas *L. quadrioculata* and *L. braziliensis* have two pairs in a trapezoidal arrangement.

A pair of antennae and a pair of palps, all short, are inserted dorsolateral and ventrolateral (lined up with the oral aperture, which is ventral), respectively, on the prostomium. Dorsolateral antennae are about twice the length of palps; antennae may be digitiform, filiform, papilliform, fusiform, oval, or conical. The median antenna is difficult to observe because it is very fragile and can be easily broken; however, if stained with Shirlastain A®, for example, an insertion scar may be visible medially at the prostomium. The prostomium can be distinctly separated from the tentacular segment. A pair of nuchal organs form a ciliated collar between the prostomium and the tentacular segment, which can be seen dorsolaterally or ventrally in some species, as seen in *Lacydonia hampsoni* (Blake 1997, p. 183).

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Pharynx. The pharynx is a muscular bulb, unarmed, although jaws may be present. The pharynx can be seen through the body wall; it is a muscular axial proboscis that is rarely seen everted (Rouse and Pleijel 2001, fig. 26.2c). A terminal papillose ring may be present (Marion and Bobretzky 1875, p. 60). The pharynx lies between a pair of large lateral glands, extends through chaetigers 1–6, and can be used as a diagnostic feature to separate closely related species. The lateral glands can be roughly cylindrical or tapered anteriorly, with median and posterior regions of about the same diameter. A tangle of sclerotized channels is reported in the anterior part of the pharynx in some *Lacydonia* species, such as *Lacydonia miranda* and *Lacydonia braziliensis* (Fig. 7.13.6.1E). These channels are situated between the first and the second chaetigers when the pharynx is introverted. They arise from each lateral gland, divide into two slightly thicker channels, and finish in a pair of small pectinate blade-shaped structures (see also Marion and Bobretzky 1875, fig. 17D, plate 8). Brownish granulate patches associated with the posterior end of the lateral glands are present in *L. miranda* (see Marion and Bobretzky 1875, figs. 17 and 17D, plate 8). The nature and the function of the small pectinate blade-shaped structures and lateral glands are still unknown; they may aid food capture and digestion. The jaw apparatus in *Lacydonia* shares some similarities with the Lopadorhynchidae Claparède, 1868 (Marion and Bobretzky 1875). The gut is a straight tube that ends in a terminal anus.

The first segment is achaetous and defined as the tentacular segment. This segment is shorter than the following chaetigers in all known species. It has one pair of ventrolateral conical, digitiform, or papilliform tentacular cirri.

Parapodia and chaetae. Three pairs of anterior uniramous parapodia (segments 2–4) have neuropodial lobes and dorsal and ventral cirri, globular to conical, dorsal cirrus inserted near to parapodial base, and ventral cirrus near the middle of the parapodial lobe. Parapodia of remaining segments are biramous with notopodial and neuropodial rami separated; notopodia are shorter than neuropodia. In species having a body length of less than 2 mm, parapodial lobes are usually truncate or blunt, short, and sometimes distally bilobed (e.g., *Lacydonia jacki*), whereas in those with long bodies, lobes are elongated (e.g., *Lacydonia* cf. *papillata*). Conical and thickened notopodial lobes usually have two lamellae, prechaetal and postchaetal, both of the same length. Neuropodial lobes are usually 1.5 times longer than notopodial ones and may be conical, narrow, or sometimes distally pointed (e.g., *Lacydonia oculata*). Dorsal and ventral cirri are short, inserted near to the middle of the noto- and neuropodial lobe, respectively; it might be easily detached in some species (as in *L. jacki* for example) or nondeciduous. Dorsal cirri have been described as oval, globular, conical, ovoid, or acute. Ventral cirri may present similar length to the dorsal ones or may be slightly shorter; they can be slender, elongated, ovoid, or tapered. Noto- and neuropodial lobes are supported by a straight to slightly curved acicula, not projecting beyond the corresponding lobes.

Lacydoniids have only two main types of chaetae: notochaetae are capillaries, and neurochaetae are compound spinigers. The capillaries may be smooth (as in *Lacydonia oculata*) or serrated; in the latter type, they can be thicker basally, tapered distally with a coarsely serrated margin (as *Lacydonia jacki* and *Lacydonia miranda*); however, in some species, they are distally enlarged and finely serrated (*Lacydonia cirrata*). Capillaries can be diagonally striated (when viewed under oil immersion), as in *L. cirrata*. The compound spinigers may have blades of slightly different lengths. Shafts have one large apical tooth on one edge and one or two smaller additional teeth on the other edge, at a ratio of 2:1 (i.e., *L. cirrata*). It is possible that the presence of the two small teeth has been overlooked in most species and future SEM imaging is recommended. Blades are finely serrated.

Pygidium. The pygidium of lacydoniids has a terminal anus with a pair of cirri, and usually one midventral papilla (sometimes named as a cirrus) located between them. Specimens of *L. miranda* were described and illustrated having one or two ventral papillae (Marion and Bobretzky 1875). The anal cirri are usually filiform and long (reaching the last three chaetigers; i.e., *L. laureci*),or can be oval to globular (not extending beyond the last chaetiger; i.e., *L. miranda* and *L. oculata*). The midventral papilla can be as long as the paired cirri and, sometimes, more similar to a cirrus than to a papilla (i.e., *L. laureci and L. papillata)*. *Lacydonia miranda* and *L. oculata* have a typical papilla; *L. mikrops* has the short paired cirri and a papillate midventral cirrus. *Lacydonia quadrioculata* has a typical midventral papilla, and SEM images show sensory cilia along the distal part and paired cirri lacking such cilia (Magalhães et al. 2012, fig. 3C). Some species can have two pigmented spots, one on each cirrus, subdistal or lateral on the pair of cirri (*Lacydonia anapaulae*), in addition to a pair of subdermal pigmented spots on the pygidium (i.e., *L. braziliensis* and *L. cirrata*).

Color. Preserved specimens are usually shades of white, yellow, or green but some can be brownish. Red-brown

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pigment spots are usually present, mainly on the prostomium, first chaetiger, parapodial base (usually one or two spots), dorsolaterally on parapodia, dorsal cirri, and pygidium. Lateral anal cirri can have one pair of red-brownish pigment spots distally as mentioned above. Sometimes, glands are arranged as two or three longitudinal series, in dorsolateral and central position (as seen in *L. cirrata* and *L. braziliensis)*. *Lacydonia papillata* seems to be the only species with four large circular dark spots on the dorsal side of the second chaetiger.

Biology and ecology

There are no studies on the reproduction or feeding biology of lacydoniids. However, they have been considered carnivorous or omnivorous based on buccal morphology (Gathof 1984, Pleijel and Fauchald 1993, Wilson 2000). Recently, this family was tentatively listed as motile carnivorous (Jumars et al. 2015). Observations on preserved specimens have led to the conclusion that lacydoniids are gonochoric (Rouse and Pleijel 2001) with internal fertilization; for example, females of *Lacydonia quadrioculata* (Magalhães et al. 2012) have been observed with large (0.2 mm in diameter) and whitish intracoelomic embryos.

Lacydonids are rare polychaetes and usually found in low numbers (less than five individuals per sampling station) (Hartman and Fauchald 1971, Sardá 1982, Gathof 1984, Hartmann-Schröder and Rosenfeldt 1992, Pleijel and Fauchald 1993). Therefore, it is common to find species descriptions based on the holotype. This is the case of *L. oculata* (Hartman 1967) initially described as belonging to the genus *Scalispinigera* within the family Scalibregmatidae, and likewise for *Lacydonia laureci, Lacydonia elongata, Lacydonia antarctica* (= *L. oculata*), and *Lacydonia anapaulae*. Most species in this family are found at depths between 200 and 5,500 m, whereas *Lacydonia miranda, Lacydonia antarctica, Lacydonia mikrops, Lacydonia oculata, Lacydonia gorda, Lacydonia quadrioculata*, and *Lacydonia jacki* are found in shallower waters (<200 m).

Phylogeny and taxonomy

The Lacydoniidae and the Paralacydoniidae have an overlapping taxonomic history. The genus *Lacydonia* was described by Marion and Bobretzky (1875), and the authors discussed its similarities with phyllodocids, alciopids, and lopadorrhynchids. The relationship with phyllodocids was explained based on the shape of parapodia and chaetae, especially those found in *Notophyllum* Örsted, 1843. The authors also highlighted the resemblance of *Lacydonia* with alciopids based on the presence of three anterior rudimentary segments and with lopadorrhynchids mainly on the similar structures of the pharynx. Lacydoniids were recognized as a separate family from the Phyllodocidae in Bergström (1914). Fauvel (1913) described *Paralacydonia* and later grouped it with *Lacydonia* to form the subfamily Lacydoniinae within the Phyllodocidae (Fauvel 1923). Subsequent publications either accepted the Lacydoniidae (including *Paralacydonia*) as a separate family (e.g., Day 1967, Fauchald 1977) or considered them as part of the Phyllodocidae.

Currently, the Lacydoniidae and Paralacydoniidae are considered as separate families, but Rouse and Pleijel (2001) considered the family names redundant because both are monotypic. Morphological and molecular phylogenies agree that lacydoniids and paralacydoniids belong to the order Phyllodocida (e.g., Rouse and Fauchald 1997, Struck et al. 2007, Böggemann 2009). Rouse and Fauchald (1997) recovered the lacydoniids as sister group to the phyllodocids, whereas the paralacydoniids as sister taxon to glycerids and goniadids. Pettibone (1963) considered paralacydoniids as related to Nephtyidae, and Pleijel and Dahlgren (1998) considered them as sister to the clade composed of nephtyids, goniadids, and glycerids. Struck and Halanych (2010), using 18S and 28S rRNA data, showed Paralacydonidae as sister to Hesionidae. Böggemann (2009) presented 18S, 16S, and COI sequences for *Paralacydonia paradoxa, Lacydonia laureci*, and *Lacydonia* sp. from abyssal regions of the southeastern Atlantic. The author found a well-supported clade composed of lacydoniids and paralacydoniids using maximum likelihood.

The main morphological characters used to separate *Lacydonia* species have been the presence of eyes and its relative size, the proportions of the prostomium (width-length ratio), and length of anal cirri. Although the proportion of the prostomium had been widely used, some species may show intraspecific variation. Therefore, this characteristic should be used carefully altogether the other characteristics. The patterns of pigmentation, although difficult to observe in preserved specimens, can be a useful feature to distinguish *Lacydonia* species. There are species such as *Lacydonia miranda* that are colorless, and others with defined pigment patterns, for example, pigments basally and dorsolaterally on parapodial lobes, on the prostomium, or pygidium. The presence of glandular patches has been observed in most species, and this could be an additional character that needs further investigation.

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A pair of lateral glands and a striated pharynx between these glands as part of the pharyngeal apparatus have been observed for some species and possibly overlooked in others. In addition, *Lacydonia miranda* and *Lacydonia braziliensis* have chitinous channels with a distal, small pectinate structure associated with the lateral glands usually in the first chaetiger. The presence of these channels and pectinate structures in other species is questionable because they are difficult to observe with light microscopy. The internal anatomy of the anterior portion of the digestive tract was well described by Marion and Bobretzky (1875) for *L. miranda*. Since then, no other study has addressed the structure of the digestive tract or assessed the relevance to understanding its phylogenetic relationships. This omission can be explained by the scarcity of specimens to conduct dissection and histological studies.

The length of parapodia might be related to species size; thus, species with long bodies apparently have longer parapodia, whereas species with short bodies tend to have shorter parapodia. It has also been noticed that the dorsal and ventral cirri are apparently different among species, not only in shape or size. Cirri in lacydoniids seem to be of two types, those similar to phyllodocids, and defined as deciduous, and those that seem to be an extension of the parapodial lobes and cannot be easily lost (not deciduous). Species with large body size seem to have cirri from the second type such as *Lacydonia gorda* and *Lacydonia papillata*. Similarly, the chaetae of lacydoniids have received little attention as useful characters for distinguishing species. The capillary notochaetae can be marginally smooth or serrated; when serrated, they can be finely or coarsely serrated along the entire margin, or only along the distal region. The same seems to occur with the neurochaetae, which have two unequal teeth on the shaft's distal region. The proportion of these teeth might be used as a criterion to distinguish closely related species.

The species of *Lacydonia* could be separated into two groups or genera by the types of chaetal surface, i.e., finely versus coarsely spinulose. If notochaetae could be used to separate species groups, then those with finely spinulose capillaries would be *Lacydonia anapaulae, Lacydonia braziliensis, Lacydonia cirrata, Lacydonia oculata*, and *Lacydonia papillata*, and with coarsely spinulose or denticulate notochaetae would be *Lacydonia jacki, Lacydonia laureci*, and *Lacydonia miranda*. If neurochaetae are to be used, then those with finely spinulose neurochaetal blades are *L. braziliensis, L. miranda*, and *L. papillata*, and with coarsely spinulose blades *L. cirrata, L. jacki, L. laureci*, and *L. oculata*. An evaluation of type material for all described species and an evaluation of other phylogenetically informative characters must be done for this potential taxonomic change.

In conclusion, many taxonomically informative characters have been overlooked in previous studies. Exploring the potential use of these characters could significantly contribute to the assessment of the phylogenetic relationships within *Lacydonia* based on morphological characters.

Lacydoniidae Bergström, 1914

Lacydonia Marion and Bobretsky in Marion, 1874

Scalispinigera Hartman, 1967: 134.

Type species: *Lacydonia miranda* Marion and Bobretsky *in* Marion, 1874; by monotypy.

Diagnosis (after Rizzo et al. 2015): Prostomium rounded, palps ventral, one median and two lateral antennae, all short; eyes present or absent; nuchal organs present. Tentacular segment (=achaetous segment 1) reduced, bearing a single pair of short cirri. First three segments uniramous, all subsequent ones biramous. Parapodia well developed, with dorsal and ventral cirri. Notochaetae capillaries; neurochaetae compound spinigers. Pygidium with two lateral cirri and one median, ventral papilla or cirrus.

Twelve species are currently valid:

1. *Lacydonia anapaulae* Rizzo, Magalhães & Santos, 2015, southern Brazil, 1272 m.
2. *Lacydonia braziliensis* Rizzo, Magalhães & Santos, 2015, southern Brazil, 680–1379 m.
3. *Lacydonia cirrata* (Hartman & Fauchald, 1971), off New England, 2022 m.
4. *Lacydonia gorda* Hartmann-Schröder, 1993, Antarctic Peninsula, 165–177 m.
5. *Lacydonia hampsoni* Blake, 1994, off northern California, 985–1990 m.
6. *Lacydonia jacki* Rizzo, Magalhães & Santos, 2015, southern Brazil, 72–103 m.
7. *Lacydonia laureci Laubier, 1975,* Matapan trench, 4690 m.
8. *Lacydonia mikrops* Ehlers, 1913, Eastern Antarctica, 382–385 m.
9. *Lacydonia miranda* Marion & Bobretzky in Marion, 1874, Gulf of Marseille, shallow waters.
10. *Lacydonia oculata* (Hartman, 1967), Antarctic Peninsula, shallow waters.
11. *Lacydonia papillata* Uschakov, 1958, Kurile trench, 3352–5690 m.
12. *Lacydonia quadrioculata* Magalhães, Bailey-Brock & Rizzo, 2012, Hawaii, 27–65.5 m.

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Invalid and questionable species:

1. *Lacydonia antarctica* Hartmann-Schröder & Rosenfeldt, 1988. Off King George Island, Antarctica, 265 m. Referred to as a junior synonym of *L. oculata* by Pleijel and Fauchald (1993).
2. *Lacydonia eliasoni* Hartmann-Schröder, 1996. Skagerrak, Norway. Magalhães et al. (2012) questioned the validity of this species because it was named based on a previous description and with no deposition of type material. However, this species has been considered as accepted in WoRMS (Read and Fauchald 2021).
3. *Lacydonia elongata* Hartmann-Schröder & Rosenfeldt, 1992. Antarctica Peninsula, 634 m. Referred to as a synonym of *L. papillata* by Böggemann (2009).
4. *Lacydonia incognita* Rullier, 1965. West Africa. Original description was based on a posterior end fragment and considered as a *nomen dubium* by Blake (1994). Böggemann (2005) suggested it could be a posterior fragment of *Goniada congoensis*.

Key to species of *Lacydonia* (Extracted from Rizzo et al. 2015)

1. Eyes present 2
   — Eyes absent 7
2(1). Eyes small, punctiform 3
   — Eyes large 5
3(2). One pair of eyes, laterally positioned; prostomium as wide as long *Lacydonia mikrops*
   — Two pairs of eyes, in trapezoidal arrangement; prostomium variable 4
4(3). Prostomium usually as wide as long; antennae and anal cirri short; notochaetae smooth *Lacydonia quadrioculata*
   — Prostomium usually twice wider than long; antennae and anal cirri long; notochaetae finely serrated *Lacydonia braziliensis*
5(2). Prostomium usually as wide as long; body without pigmented spots *Lacydonia miranda*
   — Prostomium usually 1.5–2.0 times wider than long; body with pigmented spots 6
6. Prostomial anterior margin without incisions; notochaetae finely serrated *Lacydonia oculata*
   — Prostomial anterior margin with two lateral incisions; notochaetae coarsely serrated *Lacydonia jacki*
7(1). Prostomium usually as wide as long 8
   — Prostomium usually twice wider than long 11
8(7). Prostomial posterior edge with two lateral lobes *Lacydonia laureci*
   — Prostomial posterior edge without lobes 9
9(8). Prostomium not widely separated from the tentacular segment; parapodia short *Lacydonia cirrata*
   — Prostomium widely separated from the tentacular segment by ciliated nuchal organ; parapodia elongated 10
10(9). Prostomium 1.5 times wider than long, with two dorsolateral depressions; second chaetiger with four large dorsal dark spots; dorsal and ventral cirri rounded, rudimentary, not deciduous *Lacydonia papillata*
   — Prostomium about twice wider than long, without dorsolateral depressions; second chaetiger without dorsal dark spots; dorsal and ventral cirri globular to conical, deciduous *Lacydonia elongata*
11(7). Prostomium with a slit on the median anterior edge; without lobes in the posterior edge *Lacydonia anapaulae*
   — Prostomium without slit on the median anterior edge, lobes in the posterior edge 12
12(11). Prostomium 1.5 times wider than long; antennae digitate *Lacydonia hampsoni*
   — Prostomium three times wider than long; antennae oval *Lacydonia gorda*

Acknowledgments

The authors thank Dr. Cinthya S. G. Santos for the use of some figures extracted from our publication.

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Alexandra Elaine Rizzo and Wagner F. Magalhães

7.13.7 Paralacydoniidae Pettibone, 1963

Introduction

Paralacydonia is a genus described by Fauvel (1913) initially included in the Phyllodocidae and later transferred to the subfamily Lacydoniinae in Phyllodocidae (Fauvel 1914, 1923, 1953). Hartman (1959) and Hartman and Barnard (1960) considered the genus as belonging to the Lacydoniidae. Pettibone (1963) established the family Paralacydoniidae to accommodate the monotypic genus *Paralacydonia*. For the establishment of Paralacydoniidae as a separate family, based on morphological data, Pettibone (1963) noted similarities between paralacydoniids and nephtyids, such as the long parapodial supporting lamellae, and the separated rami with cilia between the notopodium and the neuropodium. This finding persuaded subsequent authors to maintain this species within the Paralacydoniidae.

Only the type species *Paralacydonia paradoxa* Fauvel, 1913, described from the Mediterranean, is usually accepted in Paralacydoniidae. Two other species, *Paralacydonia weberi* Horst, 1923 and *Paralacydonia mortenseni* Augener, 1924, and the subspecies *P. paradoxa japonica* Kitamori, 1965 were synonymized with *P. paradoxa* (Uschakov 1958, 1972). However, no revision has been done to confirm or reject these proposed synonymies (Blake 1997), perhaps because of the difficulty in locating the type material. The species *P. weberi* is listed as valid in the WoRMS database (Read and Fauchald 2021), but the difference between this species and *P. paradoxa* is only related to size. Specimens of *P. weberi* from Indonesia are larger (ca 40 mm length) than those from the Mediterranean Sea (ca 20 mm) (Horst 1923).

Paralacydoniids are small worms that burrow in soft sediments, and although they inhabit deep water (up to 5,498 m depth), they have also been recorded at only 2 m depth (Kitamori 1965). Their body is elongated; the first parapodium is uniramous and the following parapodia are biramous. The notochaetae are all simple capillaries, and the neurochaetae are compound spinigers usually with one or two companion capillaries. *Paralacydonia paradoxa* has been recorded in the Pacific, including the Indo-Pacific and the Atlantic oceans. In the Atlantic, this species was known from the North Atlantic to the Gulf of Mexico until 2007, when Rizzo and Amaral recorded it for the first time for the South Atlantic Ocean (Brazil), and posteriorly in 2011 by Rizzo and Oliveira.

Morphology

Size. Adults of *Paralacydonia paradoxa* can reach 19 mm in length and 74 chaetigers. The number of chaetigers is related to the length of the body (Rizzo and Oliveira 2011).

Color. Coloration is whitish on small specimens, yellowish on larger ones with the pharyngeal region having a rosaceous color in alcohol; brownish punctate pigments may be present on prostomium, also in the subdistal end of the lamellae, and ventrally and dorsally in the intersegmental region. The body is elongate and slender (Figs. 7.13.7.1A and 7.13.7.2A).

Prostomium. The prostomium is subconical, wider than long, slightly blunt, and with four small appendages, all biarticulate and of the same length. The antennae are dorsal and the palps ventral, a median antenna is absent (Fig. 7.13.7.2B). A pair of eyespots may be present dorsally between the prostomium and the first segment (Fig. 7.13.7.1A). A pair of nuchal organs is present on a laterodorsal depression. The proboscis is usually retracted; the peristomium is slightly fused to the prostomium and restricted ventrally to the mouth.

Pharynx. The pharynx is muscular, cylindrical, distally composed of nine soft conical papillae of the same size (Fig. 7.13.7.2B); jaws and paragnaths are absent. Anterior segments are uniannulated and become biannulated from chaetigers 15 or 16.

Parapodia and chaetae. Parapodia gradually increase in size posteriorly, becoming elongated and slender. The first segment is achaetous and indistinct from the prostomium/peristomium; tentacular cirri are absent. Chaetiger 1 is uniramous with a neuropodium and neurochaetae; subsequent chaetigers are biramous (Fig. 7.13.7.2B). The notopodia are shorter and widely separated from the neuropodia; each bears an acicula (Fig. 7.13.7.3B, C). The notopodia and neuropodia have one postchaetal and one prechaetal lamella, both rounded; also one dorsal and one ventral cirrus are present, both digitiform (Fig. 7.13.7.1B, C). The prechaetal lamella is larger than the postchaetal, with a median incision (Fig. 7.13.7.1B, C). The lower region of notopodia and upper region of neuropodia are subtriangular and distally rounded, both facing the interramal space. The dorsal cirri are one-fourth the length of the ventral cirri, whereas the ventral cirri can almost reach the length of the neuropodial prechaetal lamellae.

https://doi.org/10.1515/9783110647167-016

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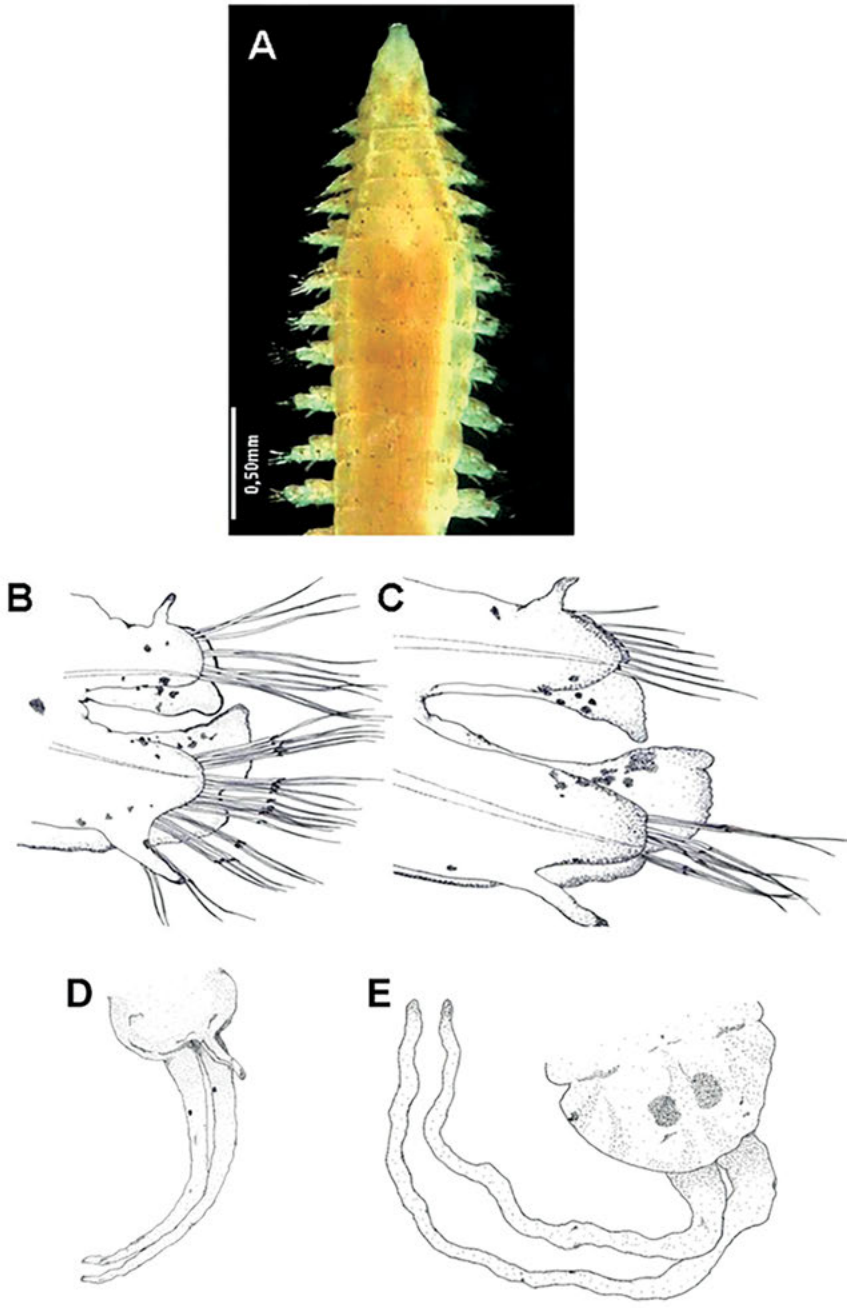


Fig. 7.13.7.1: *Paralacydonia paradoxa*. A, Anterior region, dorsal view. B, Chaetiger 15, anterior view (400×). C, Chaetiger 40, anterior view (400×). D, Pygidium with three slender anal cirri (400×). E, Pygidium with two slender anal cirri, the third one was lost, and ocellary patches (400×).

The notochaetae are simple capillaries numbering 6–11 (Fig. 7.13.7.3A); the neurochaetae include 18–20 spinigers, each with a heterogomph shaft subdistally robust, tapering distally (Fig. 7.13.7.3B). One or two simple capillary neurochaetae may be present in an inferior bundle. Notopodial capillaries and neuropodial spinigers are marginally serrated.

Pygidium. The pygidium is bulbous, slightly rounded, with three slender anal cirri, including a pair of long cirri in lateral position and single short cirrus (one-sixth length of lateral cirri) in central position (Fig. 7.13.7.3D); a single anal cirrus, when present, is positioned above the lateral cirri (usually lost in adult specimens). Juvenile specimens have two pigmented patches on the pygidium (Fig. 7.13.7.1E).

Biology and ecology

The type locality of *Paralacydonia paradoxa* is South of Monaco (Mediterranean Sea), between 48 and 52 m depth.

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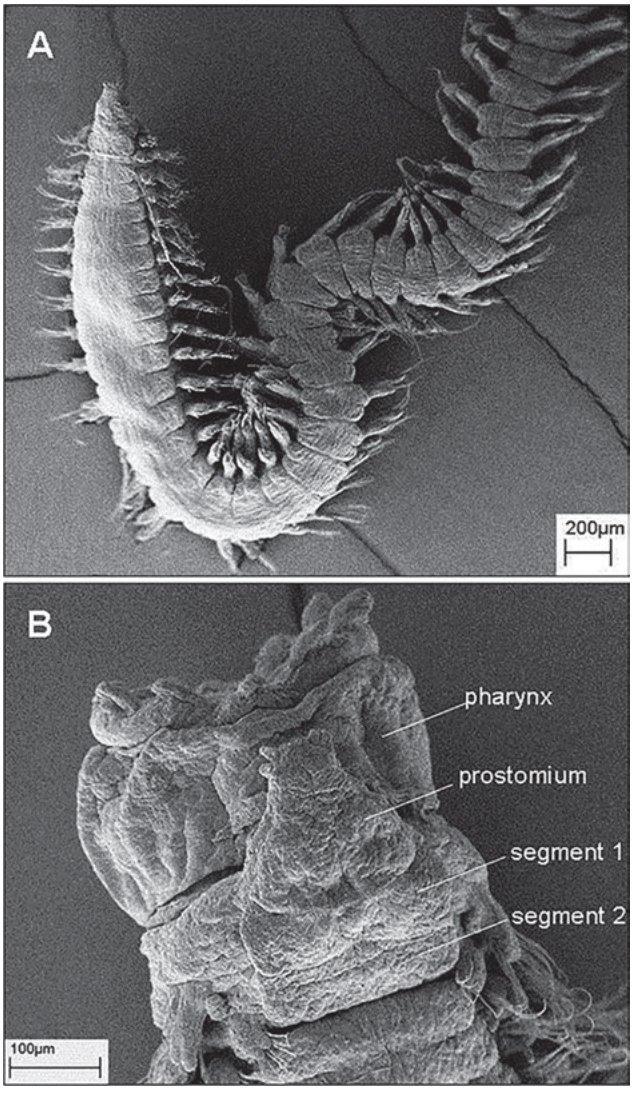


Fig. 7.13.7.2: *Paralacydonia paradoxa* (SEM). A, Anterior and median region, dorsal view. B, Prostomium, first and second segments, and eversible pharynx, dorsal view.

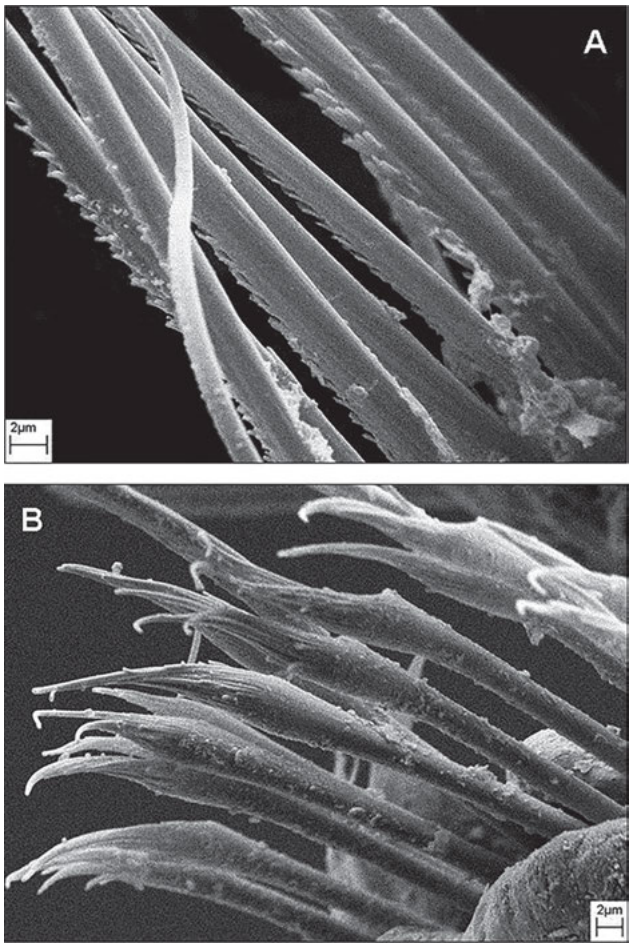


Fig. 7.13.7.3: *Paralacydonia paradoxa* (SEM). A, Details of simple notochaetae, capillary. B, Details of compound neurochaetae, spiniger (upper: blade; lower: shaft).

The holotype was not designated from any of the three specimens collected (Fauvel 1913, p. 55). The species was recorded for the first time for the South Atlantic (southeastern Brazil) in depths from 156 to 400 m by Rizzo and Amaral (2007). Because the comparison is based on phenotypic characters, this species has been considered eurybathic, having been recorded from 2 to 5498 m, with a circumtropical distribution and incursions into temperate waters. However, recent genetic studies of other polychaete families have pointed to complexes of cryptic species (e.g., Westheide and Hass-Cordes 2001, Westheide and Schmidt 2003), and it may be the case for the widely distributed *P. paradoxa*. Despite feeding preference, its morphology suggests motility, and it was supposed that they are predators using unarmed pharynx to capture prey (Jumars et al. 2015).

Phylogeny and taxonomy

See discussion about phylogeny under Lacydoniidae. Rizzo and Oliveira (2011) discussed the morphological differences between the material collected in southern Brazil and the available descriptions of *Paralacydonia paradoxa*. Differences in relation to the nuchal organ and its position on the prostomium were observed with SEM images. In the Brazilian material, a pair of nuchal organs that are present as small, slightly inflated knobs located laterally on the prostomium was clearly seen, whereas Rouse and Pleijel (2001, fig. 31.2b) found, in addition to a lateral pair, possibly a second pair, in a lateral depression on the posterior side of the prostomium. The prostomial appendages have generated controversy among researchers, having been sometimes called antennae (Fauvel 1913, Hartman and Barnard 1960, Pettibone 1963, Hartman 1965, 1968, Day 1967, Gallardo 1968, Blake 1997, Redondo and San Martín 1997) or cephalic appendages or tentacles (Fauvel 1923,

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Uschakov 1974). This may be problematic when trying to resolve the phylogenetic position of paralacydoniids in relation to other polychaete families using morphology. Nowadays, the presence of a dorsal pair of antennae and a pair of ventral palps is well accepted (Wilson 2000, Rouse and Pleijel 2001). Palps are homologous structures that are largely supported in cladistic analyses, including paralacydoniids (Rouse and Fauchald 1997). An issue that still needs to be resolved is related to the peristomium, whether it is limited only to the ventral side of mouth (Rouse and Pleijel 2001) or forming a complete ring.

The presence of small subdermal eyespots was noted in both juveniles and adults (Rizzo and Oliveira 2011). Small eyespots were also noted by Day (1967), Gathof (1984), and Redondo and San Martin (1997) but were not reported in other studies (Fauvel 1953, Hartman and Barnard 1960, Hartman 1965, Gallardo 1968, Uschakov 1974, Blake 1997, Wilson 2000). The chaetae have not been examined in detail by earlier authors, and it is possible that they may show differences. Observations based on optical microscopy have indicated the presence of simple capillary notochaetae and compound spiniger neurochaetae. However, details seen only by means of SEM, such as transverse rows of minute spines located on the inferior face of the capillary chaetae and the presence of a fringe on the basal article of the spinigers, are characters that have been insufficiently observed.

Although a median papilla on the pygidium was mentioned by Rouse and Pleijel (2001), it has not been reported by other researchers. It is possible that the median papilla mentioned by these authors is the scar of insertion of the third cirrus located centrally. A third anal cirrus can be observed, about one-sixth the length of the lateral pair (Gallardo 1968, p. 59). This structure cannot be considered a papilla because it is not a short rounded protuberance but rather resembles one of the lateral cirri, only shorter (Fig. 7.13.7.3D). However, this third cirrus is usually lost in adult specimens (Pettibone 1963). Other authors have mentioned only a pair of long anal cirri (Uschakov 1974, fig. 8, Blake 1997, Redondo and San Martín 1997, Wilson 2000, Rizzo and Amaral 2007). These and other morphological characters, along with molecular studies, will be required to confirm or reject the hypothesis that *Paralacydonia paradoxa* may be a single species with intraspecific variations, or a complex of cryptic species.

Paralacydoniidae Pettibone, 1963

Paralacydonia Fauvel, 1913

Type species: *Paralacydonia paradoxa* Fauvel, 1913; by monotypy.

Diagnosis (after Rizzo and Oliveira 2011): Prostomium conical and elongated, bearing distally two pairs of biarticulated cephalic appendages: one dorsal pair of antennae and one ventral pair of palps. Muscular pharynx, unarmed, smooth, distally papillate. First segment achaetous, appendages absent. First chaetiger with neuropodium only, following chaetigers biramous, with notopodium and neuropodium connected by a ciliated ridge. Parapodium well developed, with postchaetal and prechaetal lobes.

Notochaetae simple, capillary; neurochaetae compound, spiniger. A single species is considered as valid:

1. *Paralacydonia paradoxa* Fauvel, 1913, South of Monaco, Mediterranean, 48–52 m.

Invalid and questionable species and subspecies:

1. *Paralacydonia mortenseni* Augener, 1924, New Zealand. Considered as a synonym of *P. weberi* by Augener (1927).
2. *Paralacydonia weberi* Horst, 1923, Indonesia. Considered as a synonym of *P. paradoxa* by Fauvel (1953) and Uschakov (1958), but valid on WoRMS (Read and Fauchald 2021).
3. *Paralacydonia paradoxa japonica* Kitamori, 1965, Japan. According Kitamori (1965), this subspecies differs from *P. paradoxa* by the presence of a small depression on prostomium, biarticulate antennae, a small median papilla on pygidium (see comments above about the presence of anal median papilla), and a pair of long anal cirri. Examination of the type material would be necessary in order to verify the differences of this subspecies with *P. paradoxa*.

Acknowledgments

The authors thank Jamil R. Oliveira for the use of some figures from our publication and Chris Glasby for references.

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7.13.8 Nephtyidae Grube, 1850

Introduction

The family Nephtyidae Grube, 1850 belongs to the order Phyllodocida Dales, 1962 and includes about 140 species described within four valid genera, *Aglaophamus* Kinberg, 1865; *Inermonephtys* Fauchald, 1968; *Micronephthys* Friedrich, 1939; and *Nephtys* Cuvier, 1817. A fifth genus,

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Bipalponephtys Ravara, Wiklund, Cunha & Pleijel, 2010, was recently proposed based on the presence of bifid palps and capillary preacicular chaetae on posterior segments (instead of barred). However, its validity has been contested and must be further investigated (Dnestrovskaya and Jirkov 2010). *Aglaophamus* and *Nephtys* include most of the known species (more than 80%).

Nephtyids have a bad reputation among workers who usually need fast identifications for monitoring and impact assessment purposes (Rouse and Pleijel 2001). They may be dominant animals in benthic surveys (e.g., Lvova 1976 recorded 8,000 individuals/m^2 of *Micronephthys minuta* in the White Sea), and different species may co-occur in the same samples. Furthermore, the high morphological homogeneity within the family is an obvious difficulty in distinguishing genera and species. This difficulty is increased in the case of smaller forms with poorly developed parapodial structures.

As a group, nephtyids are likely to be monophyletic and can be separated from other polychaetes mainly by the presence of an interramal branchia attached to the ventral notopodial margin and a single median pygidial cirrus, which are unique features within the order Phyllodocida (Rouse and Pleijel 2001). Other diagnostic characters include the widely separated parapodial rami with a large number of barred chaetae. The most important characters for species discrimination include the shape of the branchiae and the segments on which they occur, the shape and proportions of parapodial lamellae, and the arrangement of papillae on the pharynx.

Morphology

Nephtyids are elongated worms, with slightly wider anterior region and tapering posteriorly (Fig. 7.13.8.1A). Their body is highly muscular and square to rectangular shape in transverse section.

Color. Body coloration in living nephtyids varies from white to dark orange. An iridescent cuticle is common in larger specimens. Marked pigmentation patterns are usually lacking, but live adult specimens may be assigned to species by the presence of pigmented bands or spots on prostomium and/or anterior segment, as in the case of *Nephtys caecoides* Hartman, 1938; *Nephtys californiensis* Hartman, 1938; *Nephtys ferruginea* Hartman, 1940; *Nephtys picta* Ehlers, 1868; and on the pygidium [e.g., *Micronephthys minuta* (Théel, 1879) and *Micronephthys neotena* (Noyes, 1980)], as shown by Dnestrovskaya and Jirkov (2010). Dorsal and ventral blood vessels are often conspicuous in live animals. Unfortunately, these diagnostic features have not always been duly mentioned in the current taxonomical literature. Also, pigmentation fades after prolonged storage.

Prostomium. The prostomium is dorsoventrally flat, with rectangular to rounded outline, and narrower than the first segments (Figs. 7.13.8.1B and 7.13.8.2A, B); its posterior margin is U- or V-shaped, extending over the first segment. The fixation routines and the degree of pharynx eversion may strongly influence the shape of the prostomium and the associated nuchal organs (Dnestrovskaya 2013). Nephtyids possess a pair of unarticulated, frontal antennae, absent only in *Inermonephtys*, and a more ventrally located pair of palps (Figs. 7.13.8.1B, C, E and 7.13.8.2B). Antennae and palps may be subequal in shape and length, or more frequently, palps are slightly larger than antennae. Palps can be simple or bifid (Fig. 7.13.8.1E) and may be inserted anteriorly, slightly behind the antennae, or ventrolaterally and further back on the prostomium (Dnestrovskaya 2013). Their relative position on the prostomium varies between species and may be used as a distinguishing character (Ohwada 1985). Median antennae are always absent. One or two pairs of subdermal eyes, associated with brain lobes (Wesenberg-Lund 1949, Rainer and Kaly 1988), may be visible on the prostomium or anterior segments, especially in juveniles, but are often externally invisible in adults. A pair of ciliated nuchal organs, which look either spherical (*Aglaophamus*, *Micronephthys*, *Nephtys*) or cirriform (*Inermonephtys*), are dorsolaterally positioned near the posterior margin of the prostomium (Figs. 7.13.8.1D and 7.13.8.2A, B).

Pharynx. The pharynx is muscular and eversible, with a conspicuous terminal ring of papillae and rows of subterminal papillae (absent in *Inermonephtys*) (Figs. 7.13.8.1F, G and 7.13.8.2A, B). The terminal ring has a series of 10 bifid distal papillae on each side of a dorsoventral slit (Wilson 2000, Laborda 2004), separated dorsally and ventrally by a gap or a simple conical papilla. The subdistal region has about 14 to 22 rows of conical to cirriform papillae that may occupy only the distal part of the pharynx or extend to its base. A single middorsal long papilla and/or a single midventral short papilla may also be present distally to the subterminal papillae. The median and/or posterior surface of the pharynx may be smooth or covered by verrucae (structures often referred to as "prickles" or "tubercles" in older nephtyid descriptions and also as "warts"). The number of rows of subdistal papillae and the number of papillae per row, as well as the presence or absence of a single middorsal papilla and verrucae in the proximal part of the pharynx, are important diagnostic characters at species level (Ravara et al. 2010a, Dnestrovskaya 2013). However, the number of subterminal rows of papillae may vary

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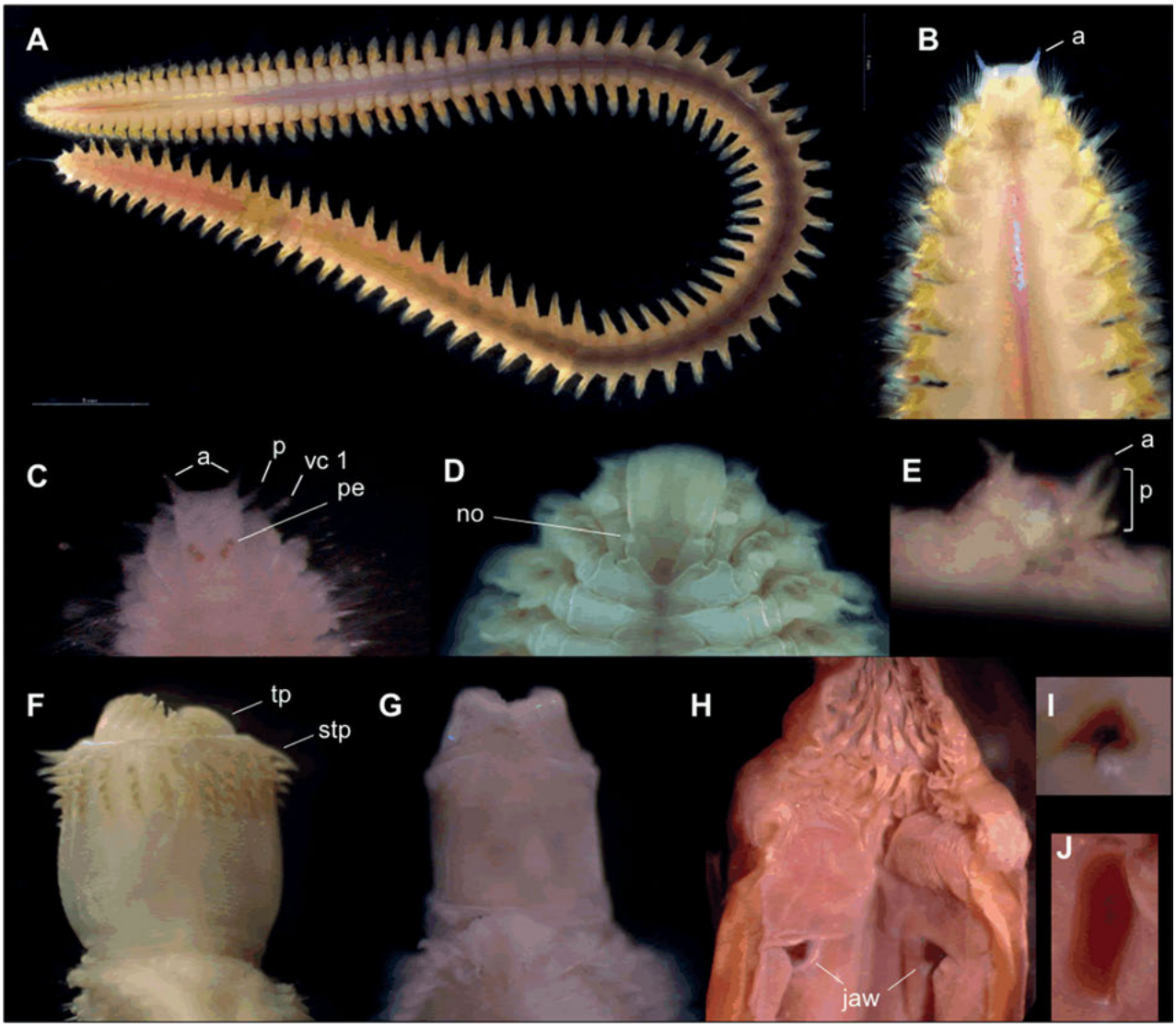


Fig. 7.13.8.1: *Nephtys* cf. *tulearensis* Fauvel 1919. A, Living specimen, dorsal view (© A. Zhadan). B, Living specimen, dorsal anterior view (© A. Zhadan). *Micronephthys oculifera* Mackie, 2000. C, Preserved specimen, prostomium, dorsal view (© A. Ravara); *Inermonephtys foretmontardoi* Ravara, Cunha & Pleijel, 2010. D, Preserved specimen, prostomium, dorsal view (© A. Ravara). *Nephtys cornuta* Berkeley & Berkeley, 1945. E, Preserved specimen, prostomium, ventral view (© A. Ravara). *Nephtys pente* Rainer, 1984. F, Preserved specimen, pharynx, ventral view (© A. Ravara). *Inermonephtys inermis* (Ehlers, 1887). G, Preserved specimen, prostomium and pharynx, dorsal view (© A. Ravara). *Nephtys longosetosa* Örsted, 1842. H, Preserved specimen, dissected pharynx (© A. Ravara). *Nephtys serrata* Imajima & Takeda, 1987. I, Jaw (© A. Ravara). *Inermonephtys inermis* (Ehlers, 1887). J, Jaw (© A. Ravara). a, antenna; no, nuchal organ; p, palp; pe, prostomial eyes; tp, terminal papillae; stp, subterminal papillae; vc1, ventral cirri of chaetiger 1.

depending on the developmental stage of the organism. For example, Dnestrovskaya (2003) reports that although adults of *Nephtys paradoxa* Malm, 1874 and *Nephtys kersivalensis* McIntosh, 1908 usually have 22 rows of subterminal papillae, there are individuals with 21 rows, and similarly, that juveniles of *Nephtys ciliata* (Müller, 1789) have 20 rows, but up to 24 rows may be present in adults.

A pair of internally located lateral jaws is present in all nephtyids, although their shape and development may vary (Fig. 7.13.8.1H–J). Jaws are usually not visible without dissection. According to Fauchald (1968), jaw shape is a good generic and specific diagnostic character. *Nephtys* jaws have a roughly triangular base with a spur on the posterior edge and a recurved tip (Figs. 7.13.8.1I and 7.13.8.2C). *Aglaophamus* jaws have the same general shape but differ by having an inner supportive ridge. *Micronephthys* jaws have a more elongated base with a poorly developed spur and also have an inner supportive ridge. *Inermonephtys* jaws have a spindle-shaped base and a straight free edge, lacking a spur, and the recurved tip is absent (Fig. 7.13.8.1J). Apart from jaws, *Nephtys glabra* (Hartman, 1950) has an additional pair of hard trepans carrying a row of

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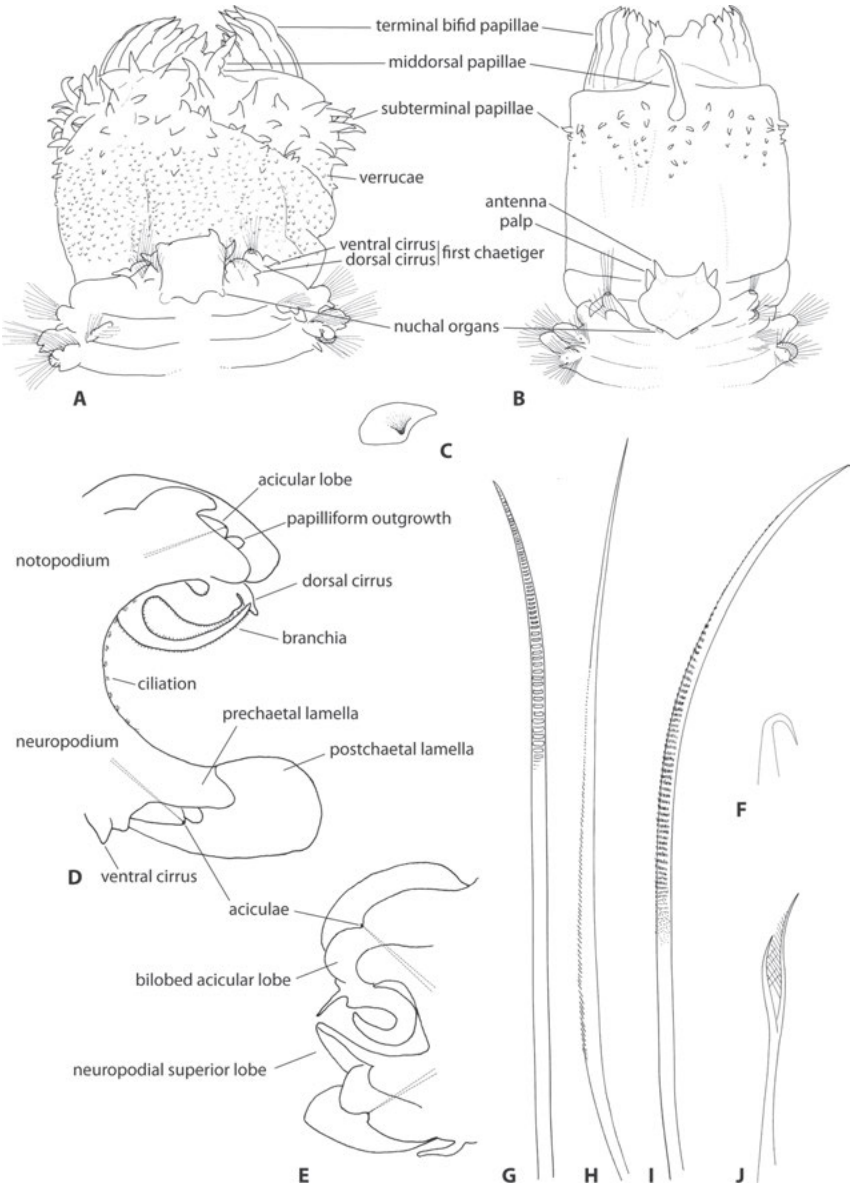


Fig. 7.13.8.2: Family Nephtyidae, general morphology (schematic figure). A and B, Prostomium and pharynx. C, Jaw. D and E, Parapodia. F, Acicula tip. G, Barred preacicular chaeta. H, Serrated postacicular chaeta. I, Spinulated postacicular chaeta. J, Lyrate chaeta (© A. Ravara).

teeth (Fauchald 1968, Imajima and Takeda 1987), a feature that may have been overlooked in other species. The jaws possess distinct rings, which most probably are laid down seasonally or annually, and may thus provide a record of an individual's age (Olive and Morgan 1983).

Peristomium. The peristomium is reduced, not visible dorsally, and ventrally limited to lips around the mouth. Laterally, the mouth may be framed by the parapodia of anterior segments. Body segments in the anterior region may be little differentiated dorsally but are always well marked on median and posterior regions.

Parapodia and chaetae. The parapodia of the first segment are less developed and usually smaller than subsequent ones, often anteriorly directed. The following parapodia gradually increase in size, attaining their maximum size and development at midbody. All parapodia are distinctly biramous, with well-separated rami (Figs. 7.13.8.2D, E, 7.13.8.3A, B, and 7.13.8.4A,). Each ramus is sustained by one or more (in *Inermonephtys*) aciculae extending through acicular lobes and carries pre- and postchaetal lamellae as well as dorsal (notopodial) and ventral (neuropodial) cirri. Acicular lobes may be acutely pointed (*Aglaophamus* and *Inermonephtys*), conical (*Micronephthys* and some species of *Nephtys*), or rounded to bilobed (other species of *Nephtys*). Some *Nephtys* species have outgrowths on the outer parts of acicular lobes (dorsally in notopodia, ventrally in neuropodia; near aciculae) (e.g., *Nephtys assimilis* Örsted, 1843; *Nephtys hombergii* Savigny in Lamarck, 1818; and *Nephtys gravieri* Augener, 1913) (Fig. 7.13.8.2D). The prechaetal lamellae may be simple or bilobed,

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rudimentary to well developed. The postchaetal lamellae may also be simple or bilobed and are usually well developed, as long as or longer than the acicular lobes. *Micronephthys* species have rudimentary or poorly developed parapodial lamellae, a feature that characterizes the genus. The shape and proportion of parapodial lamellae are important diagnostic characters at the specific level, although a degree of variation is present along the body (Ravara et al. 2010b). Dorsal and ventral cirri are present on the ventral side of noto- and neuropodia, respectively. Ventral cirri have poor distinctive value, whereas dorsal cirri may have different shapes (conical to cirriform, lamelliform) and sizes and thus contribute to species distinction. A neuropodial superior lobe may be present on anterior and median parapodia or along almost all body (in some species of *Aglaophamus*), located on the dorsal side of the neuropodia in a similar position to dorsal cirri (Figs. 7.13.8.2E and 7.13.8.3B); these are often referred to in the literature as "ventral interramal cirri" or neuropodial or ventral "interramal branchiae" and can be digitiform or tonguelike, with ciliated margins and involute, and may be similar in structure to, but smaller than, the notopodial interramal branchiae [e.g., those of *Aglaophamus verrilli* (McIntosh, 1885)]. The ciliation present along the interramal space may form a continuous row or be gathered in tuffs or ciliated pads (Fig. 7.13.8.2D).

The distinctive and usually conspicuous branchiae, also called interramal cirri, may be present or absent (some *Micronephthys*). When present, they are attached to the ventral side of the notopodia (below dorsal cirri; Figs. 7.13.8.2D, E and 7.13.8.3A, B) and may be involute (coiled inwards) or recurved (coiled outwards). Branchiae have more or less conspicuous ciliated margins and may vary in length and shape from thin and cirriform to thick and digitiform, sometimes with membranous expansions (often referred to as "foliaceous"). A small basal accessory cirrus may also be present dorsal to branchia (Fig. 7.13.8.4A). The anteriormost (2–12) and posteriormost (10–30 preanal) segments may have greatly reduced branchiae or even lack them (Rainer 1991a, Dnestrovskaya and Jirkov 2001). Furthermore, the anteriormost chaetiger where branchiae first appear may differ slightly for left and right sides of the body (Dnestrovskaya and Jirkov 2012). Branchial shape and the chaetiger from which they start and end are important characters to distinguish species, although some variation may occur in some species. In some smaller nephtyid forms, as *Aglaophamus elamellatus* (Eliason, 1951) and *Aglaophamus pulcher* (Rainer, 1991a), the number of chaetigers with branchiae varies with body length and branchiae may even be absent in smallest specimens (Ravara et al. 2010b).

The most consistent chaetal terminology currently available was proposed by Dnestrovskaya and Jirkov (2010, 2011). Noto- and neurochaetae are similar in shape and arrangement. All chaetae are simple and arranged in preacicular and postacicular bundles (Figs. 7.13.8.2B and 7.13.8.4A–B), which may be spinose (spines scattered in irregular or regular transverse rows) (Fig. 7.13.8.2I), serrated (spines scattered in one longitudinal lateral row) (Figs. 7.13.8.2H and 7.13.8.3D), or smooth (with undetectable spines) capillary chaetae. Lyrate neurochaetae may be present in species of *Aglaophamus*, *Inermonephtys*, and *Micronephthys* (Figs. 7.13.8.2J and 7.13.8.3E). On some small nephtyid forms, preacicular barred chaetae may be replaced by smooth or lightly spinose chaetae on posterior segments [e.g., *Aglaophamus australiensis* (Fauchald, 1965); *Aglaophamus gippslandicus* Rainer & Hutchings, 1977; *Nephtys fluviatilis* Monro, 1937; *Nephtys mesobranchia* Rainer & Hutchings, 1977; *Nephtys palatii* Gravier, 1904; *Nephtys semiverrucosa* Rainer & Hutchings, 1977; *Nephtys sukumoensis* Kitamori, 1960; and some species of *Micronephthys*]. On species of *Inermonephtys*, barred chaetae may be either absent [*Inermonephtys foretmontardoi* Ravara, Cunha & Pleijel, 2010; *Inermonephtys inermis* (Ehlers, 1887); and *Inermonephtys tetrophthalmus* Rainer & Kaly, 1988], present on anterior and median segments (*Inermonephtys brasiliensis* Martin, Gil & Lana, 2009; *Inermonephtys gallardi* Fauchald, 1968; *Inermonephtys patongi* Nateewathana & Hylleberg, 1986; and *Inermonephtys soldius* Franco & Rizzo, 2016) or also spinulated (*Inermonephtys japonica* Imajima & Takeda, 1985 and *Inermonephtys palpata* Paxton, 1974). On *Micronephthys stammeri* (Augener, 1932), the barred chaetae of the first chaetiger are modified by the development of a peak in the middle region of each bar (and often referred to "dentate chaetae"). The presence or absence of lyriform or modified chaetae are important diagnostic characters at generic and specific levels, whereas the presence of barred and spinose/serrated chaetae (which range in appearance from coarse to finely spinulated) may be useful at species level but somewhat subjective and frequently overlooked (Ravara personal observation). According to Rainer and Hutchings (1977), the distribution and number of the various types of chaetae along the body is also useful in distinguishing closely related species, although some size-related variation within species may occur. Aciculae are thick and usually have recurved tips at least in median and posterior parapodia (Fig. 7.13.8.2F).

Pygidium. The pygidium includes a terminal anus and single filiform cirrus located ventrally (Fig. 7.13.8.4B) that is a unique trait within the Phyllodocida (Rouse and Pleijel 2001).

Character variability. Except for a few exclusive characteristics such as the absence of antennae and pharyngeal papillae and the presence of cirriform nuchal organs for the

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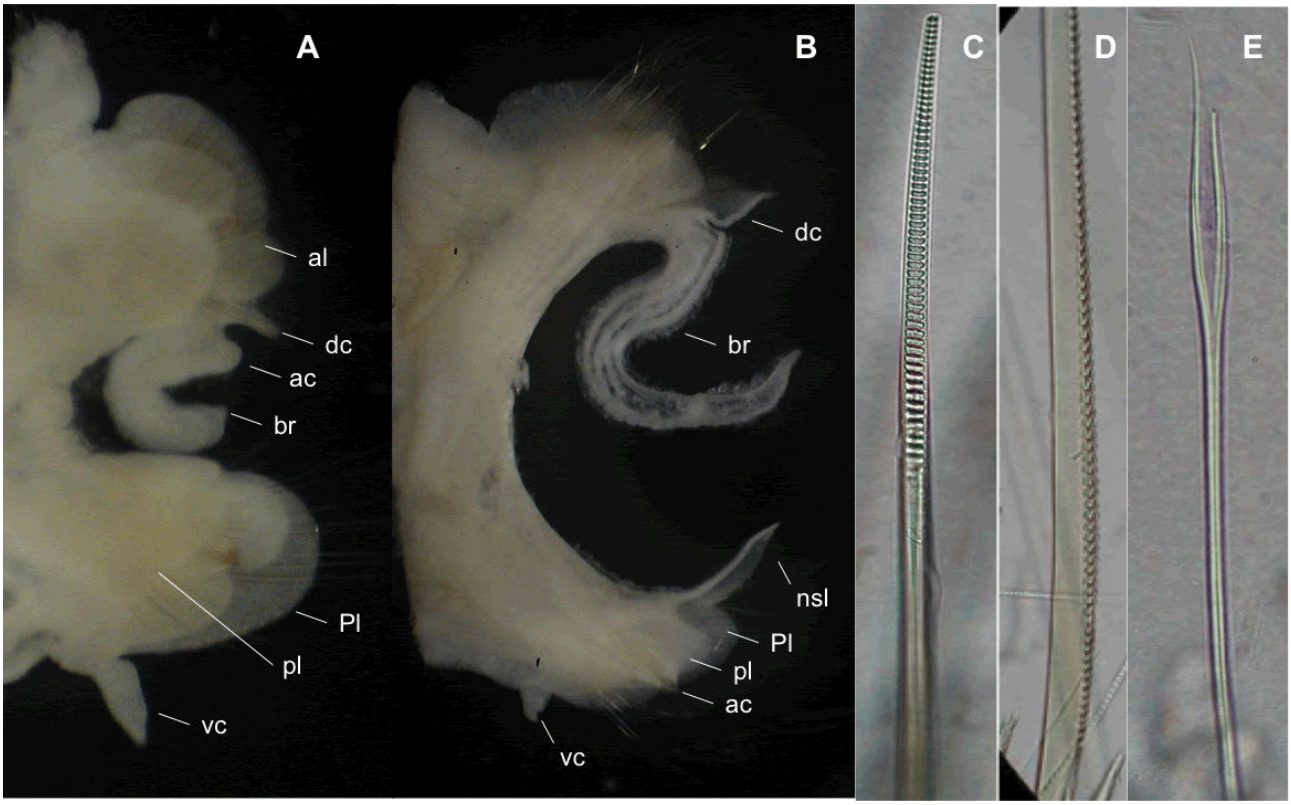


Fig. 7.13.8.3: *Nephtys pente* Rainer, 1984. A, Parapodium 30, anterior view (© A. Ravara). *Nephtys monroi* Hartman, 1950. B, Parapodium 24, anterior view (© A. Ravara). C, Barred preacicular chaeta (© A. Ravara). *Nephtys serrata* Imajima & Takeda, 1987. D, Postacicular chaeta (© A. Ravara). *Aglaophamus munamaorii* (Gibbs, 1971). E, Lyrate postacicular chaeta (© A. Ravara). ac, accessory cirri; al, acicular lobes; br, branchiae; dc, dorsal cirri; nsl, neuropodial superior lobe; pl, prechaetal lamellae; Pl, postacicular lamellae; vc, ventral cirri.

genus *Inermonephtys*, most characters vary within genera and some are common to more than one genus. It is therefore crucial that a combination of traits is used to properly assign a species to a genus. Diagnostic characteristics for the different genera within the Nephtyidae are summarized in Tab. 7.13.8.1. Species distinction is based mostly on branchial shape and placement along the body, parapodial features (acicular lobes shape, dorsal and ventral cirri, and lamellae shape and proportions), and pharyngeal papillae number and arrangement. Secondary characteristics are used to confirm identity and distinguish morphologically similar species. Among these, the antennae and palps shape and placement, length, and proportion of dorsal and ventral cirri of the first chaetiger and the presence or absence of lyrate chaetae are often used. There are also atypical characteristics for some species such as the presence of prostomial eyes, spinose preacicular chaetae on posterior chaetigers, modified chaetae, dorsal expansions near base of parapodia, and pigmentation patterns. Not all characters are well developed in juvenile forms (Dnestrovskaya and Jirkov 2012), making their identification to species level difficult, mainly when more than one species occurs in the same sample. Dnestrovskaya (2013) has prepared a useful table with taxonomic weight of morphological characters at genus and species levels. Stains such as methylene blue or Shirlastain may be useful to highlight certain morphological characters, for instance, pharyngeal papillae or post- and prechaetal lamellae (Dnestrovskaya and Jirkov 2012, Dnestrovskaya 2013).

Biology and ecology

Nephtyids are cosmopolitan and have a large bathymetric and latitudinal distribution, inhabiting estuarine, coastal waters, and offshore waters (Rainer 1991a, Murray et al. 2015). However, they are most abundant in shallow water and typically occur in muddy or sandy bottoms rather than other habitats (Murray et al. 2015), for which reason they are sometimes known as sand worms (Pettibone 1963). Most are restricted to species-specific habitats, although species may co-occur (Hylleberg and Nateewathana 1984). Shallow-water species may tolerate a wide range of salinities and some occur in nearly freshwater (Fauchald 1968, Lana 1986), as *Nephtys fluviatilis, Nephtys polybranchia* Southern, 1921, and *Micronephthys oligobranchiata* (Southern, 1921).

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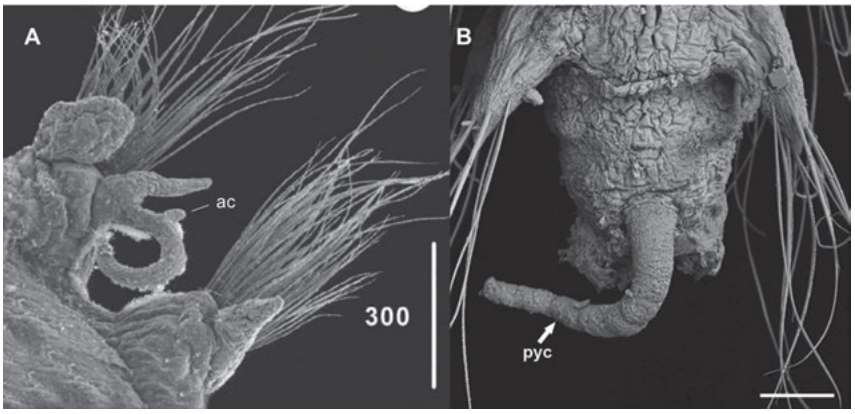


Fig. 7.13.8.4: *Inermonephtys brasiliensis* Martin, Gil & Lana, 2009. A, SEM photo, parapodium 10, posterior view, scale bar in µm (Martin et al. 2009). *Micronephthys oculifera* (Mackie, 2000). B, SEM photo, posterior end, ventral view, scale bar: 0.05 mm (Mackie 2000). ac, accessory cirri; pyc, pygidial cirrus.

Because of their strong muscular body, nephtyids are active burrowers usually living just beneath the water-sediment interface. The longitudinal musculature of these animals presents extra stiffness provided by unique intracellular calcium phosphate granules and functions like a flexible internal skeleton (Gibbs and Bryan 1984), allowing lateral sinuous movements. Such intracellular calcium granules rich in phosphorus may be found throughout the animal kingdom but not in the abundance found in nephtyids. These worms are able to borrow to a depth of at least 20 cm but do not construct permanent galleries (Wilson 2000). Although benthic in most of their life strategies, they are good swimmers when disturbed or mechanically moved into the water column. The frequency with which nephtyids swim is, within limits, a linear function of light intensity (Clark 1956). Although their ganglionic eyes are directional receptors, these worms do not orientate themselves towards a light beam, with exception for individuals of the very small species *Nephtys cornuta* Berkeley & Berkeley, 1945, which display eyes close to the surface of the brain. There are both morphological and behavioral grounds for concluding that the prostomial eyes, when present, are homologous with the eyes of *Nereis* Linnaeus, 1758 and that they are involved in the same types of behavior (Clark 1956). Clark (1956) showed that nephtyid photoreceptors include (a) two pairs of vacuolated cells lying in pigment cups, with accessory cells, embedded in the posterior part of the supraesophageal ganglion; (b) one or two cells, which may or may not be vacuolated, on either side, lying a little anterior to the ganglion; and (c) undifferentiated epidermal cells surrounded by pigment granules, which may be photosensitive. The anterior nervous system of nephtyids was also described by Clark (1956). Mushroom-shaped *corpora pedunculata* of unknown function are present but differ from those of the hesionids, nereidids, pisionids, and other scale worms (Pleijel and Dahlgren 1998) by lacking stalks. The circulatory system is closed (Clark 1956), and the respiratory pigment is hemoglobin (Jones 1955). The excretory organs from nephtyids are protonephridia associated with ciliophagocyteal organs (Goodrich 1945), also present in glycerids, goniadids, phyllodocids, and pisionids (Pleijel and Dahlgren 1998).

In most published studies (e.g., Schubert and Reise 1986, Jumars et al. 2015), nephtyids are considered to be carnivores, feeding on mollusks, crustaceans, and other polychaetes (which may include smaller conspecifics). They use the strong muscular pharynx, armed with two well-developed jaws to capture their preys. According to Schubert and Reise (1986), nephtyids seem to prey preferentially on adult individuals, and hunting occurs within the sediment thus excluding most surface-dwelling fauna and tube-building polychaetes. However, their feeding behavior seems to vary from actively hunting to sit-and-wait predation (Jumars et al. 2015). Scanning electron microscopy has revealed a very unusual interlacing muscle fiber pattern in the pharynx of nephtyids, challenging known patterns of gut architecture and feeding behavior in shallow-water polychaetes (Dinley 2012). This so-called ventral coelomic muscle may be a primary driving force for proboscis extrusion. In contrast with most polychaetes, increases in coelomic pressure caused by the combined action of longitudinal and circular muscles seem to be less relevant for proboscis extrusion in nephtyids. Such "ventral retensor" muscles that probably act in the retraction of an extruded pharynx are not yet known in other polychaetes. Deposit-feeding strategies have been suggested for a few species (Noyes 1980, Jumars et al. 2015) mainly on the basis of the presence of sediment in the gut. However, true detritus-feeding behavior seems unexpected for the family and needs empirical confirmation (Noyes 1980, Hilbig 1997, Dnestrovskaya and Jirkov 2012, Jumars et al. 2015). According to Clark (1962), deposit-feeding behavior appears when dense assemblages of species occur, and competition forces individuals into

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Tab. 7.13.8.1: Diagnostic character summary for nephtyid genera (based on Ravara et al. 2010b; emended by Murray et al. 2015).

	Aglaophamus	*Inermonephtys*	*Micronephthys*	*Nephtys*
Antennae	Present	Absent	Present	Present
Palps	Simple	Simple, small	Simple/bifid	Simple
Nuchal organs	Rounded	Cirriform	Rounded	Rounded
Acicular lobes	Acutely pointed	Conical/acutely pointed	Conical	Conical/rounded/bilobed
Parapodial lamellae	Usually well developed	Well developed	Poorly developed	Well developed
Neuropodial superior lobes	Often present	Present/absent	Absent	Sometimes present
Branchiae	Involute/recurved	Long, thin, involute	Absent/poorly developed	Recurved
Preacicular chaetae	Barred	Spinulated	Barred/smooth	Barred
Spinulation postacicular chaetae	Light	Light	Light/smooth	Light/coarse
Lyrate chaetae	Present/absent	Present	Present/absent	Absent
Pharynx papillae	Present	Absent	Present	Present
Subterminal papillae per row	More than 10, close together; proximal ones often in small groups	–	Up to 10	Less than 10 (usually 5–7)
Pharynx middorsal papillae	Present/absent	–	Present/absent	Present/absent
Pharynx proximal region	smooth/with verrucae	–	smooth/with verrucae	smooth/with small verrucae
Jaws	Conical	Spindle shaped	Conical	Conical

fine sediments with higher organic carbon content. Also, omnivorous feeding is suggested to occur in certain habitats when population densities become high (Schubert and Reise 1986). Nephtyids are known to be an important item in the diet of other polychaetes (e.g., nereids), crabs, fish, and birds (Schubert and Reise 1986).

Reproduction and development

Nephtyids are gonochoric and iteroparous but do not breed necessarily every year. All mature worms in a population breed synchronously (sometimes during a single day). Some species display some degree of epitoky, with modified elongated parapodial lobes and chaetae (Garwood and Olive 1981). Dnestrovskaya and Jirkov (2011) indicated that epitokous individuals have increased numbers of elongated chaetae, but they did not report specialized chaetae or parapodial modifications. Gametes are discharged through the anus at the water-sediment interface, where fertilization occurs (Rouse and Pleijel 2001). The planktonic larvae feed on phyto- and zooplankton (Yokouchi 1991) and may spend up to 5 weeks in the water column before settling down on the bottom sediments where metamorphosis takes place (Noyes 1980). There are few available descriptions of nephtyid metamorphosis from planktonic larvae to benthic juveniles. Noyes (1980) presented one of the most complete life history studies as yet available and described the larval stages of *Aglaophamus neotenus* Noyes, 1980 (Trochophore, Metatrochophore I and II and juvenile; Fig. 7.13.8.5). Little is known about the survival time of the larvae, or their potential to disperse rather than settling locally. Recent molecular analyses of *Aglaophamus australiensis* and *Nephtys longipes* Stimpson, 1856 from southeastern Australia were carried out to assess whether geographically distinct populations show genetic differences (Smith et al. 2015). Little evidence of genetic differentiation among populations was found, despite a high level of genetic diversity within each species. The results suggested that both species were able to disperse to distant estuaries with the aid of tidal flushing and coastal ocean currents. Several studies described gametogenic cycles and early development for particular species (e.g., Wilson 1936, Rasmussen 1973, Olive 1978, Mathivat-Lallier and Cazaux 1991), whereas Clark and Clark (1962) described growth and regeneration process. Reproductive failures in spawning or recruitment seem to be common in nephtyids (Olive and Morgan 1983), which explains why so many populations are dominated by large and old individuals.

Nephtyids are long-lived and slow-growing animals, and offspring have a low survival rate to adulthood (Olive 1985). Life span was estimated at up to 9 years for *Nephtys assimilis*, based on size models and annual growth rings

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on the jaws (Kirkegaard 1970, Rainer 1991b), but there are records of older animals. Olive (1985) found nephtyid worms up to 12 years old in a UK population, and Caron et al. (1995) reported a specimen of *Nephtys caeca* (Fabricius, 1780) from Canada with 15 visible jaw rings. Most nephtyids are no longer than 10 cm, but adults from cold-temperate species can reach up to 30–40 cm in size, 1 cm width and about 150 segments (Hilbig 1997, Rouse and Pleijel 2001). There are observations of *N. caeca* specimens with 150 cm of length (I. G. Zacks, personal communication). Tropical and subtropical species tend to be small, but they are always conspicuous in benthic samples because of their active movements.

The commercial use of nephtyids is only known for intertidal large-bodied species such as *Nephtys hombergii* and *Nephtys caeca*, which are appreciated baits for fishing. In Europe, these species are abundant and easily collected in estuaries and coastal habitats. They are commonly called "white rag worms" (*N. hombergii*) or "cat worms" in Britain (e.g., Olive 1994), on account of the typical arrangement of frontal antennae in the prostomium, and "silver rag" (*N. caeca*), on account of their iridescent body cuticle that attract fish in bright conditions. *Nephtys cirrosa* Ehlers, 1868, a smaller species frequent in clean sandy beaches in Britain and Southern Europe, is usually known as "white catworm." The slow growth, infrequent spawning, and low recruitment rates make most nephtyids species unsuitable for bait culture.

Phylogeny and taxonomy

The first nephtyid species described, *Nephtys* caeca (Fabricius, 1780) and *Nephtys ciliata* (Müller, 1789), were initially ascribed to the genus *Nereis* Linnaeus, 1758. The genus *Nephtys* was later described by Cuvier (1817) but still placed within the Nereid group. Grube (1850) erected the family Nephtyidae as "Nephtydea" to include the genus *Nephtys*. Several genera have subsequently been described by Kinberg (1865), Friedrich (1939), Fauchald (1968), Imajima and Takeda (1987), and Ravara et al. (2010a).

The earlier delineations of the genera (e.g., Hartman 1950, Taylor 1984, Rainer & Kaly 1988, Hilbig 1997) were based mainly on branchial shape (involute in *Aglaophamus*, recurved in *Nephtys* or absent in *Micronephthys*). Although not present in all members of the group, this character has been the putative support for monophyly of the family. However, a recent study by Ravara et al. (2010a) relocated two species previously assigned to the genus *Nephtys* (*Nephtys pulchra* and *Nephtys australiensis*) into the genus *Aglaophamus* revealing homoplasy for the branchial shape character. It became necessary that a combination of characters be used to properly assign a species to a genus as there are no obvious apomorphies for the genera and their delineation still lack stability (Rouse and Pleijel 2001, Ravara et al. 2010a). Furthermore, there are still many doubts about the correct allocation of many species, and there is some evidence that the present genera may need to be subdivided (Ravara et al. 2010a).

When originally erected, the family Nephtyidae was placed among other errant groups of polychaetes such as "Aphroditea," "Amphinomiacea," "Glycerea," "Phyllodocea," "Eunicea," and "Syllidea." Levinsen (1883) split all these families into several groups and included the Nephtyidae within the "Phyllodociformia," whereas Hatschek (1893) regrouped the same families as "Nereimorpha." Uschakov (1955) distinguished again a "Phyllodocemorpha" group that included the Nephtyidae, from a "Nereimorpha" group. After the erection of orders by Dales (1962), based on structural relations of pharynx and nephridia, the Nephtyidae remained within the Phyllodocida group. More recently, phylogenetic-based studies by Rouse and Fauchald (1997) and Rouse and Pleijel (2001) confirmed Nephtyidae within Phyllodocida, as a sister-group of Phyllodocidae, Lacydoniidae, Pisionidae, Paralacydoniidae, Goniadidae, and Glyceridae. On the other hand, Pleijel and Dahlgren (1998) mentioned the unique pygidial cirrus as an additional evidence for monophyly and placed the family in the same clade as Glyceridae and Goniadidae. The position of Nephtyidae within Phyllodocida remains uncertain, but more recent analyses suggest that they may be closely related to the Hesionidae and the Pilargidae (Rousset et al. 2007, Struck et al. 2007, Zrzavý et al. 2009).

The family contains about 140 species distributed in four genera: *Aglaophamus*, *Inermonephtys*, *Micronephthys*, and *Nephtys*. Most described and accepted species belong to *Aglaophamus* (ca. 50 species) or *Nephtys* (ca. 70 species), whereas the other two genera have 10 and 15 species each (WoRMS, consulted on 31 August 2021). The genus *Bipalponephtys* recently erected by Ravara et al. (2010a) was considered to be a junior synonym of *Micronephthys* by Dnestrovskaya and Jirkov (2010), and the synonymy of the genus *Dentinephtys* with *Nephtys* by Ravara et al. (2010a) was not recognized by Alalykina and Dnestrovskaya (2015). The validity of these two genera must be further investigated with the examination of more taxa. Two fossil records from the Carboniferous Period, of *Astreptoscolex anasillosus* Thompson, 1979 and *Didontogaster cordylina* Thompson, 1979, were attributed to Nephtyidae (Fitzhugh et al. 1997). The cirriform branchiae of the Silurian *Kenostrychus clementsi* Sutton, Briggs, Siveter & Siveter, 2001, preserved with a fidelity unknown among other polychaetes, may be homologous to extant nephtyids (Sutton et al. 2001).

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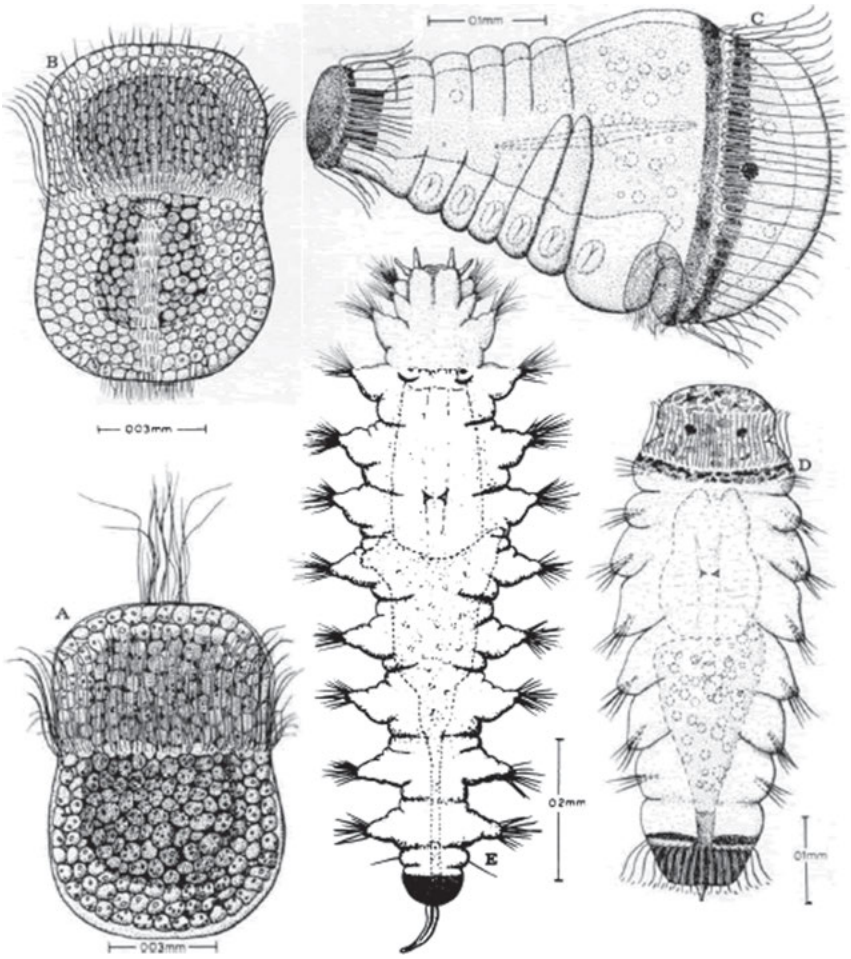


Fig. 7.13.8.5: Larvae of *Micronephtys neotena* (Noyes, 1980). A, Early trochophore. B, Trochophore. C, Metatrochophore I with diatom present in gut. D, Metatrochophore II. E, Juvenile (© Copyright The Biological Bulletin).

In the last three decades, major revisions or regional surveys have been carried out mainly in Europe (Rainer 1984, 1989, 1991a, Jirkov and Paraketsova 1996, Ravara et al. 2010b, Dnestrovskaya and Jirkov 2010, 2012), Brazil (Fauchald 1976, Lana 1986, Rizzo and Amaral 2007, Franco and Rizzo 2016), Australia (Paxton 1974, Rainer and Hutchings 1977, Rainer & Kaly 1988), Japan (Imajima and Takeda 1985, 1987), China (Jung and Hong 1997), Thailand (Nateewathana and Hylleberg 1986), California (Hilbig 1997, Lovell 1997), Gulf of Mexico (Taylor 1984), and Arctic Ocean (Dnestrovskaya and Jirkov 2001). These revisions greatly increased the number of described species, but many geographical regions remain unexplored or poorly known and doubts also remain about many records. A significant number of nephtyid species presently accepted are known only from their original description, and some are still based on a single specimen. Many others are only reported in older references, often with poor or no information on characters currently used for distinguishing species. Furthermore, the recorded geographical distribution of some species appears to be exceptionally wide, leading to the hypothesis that they in fact represent complexes of morphologically similar species, still in need of taxonomical and molecular revision.

Nephtyidae Grube, 1850

Type genus: *Nephtys* Cuvier, 1817

Diagnosis. Elongate body, quadrangular in cross section. Pigmentation patterns present or absent. Prostomium with one pair of antennae (except for *Inermonephtys*) and one pair of palps subequal in length and shape. One or two pairs of eyes visibly present or absent on prostomium or in anterior region. Pair of nuchal organs present near the posterior corners of the prostomium. Pharynx smooth or covered with verrucae, with or without papillae; jaws present. When present, pharyngeal papillae arranged in terminal ring and 14–22 subterminal longitudinal rows. Parapodia biramous with well-developed acicular lobes and well or poorly developed pre- and postacicular lamellae. Branchiae and dorsal cirri attached to ventral side of notopodia (branchiae absent in some species of *Micronephthys*). Chaetae all simple: chambered preacicular chaetae; spinose or serrated postacicular chaetae; lyrate chaetae present or absent. Pygidium with terminal anus and single anal cirrus.

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***Aglaophamus* Kinberg, 1865 (sensu Hartman, 1950)**

Type species: *Aglaophamus lyratus* Kinberg, 1865, by monotypy.

Diagnosis (based on Ravara et al. 2010b; emended by Murray et al. 2015): Antennae and palps present. Pharynx usually with rows of more than 10 closely together subterminal papillae, of which the proximal ones are sometimes arranged in small groups; longer subdistal middorsal papilla absent or present; proximal region smooth or with verrucae. Jaws conical, hooklike. Nuchal organs rounded. Parapodial acicular lobes acutely pointed; lamellae usually well developed; neuropodial superior lobes may be present in anterior parapodia. Branchiae involute or recurved. Lyrate chaetae present or absent. All aciculae with curved tips.

***Inermonephtys* Fauchald, 1968**

Type species: *Inermonephtys inermis* (Ehlers, 1887), by original designation.

Diagnosis (based on Ravara et al. 2010b): Antennae absent; palps present, usually located ventrally. Pharynx smooth, without papillae; spindle-shaped jaws present. Nuchal organs present, eversible, digitiform. Parapodial acicular lobes usually conical to acutely pointed; lamellae well developed; neuropodial superior lobes may be present in anterior parapodia. Branchiae long, thin, and involute. Lyrate chaetae present. Anterior parapodia may have more than one acicula. Aciculae of posterior parapodia with curved tips.

***Micronephthys* Friedrich, 1939**

Type species: *Micronephthys minuta* (Théel, 1879), by monotypy.

Diagnosis (based on Ravara et al. 2010b; emended by Murray et al. 2015): Small bodies. Antennae and palps present. Palps simple or bifid. Pharynx with proximal region smooth or with verrucae; subterminal pharyngeal papillae present; middorsal papilla present or absent; jaws conical, hooklike. Nuchal organs rounded. Parapodial acicular lobes conical; lamellae rudimentary or poorly developed; neuropodial superior lobes absent. Branchiae usually absent or, if present, poorly developed, straight. Lyrate chaetae present or absent. Chambered (barred) chaetae present or absent. Aciculae of median and posterior parapodia with curved tips.

***Nephtys* Cuvier, 1817**

Type species: *Nephtys hombergii* Savigny in Lamarck, 1818 by subsequent designation (first designation unclear).

Diagnosis (based on Ravara et al. 2010b): Antennae and palps present. Pharynx usually with rows of less than 10 subterminal papillae (usually up to 5–7); long middorsal papilla present or absent; proximal region smooth or covered with small verrucae. Jaws conical, hooklike. Nuchal organs rounded. Parapodial acicular lobes conical, rounded or bilobed; lamellae well developed; neuropodial superior lobes may be present in anterior parapodia. Branchiae recurved. Lyrate chaetae absent. Aciculae of median and posterior parapodia with curved tips.

Remarks: According to Murray et al. (2015), currently, the only diagnostic differences between the genera *Aglaophamus* and *Nephtys* are the shape of the acicular lobe — acutely pointed in the former and conical, rounded, or bilobed in the latter — and the absence of lyrate chaetae in *Nephtys*, although they may be present or absent in *Aglaophamus*. Hartmann-Schröder (1959) described the species *Nephtys furcifera* as having lyriform chaetae in postacicular position, although securing the possibility of those being artifacts created by other broken chaetae since they were not homogeneously distributed along the body. Therefore, the taxonomical position of this species needs revision. The neuropodial superior lobes were previously considered to be absent from *Nephtys* species (Ravara et al. 2010b). However, there are seven currently accepted species (*N. bilobatus* Kudenov, 1975; *N. impressa* Baird, 1873; *N. monroi* Hartman, 1950; *N. multicirrata* Hartmann-Schröder, 1960; *N. oculata* Hartmann-Schröder, 1959; *N. singularis* Hartman, 1950; and *N. squamosa* Ehlers, 1887) that have this structure. Therefore, the possible presence of this character was included in the genus diagnosis.

Acknowledgments

The order of authors in this chapter is an academic formality or convenience. As friends and colleagues, we three were glad to share our common experience and enthusiasm for worms. We thank Anna Zhadan, Anna Murray, Pat Hutchings, Andy Mackie, and Daniel Martin for the use of some figures from their publications. We also thank Carol Schachinger, Managing Editor of the *Biological Bulletin*, for the use of figure 5, originally published in a paper by George Noyes. Our thanks to Anna Murray and Natalya Dnestrovskaya for their careful revisions and to Markus Böggemann for his patience and editorial care. Financial support was provided to the first author through FCT in the scope of the framework contract foreseen in the Decree-Laws 57/2016 and 57/2017, and from CESAM, by FCT/MEC through national funds, and cofunding by the FEDER, within the PT2020 Partnership Agreement and Compete 2020 (UIDB/50017/2020+UIDP/50017/2020).

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M. Teresa Aguado

7.13.12 Antonbruunidae Fauchald, 1977

Introduction

Antonbruunidae Fauchald, 1977 is a family of marine annelids that live within the mantle cavity of chemosynthetic bivalve mollusks from shelf to abyssal depths (Hartman and Boss 1966, Fauchald 1977, Quiroga and Sellanes 2009, Mackie et al. 2015). The family currently comprises a single genus, *Antonbruunia* Hartman & Boss, 1965, and three species: *Antonbruunia viridis* Hartman & Boss, 1966, which lives in association with *Lucina fosteri* Hartman & Boss, 1965 (Lucinidae); *Antonbruunia gerdesi* Quiroga & Sellanes, 2009, which lives within *Calyptogena gallardoi* Sellanes & Krylova, 2005 (Vesicomyidae); and *Antonbruunia sociabilis* Mackie, Oliver & Nygren, 2015, which lives within *Thyasira scotiae* Oliver & Drewery, 2014 (Thyasiridae). The systematic affiliations of this group have been quite unstable, as their adaptations to a symbiotic way of life make them morphologically similar to other symbiotic polychaete groups, such as nautiliniellids and *Calamyzas* Arwidson, 1932 (both currently within Calamyzinae, a subfamily of Chrysopetalidae) (Aguado et al. 2013, 2016). The group is herein considered to belong to Phyllodocida (Annelida, Errantia), closely related to Pilargidae (Mackie et al. 2015), although the support for this relationship is still not robust. Other authors currently consider *Antonbruunia* as a member of Pilargidae (Salazar-Vallejo and Rizzo 2021, Glasby and Salazar-Vallejo, 2021). From our point of view (Salazar-Vallejo, Rizzo, and Glasby personal communication and Aguado), different interpretations are possible, considering the current available data. The aim of this chapter is to provide a revision of this small group of symbiotic polychaetes, summarizing data about their interesting way of life, particular adaptations and changing hypotheses on systematic affiliations that could not be such extensively described in this volume if they were only included as a member of Pilargidae.

Morphology

Body shape and color. Antonbruunidae are homonomously segmented worms, small to medium size, usually about several cm long. The body is subcylindrical, ventrally flattened, and dorsally convex (Fig. 7.13.12.1A, B). Living females are green, males white (*Antonbruunia viridis*), both green (*Antonbruunia gerdesi*), or white with green gut and green gut caeca (*Antonbruunia sociabilis*, Graham Oliver pers. obs., 2018); all pale when preserved (Fig. 7.13.12.2A, B) (Hartman and Boss, 1965, Quiroga and Sellanes 2009, Mackie et al. 2015).

Prostomium. The prostomium is well developed, trapezoidal in shape, bearing a pair of anteroventral palps, a pair of dorsolateral antennae, and a posterodorsal median antenna, all cirriform or conical in shape, including palps (Figs. 7.13.12.1A and 7.13.12.3F, G). For the terminology of anterior appendages, the two pairs of anterior prostomial appendages are named in accordance with other taxa in Phyllodocida (palps and antennae), as suggested by Rouse and Fauchald (1997) and Rouse and Pleijel (2001). Eyes are missing. Nuchal organs seen in *A. sociabilis* as ciliated grooves, dorsolaterally located after the prostomium (Fig. 7.13.12.3F) (Mackie et al. 2015).

Body segments. Segment one bears a pair of dorsal and ventral cirri and has no parapodia, with dorsal cirri longer than ventral and slightly larger than those of subsequent segments (Fig. 7.13.12.1A). Short and narrow muscular pharynx everted in some specimens, globular in shape, with no distal appendages or pharyngeal armature (Fig. 7.13.12.3A, G); everted pharynx with some small distal papillae in *Antonbruunia viridis* (Hartman and Boss 1966); and digestive tube with lateral caeca from segment 3 in *Antonbruunia sociabilis* (Mackie et al. 2015).

Parapodia and chaetae. All parapodia are subbiramous, conical in shape, increasing their length towards posterior part of the body. Notopodia have one straight and pointed notoacicula (seen in *A. sociabilis*) and conical dorsal cirri (Figs. 7.13.12.1A, B, 7.13.12.3B, I, and 7.13.12.4A, C). Neuropodia are well developed and conical in shape (Fig. 7.13.12.3A); those from midbody segments are slightly longer, without parapodial distal lobes and with chaetal fascicles (Fig. 7.13.12.4F, G). Neuropodia have two stout and distally pointed neuroaciculae and ventral cirri shorter in length than dorsal ones (Figs. 7.13.12.1A, B, 7.13.12.3B, I, and 7.13.12.4G). The ventral surface of midbody neuropodia has pores in *Antonbruunia gerdesi* (Fig. 7.13.12.4E, F). Chaetal fascicles have numerous chaetae, mainly in midbody fascicles (Figs. 7.13.12.3C, E, J, K and 7.13.12.4D, E). The chaetae of anterior and midbody segments in *A. gerdesi* and *A. sociabilis* are organized in two bundles (Figs. 7.13.12.3I, J and 7.13.12.4B, F, I), bundles less evident in *Antonbruunia viridis* (Fig. 7.13.12.3B, C, E). Neurochaetae are simple, bifid, with two long, distal, curved teeth, one of them wider than the other (Figs. 7.13.12.1C, 7.13.12.3C–E, K, and

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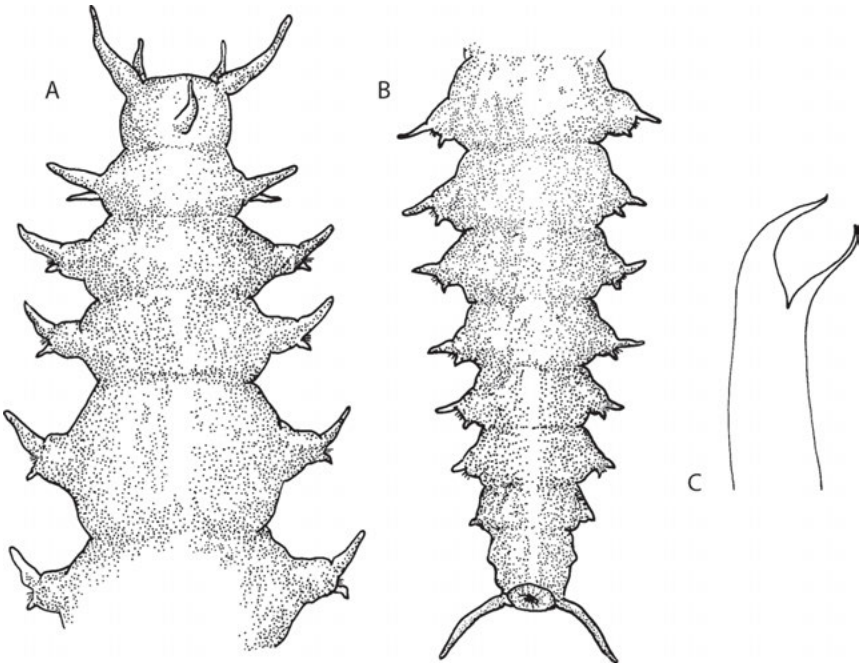


Fig. 7.13.12.1: *Antonbruunia viridis*. A, Anterior end, dorsal view. B, Posterior end, ventral view. C, Midbody chaeta. A and B modified from Hartman and Boss (1965); C drawn from micrograph.

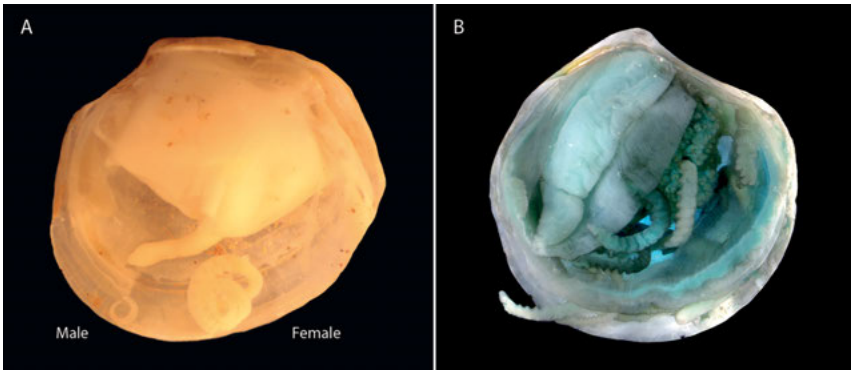


Fig. 7.13.12.2: A, Female and male of *Antonbruunia viridis* (paratypes LACM-AHF POLY 162) in opened host *Lucina fosteri* (photo: M. Capa). B, *Antonbruunia sociabilis* (NMW specimens; methyl green staining) in opened host *Thyasira scotiae* (photo: P.G. Oliver).

7.13.12.4H, I). Posteriormost segments have shorter parapodia and few chaetae.

Pygidium. The pygidium has two cirriform anal cirri (Figs. 7.13.12.1B and 7.13.12.3H).

Biology and ecology

The three species have been found in different bivalve hosts and are from distant geographic areas, as well as different depths: *Antonbruunia viridis* was found within *Lucina fosteri*, from southwest Madagascar (Western Indian Ocean), hypoxic sediments of black-brown oozy mud and detritus, at 68–82 m deep; *Antonbruunia gerdesi* was found within *Calyptogena gallardoi*, cold seep location off central Chile (from Southeastern Pacific Ocean), sticky dark grey sediments smelling of sulfide, at 795–846 m deep; and *Antonbruunia sociabilis* was found within *Thyasira scotiae*, from west Isle of Harris, Scotland (Northeastern Atlantic), in sulfidic sediments, at 1187–1200 m deep (Hartman and Boss 1965, Quiroga and Sellanes 2009, Mackie et al. 2015). Specimens of *A. viridis* were mostly found in one pair (male and female) per each infested bivalve (Fig. 7.13.12.2A), whereas specimens of *A. gerdesi* and *A. sociabilis* were found in larger numbers within their hosts (Fig. 7.13.12.2B).

A sexual dimorphism has been reported for *Antonbruunia viridis*. Females of *A. viridis* are larger, approximately double in size than males (Hartman and Boss

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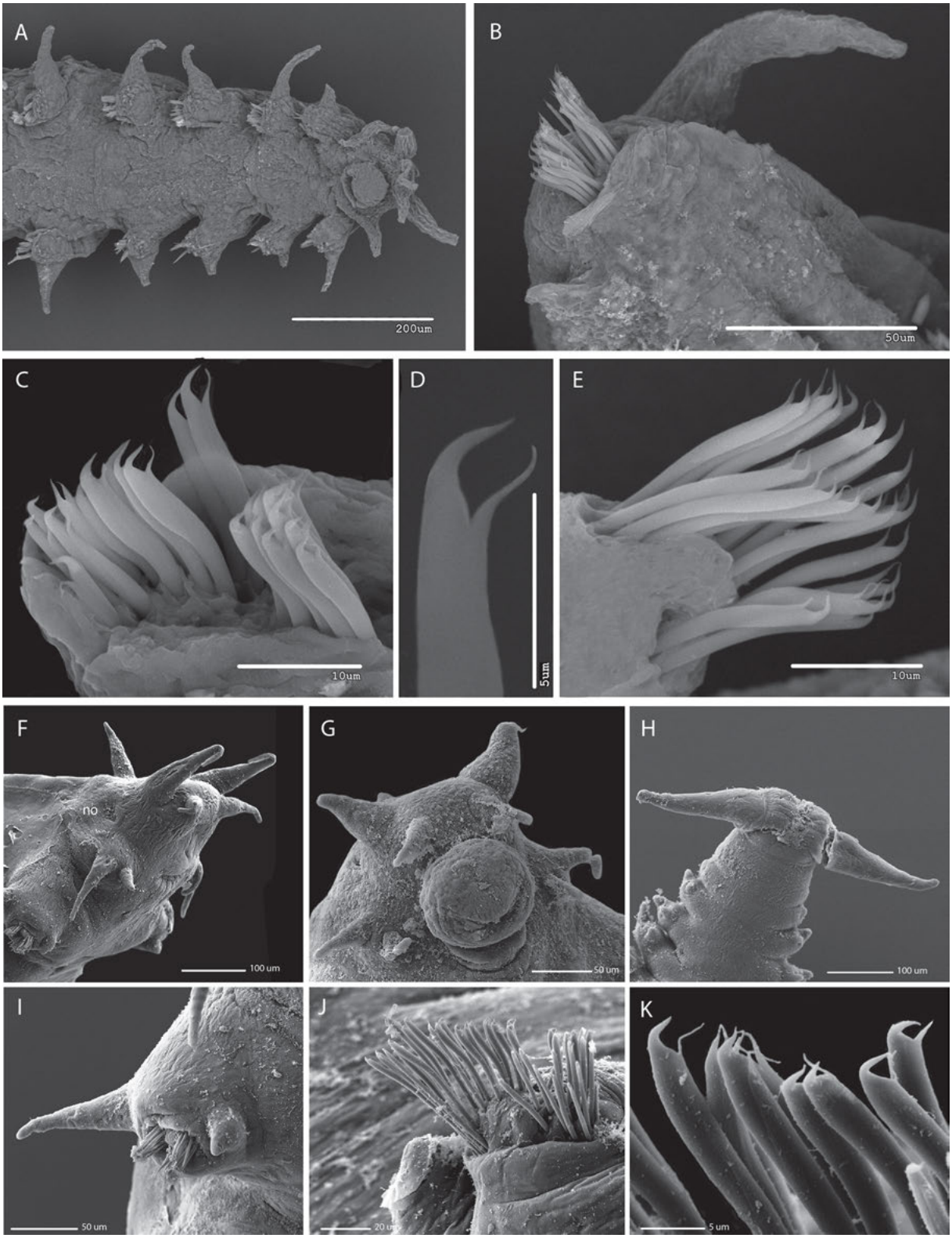


Fig. 7.13.12.3: Morphology of *Antonbruunia*. SEM. A–E, *Antonbruunia viridis* (paratype LACM-AHF POLY 161). A, Anterior end, ventral view. B, Midbody parapodium, lateral view. C–E, Midbody chaetae. *Antonbruunia sociabilis* (from Mackie et al. 2015)(F and H–K, NMW-Z.2012.074.10; G, NMW-Z.2012.074.12). F, Anterior region, anterolateral view (no, nuchal organ). G, Anterior region, ventral view, showing protruded proboscis. H, Pygidium, ventral view. I, Chaetiger 1, anteroventral view. J, Parapodium, ventral cirrus and chaetae, chaetiger 9, anterior view. K, Chaetae, chaetiger 9, from upper posterior part of subacicular bundle.

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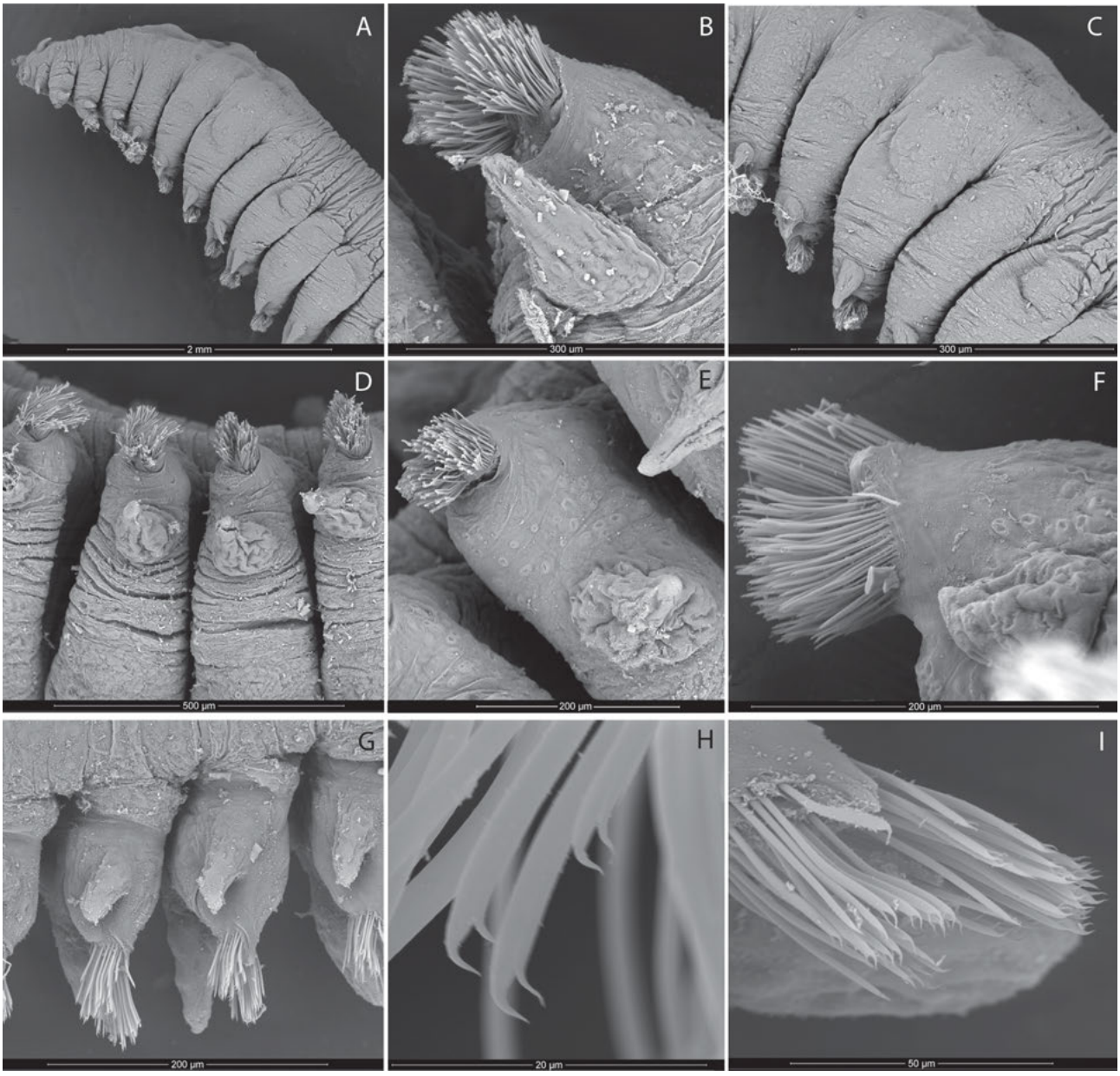


Fig. 7.13.12.4: Morphology of *Antonbruunia gerdesi* (AGT6-9/SeepOx); SEM. A, Anterior end, lateral view. B, Anterior parapodium, ventral view. C, Midbody parapodia, lateral view. D–G, Midbody parapodia, chaetal fascicles and ventral cirri, ventral and ventrolateral views. H–I, Midbody chaetae.

1965) (Fig. 7.13.12.2A), with their body full of eggs. Differences in size have been also found in the specimens of *Antonbruunia sociabilis*; however, the gender of small individuals could not be determined (Mackie et al. 2015).

Antonbruunids might feed on organic particles that enter the bivalve mantle cavity. It is speculated that they are also dependent on the bacterial communities associated with the bivalves (Mackie et al. 2015). However, a clear evidence about their kind of diet is still missing.

Phylogeny and taxonomy

Currently, the family Antonbruunidae is considered as an independent group within Phyllodocida (Annelida,

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Errantia). Its phylogenetic relationships have been recently investigated through phylogenetic analyses, including molecular information (16S RNA and 18S RNA) (Mackie et al. 2015), whose results indicated a close relationship with Pilargidae. However, this affiliation is still not completely stable.

The systematic position of this group of annelids has been quite unstable since they were firstly described. Hartman and Boss (1965) were the first noticing about similarities between *Antonbruunia viridis* and Pilargidae, although they considered that both were different groups. Some years later, Fauchald (1977) erected the family Antonbruunidae with *A. viridis* as the single species. However, Salazar-Vallejo (1986) and Salazar-Vallejo and Orensanz (1991) placed the genus *Antonbruunia* Hartman & Boss, 1965 within Pilargidae. By contrast, Miura and Laubier (1990) considered Antonbruunidae as a family close to Nautiliniellidae, both similar to Pilargidae. They pointed some morphological similarities between Antonbruunidae and Nautiliniellidae (simplified body), but also many differences (e.g., number and distribution of anterior appendages, aciculae, and chaetal composition). The major similarity between the two groups was the way of life, a symbiotic/commensal association with deep-sea bivalves (Miura and Laubier 1990). Later on, Blake (1993) considered *Antonbruunia* in its own family. Glasby (1993) included *Antonbruunia* in a phylogenetic analysis based on morphological data and found the terminal within Pilargidae, which was closely related to Nautiliniellidae. Martin and Britayev (1998) mentioned possible relationships between Antonbruunidae, Nautiliniellidae, and Pilargidae. Fauchald and Rouse (1997) and Glasby (2000) agreed in the position of *Antonbruunia* within Pilargidae. Pleijel and Dahlgren (1998) included *Antonbruunia* in a morphological phylogenetic analysis finding a nonstable position, related to either Pilargidae or Nautiliniellidae. Pleijel (2001) considered them as an *incertae sedis* taxon within Phyllodocida, unclearly related to nautiliniellids and pilargids. Aguado et al. (2013) found, in a molecular phylogenetic analysis, that nautiliniellids were, together with *Calamyzas* Arwidson, 1932, in a monophyletic group of symbiotic animals. This monophyletic group and other free-living genera were nested in a clade within Chrysopetalidae. The latter authors proposed a new subfamily for this clade, the Calamyzinae Arwidson, 1932 (Aguado et al. 2013, 2016). Finally, Mackie et al. (2015) performed the first molecular phylogenetic analyses, including one terminal of antonbruunids (*Antonbruunia sociabilis*), pilargids (*Ancistrosyllis* sp. and *Sigambra* sp.), and calamyzins (*Calamyzas amphictenicola* Arwidson, 1932; *Natsushima* sp.; and *Vigtorniella flokati* Dahlgren, Glover, Baco & Smith, 2004). The results clearly indicate that Calamyzinae and Antonbruunidae are different groups with distant phylogenetic affiliations. Their morphological similarities are mainly due to adaptations to a symbiotic way of life within bivalves associated to cold seeps and hydrothermal vents.

Antonbruunia sociabilis was found to be the sister taxon of the two included pilargids, but this relationship was only supported in the Bayesian analyses. However, support for this was not found in the less resolved maximum likelihood analyses. The topology of the Bayesian analysis (Fig. 5 in Mackie et al. 2015) also shows a long branch for *A. sociabilis*, which may contribute to its still unstable position. Mackie et al. (2015) considered Antonbruunidae as an independent group, with close affiliations to pilargids. Such interpretation has been followed herein. By contrast, as mentioned in the Introduction, other authors (Salazar-Vallejo and Rizzo 2021, Glasby and Salazar-Vallejo, 2021) currently consider the group as part of Pilargidae. The current available hypotheses (Mackie et al. 2015) allow different interpretations. The phylogenetic relationships of antonbruunids are a matter that still need further investigations; a broader taxon sampling and more genetic markers are necessary to provide more stable results.

Classification

Antonbruunidae Fauchald, 1977

Antonbruunia Hartman & Boss, 1965

Diagnosis: (modified from Mackie et al. 2015): Prostomium anteriorly bearing a pair of anteroventral palps, a pair of dorsolateral antennae, and a posterodorsal median antenna; eyes missing. Nuchal organs a pair of dorsolateral ciliated grooves. Two pairs of tentacular cirri on segment 1; parapodia and chaetae missing. Short muscular axial pharynx, with eversible short and bulbous proboscis, jaws missing; gut tubular, lateral gut caeca may be present. Body and parapodia smooth, lacking papillae and parapodial lobes. Parapodia subbiramous, with numerous bidentate neurochaetae in two bundles. Noto- and neuroaciculae present. Dorsal cirri conical larger than ventral cirri. Single pair of pygidial cirri. Sexes may be dimorphic with smaller males.

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The genus consists of three species: *Antonbruunia viridis*, *Antonbruunia gerdesi*, and *Antonbruunia sociabilis*.
Type species: *Antonbruunia viridis* Hartman & Boss, 1965.

Acknowledgments

Special thanks to Andy Mackie for the SEM pictures of *Antonbruunia sociabilis* (Fig. 7.13.12.3F–K) (from Mackie et al. 2015) and for facilitating the nonpublished photo of *A. sociabilis* in his host (Fig. 7.13.12.2B). Thanks to Graham Oliver for the photo in Fig. 7.13.12.2B and information about the color of live specimens of *A. sociabilis*. Many thanks to Javier Sellanes for sending a fragment of *Antonbruunia gerdesi* for new scanning electron microscopy (SEM) examinations (Fig. 7.13.12.4). Many thanks to Leslie Harries (LACM) and Karen Osborn (USNM) for loaning some paratypes of *A. viridis* for new morphological studies (optical microscopy and SEM) (Fig. 7.13.12.3A–E) and María Capa who examined the holotype and paratypes of *A. viridis* and took a picture under the stereomicroscope (Fig. 7.13.12.2A). Thank you also to Sergio Salazar-Vallejo, Alexandra E. Rizzo, and Chris Glasby for sharing their interpretation regarding the systematic affiliation of *Antonbruunia*.

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Maria Ana Fernández-Álamo

7.13.13 Tomopteridae Grube, 1850

Introduction

The Tomopteridae Grube, 1850 are holoplanktonic polychaetes considered as an aberrant group with problematic relationships (Bergström 1914, Støp-Bowitz 1948, Pettibone 1963, Uschakov 1972, Fauchald 1977, Pleijel and Dales 1991, Fauchald and Rouse 1997, Rouse and Fauchald 1997, Eklöf 2010, Eklöf *et al*. 2007). In fact, these worms were originally considered by Grube (1850) in the order Gymnocopa (due to the parapods lacking chaetae) with a single family, Tomopteridae, and in the same level of the Appendicularia Polychaeta, which included all those that have these structures. Later it was defined with the name of Tomopteridae into the class Polychaeta, either independently (Malaquin and Carin 1911, 1922) or in most of the works related with the order Phyllodocida (Dales 1962, Fauchald 1977) or Uschakov (1972) in the order Phyllodocemorpha. Fauchald and Rouse (1997) assumed that the presence of the acicula in the parapodia of the first two segments is the evidence of monophyly in this family.

Tomopteridae have a worldwide distribution in the pelagic realm of all oceans and seas of our planet (Rosa 1908, Dales 1957, Tebble 1960, 1962, Day 1967, Uschakov 1972), although in the sampling with trawl nets, they are usually not numerous (Southern 1911, Tebble 1960). Åkesson (1962) and Åkesson and Melander (1967) registered abundant populations off the Swedish west coast, and, therefore, tomopterids could have an important impact on the trophic chains of the marine ecosystems. By contrast, from a zoogeographic point of view, it is interesting that Ekman (1957) recorded *Tomopteris septentrionalis* Steenstrup, 1849 as an example of a cosmopolitan cold-water species; that is, it has a wide distribution in the oceans, appearing in the surface of the cold regions and in deep water in warm regions; this was also observed by Fernández-Álamo (1983, 2000) in the Eastern Tropical Pacific, always in locations where the 15°C isotherm was located less than 200 m deep.

Tomopterids have been considered voracious predators in the planktonic community (McIntosh 1921, Lebour 1923, Pettibone 1963, Åkesson 1962, Rakuza-Suzczewski 1968, Uschakov 1972).

In Tomopteridae, there is great uncertainty in the number of species that make up this taxon because many of them have not been recorded after their original description, or descriptions are so incomplete that is very difficult to define their identity. In addition to this situation, there are few papers that include lists of synonyms, which have not been included in the current databases of this family. Støp-Bowitz (1948) cleared up many nomenclatural problems, including the replacement of numerous established names with those that have priority, but which were not considered for various reasons. Dales (1956) provided an annotated list of pelagic polychaetes, including 35 species of tomopterids, and Dales and Peter (1972) reevaluated various of these species, with questionable status, and listed 45. Today in WoRMS, 51 species are listed in *Tomopteris* Eschscholtz, 1825 with status accepted (Read and Fauchald 2021).

Morphology

Body shape and color. Tomopterids are easily recognized worms, with bodies more or less transparent and flattened, with sizes from ~1.0 to 135 mm or more, and 10 to 30 pairs of complete biramous parapodia without chaetae, and with notopodia and neuropodia modified into paddle-shaped pinnules; the most distinctive characteristic is a very long pair of chaetigate processes (whiskers) directed posteriorly, almost reaching to the posterior end of the body (Ushakov 1972). When alive, they look like delicate feathers (Day 1967), as it is possible to observe in Internet videos (e.g., http:mbari.org/vars, *Tomopteris* worm). The appearance of tomopterids is highly uniform, which makes the species difficult to distinguish (Dales 1957). The body is relatively simple, but showing highly specialized adaptations to maintain its holopelagic life. It is formed by a cephalic region, a trunk, and, in some species, a tail region with rudimentary parapodia (Malaquin and Carin 1922) (Fig. 7.13.13.1A, B, C).

Prostomium and cephalic region. The cephalic region is an unusual structure formed by the prostomium as a pair of long and divergent antennae frontal, flattened with the appearance of bands or ribbons. The first two body segments are integrated into the head, each carrying a pair of cirriform appendages with an internal acicula; in adults of some species, the anterior pair is smaller than the antennae (Fig. 7.13.13.2C, D) or they could be totally lost (Fig. 7.13.13.2A), whereas the posterior pair is always present and may grow as long as the body, being a clear evidence of an adaptation connected with the pelagic mode of life (Fig. 7.13.13.1A). This second pair constitutes the most remarkable character of these worms; they have very strong bases with a long and enormous acicular bristle (Fig. 7.13.13.2B, F). The mouth is placed ventrally at the level of the base of this second pair of cirriform appendages (Fig. 7.13.13.1B).

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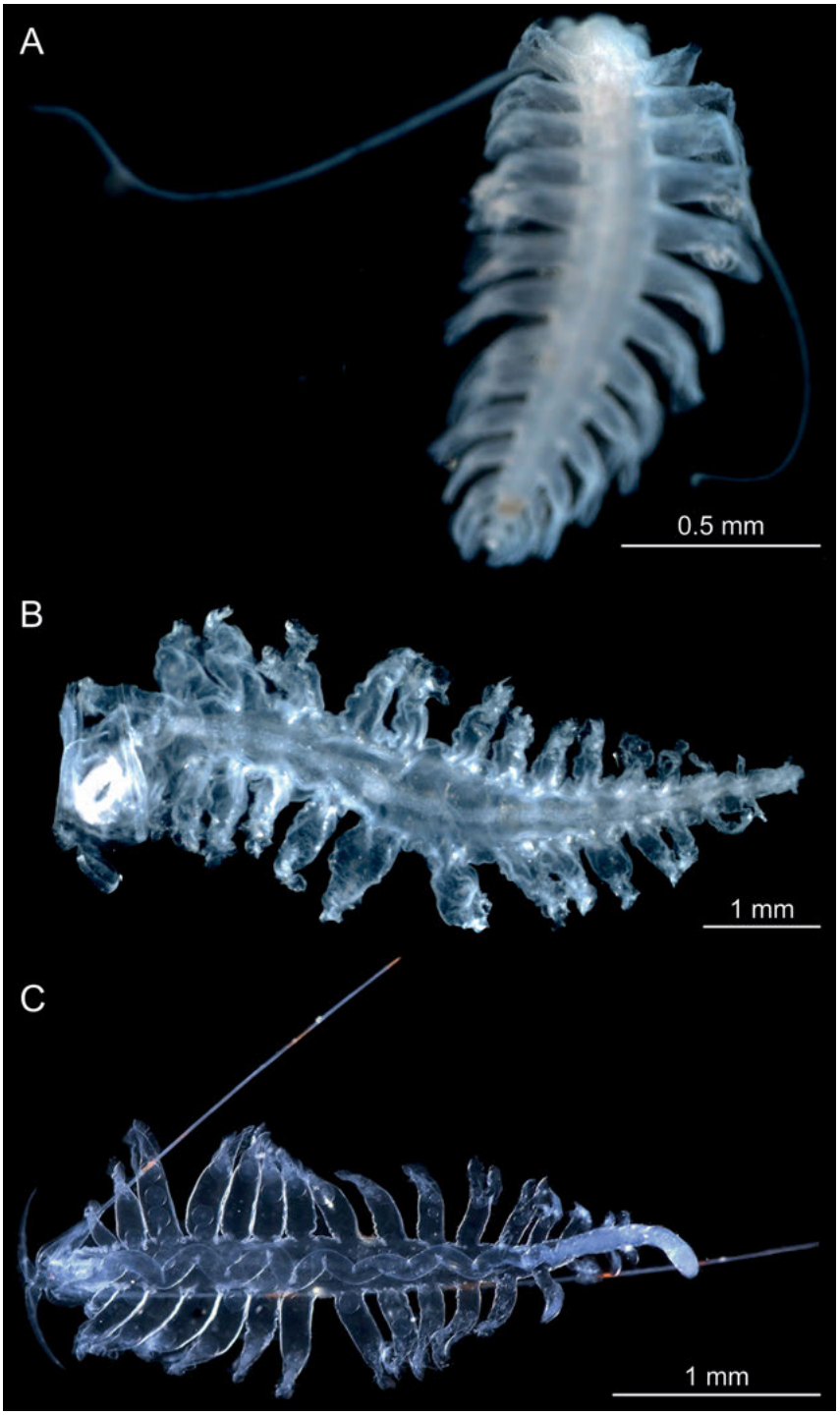


Fig. 7.13.13.1: Complete preserved specimens: tailless. A, *Tomopteris planktonis* Apstein, 1900 dorsal view; with tail. B, *Tomopteris nisseni* Rosa, 1908, ventral view. C, Live specimen of *Tomopteris sp*, dorsal view. A, B, Adrián Fernández; C, courtesy of Xavi Salvador Costa and Daniel Martin, Department of Marine Ecology, Centre d'Estudis Avançats de Blanes (CEAB-CSIC).

In the dorsal region of the head, it is possible to observe a pair of small but complex eyes (Greeff 1879, Terio 1950) embedded in the ganglionar mass. They do not have a vitreous body but have a light-refracting lens that consists of three cells and a pigment cup of seven enormous large retinal cells (Åkesson 1964, 1967) (Fig. 7.13.13.2A). Åkesson (1967) gave an excellent description of the embryonic development and histology of the eyes of *Tomopteris helgolandica*, Greeff, 1879 but little is known about the visual system (Gouveneaux et al. 2017). Also, there is a pair of notorious nuchal organs like pads with long cilia (Fig. 7.13.13.2G, H) described as fossets covered with a ciliary epithelium (Carpenter and Claparède 1860), whose shape varies with the species (Åkesson 1962). Åkesson (1967) mentioned that these structures have two distinct groups of bipolar neurons. Behind of the second pair of

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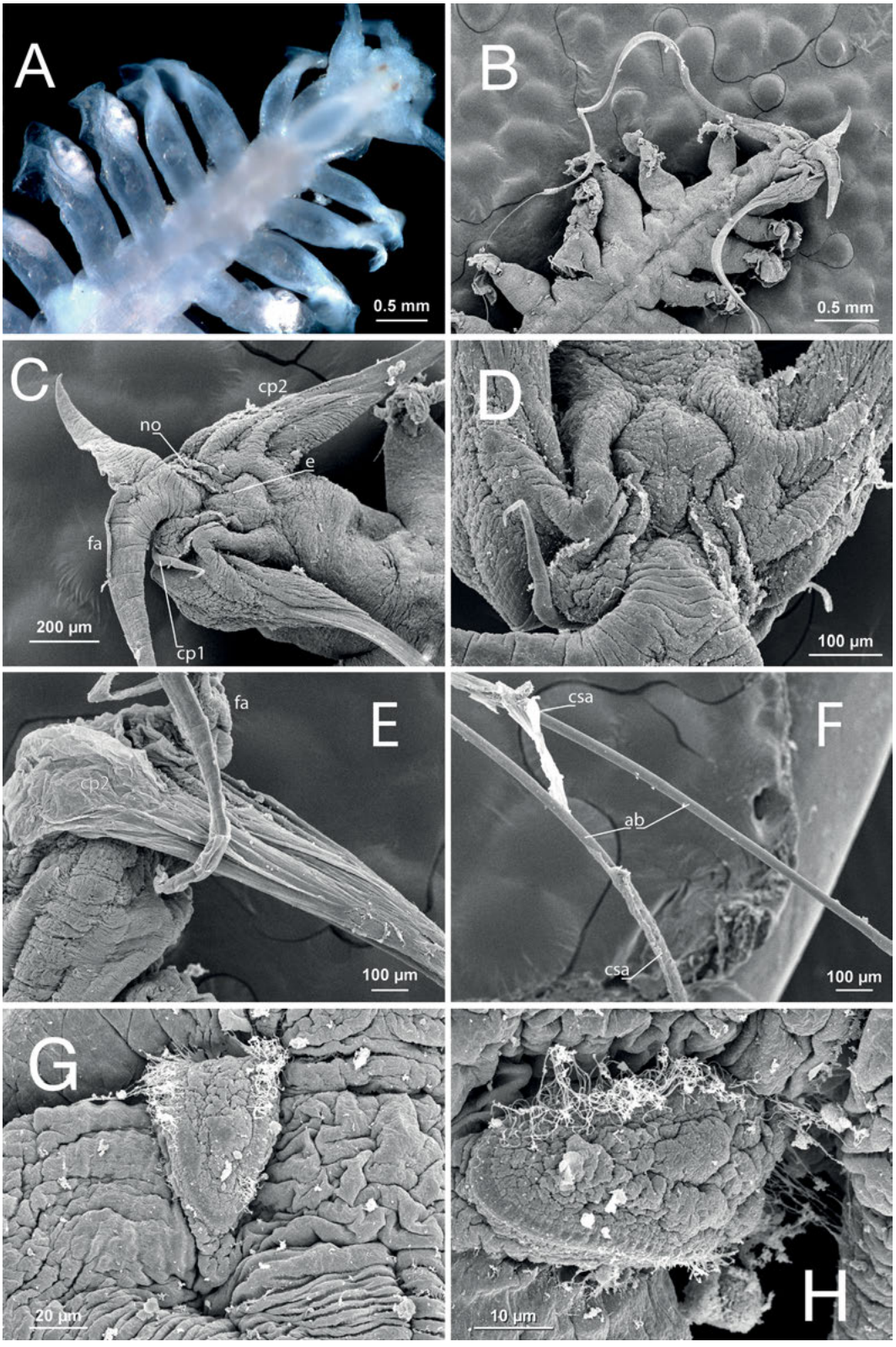


Fig. 7.13.13.2: Cephalic region of tomopterids. A, *Tomopteris planktonis* Apstein, 1900, anterior region of preserved specimen, dorsal view. SEM micrographs of *Tomopteris nationalis* Apstein, 1900. B, Anterior end, dorsal view. C and D, Head, dorsal view. E, Head lateral view. F, Acicular bristles of second pair of cirriform appendages. G and H, Nuchal organ, dorsal view with sensory cilia. fa, frontal antennae; no, nuchal organ; cp1, first cirriform appendages; cp2, second cirriform appendages; e, eyes; ab, acicular bristles; csa, cellular sheath of the acicula.

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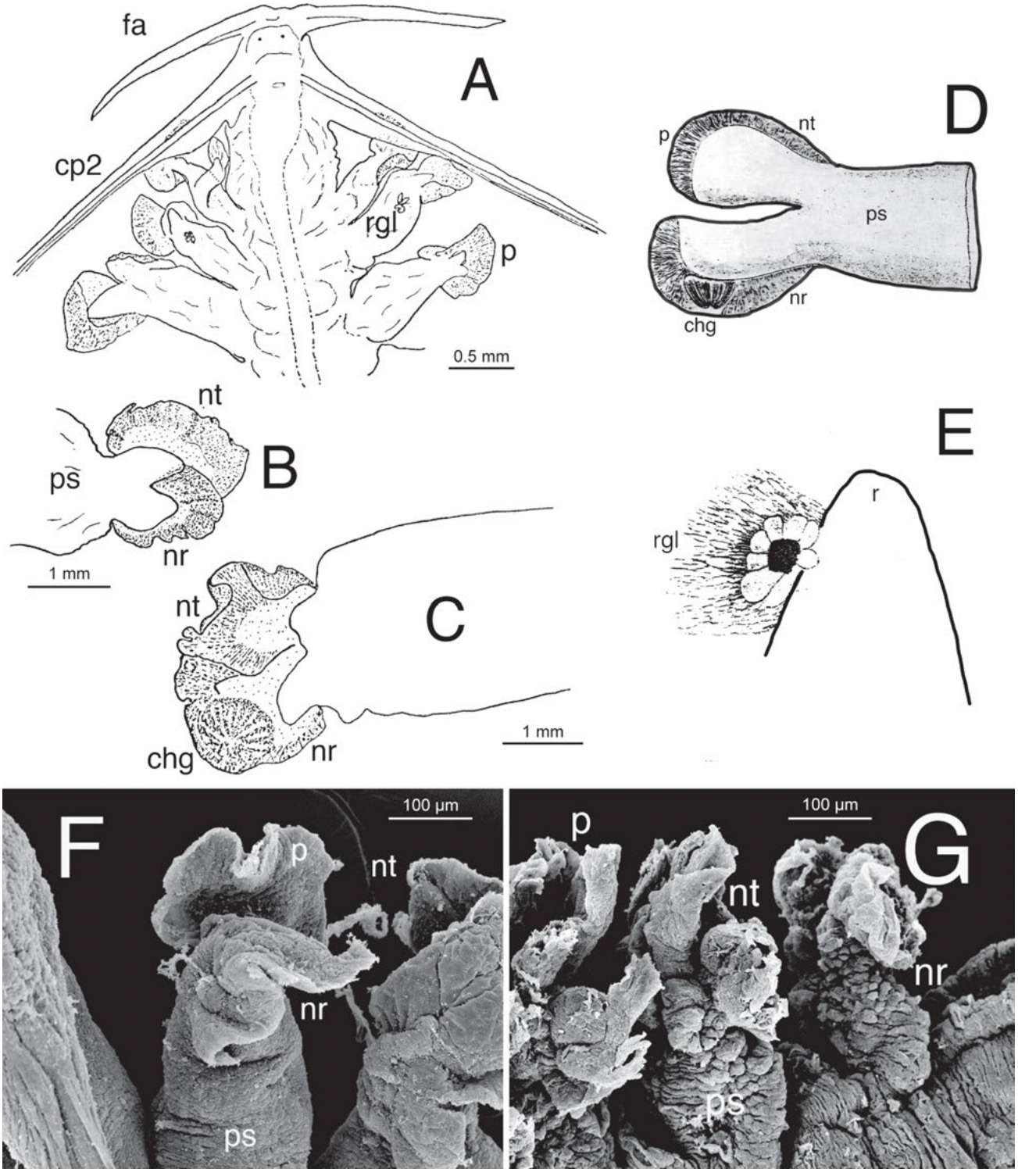


Fig. 7.13.13.3: Trunk and parapodia: A, Anterior end. B, C, First and fifth parapodia of *Tomopteris euchaeta* Chun, 1887 (Fernández-Álamo, 1983). D, Fourth parapod of *T. euchaeta* (modified from Apstein, 1900). E, Rosette gland in pinnule, near to the rami of *Tomopteris helgolandica* Greeff, 1879 (modified from Apstein, 1900). SEM micrographs: F, First parapod of *Tomopteris planktonis,* ventral view. G. First parapodia of *Tomopteris nisseni*, ventral view. ps, parapodial stem; nt, notopodial rami; nr, neuropodial rami; p, pinnula; chg, choromophile gland; rgl, rosette gland.

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cirriform appendages, there is a narrow region or neck without parapodial processes (Fig. 7.13.13.2A, C, E). Chun (1887) included an excellent figure of the complex internal anatomy of the head of *Tomopteris euchaeta* Chun, 1887 (Fig. 7.13.13.4), and Åkesson (1962) described the histology and embryological origin of these cephalic structures. It is important to point out that some information that appears in WoRMS (Read and Fauchald 2021) name details, *T. euchaeta* presents the following errors, this species was described by Chun in 1887 not in 1888, although the original description indicates that the complete citation of this work is correct with the year 1887.

In the case of *Enapteris euchaeta*, it is the same situation. This species is considered a synonym of *Enapteris euchaeta*, however Day (1967) and Fernández-Álamo (2000) argue that the taxonomical characters used by Rosa (1909) are not valid, taking consideration that the Tomopteridae family is only formed by *Tomopteris*. Therefore *Tomopteris euchaeta* is considered a valid species. This work follows these criteria.

Trunk. The trunk has the rest of the segments with their respective parapodial branches (Fig. 7.13.13.1). Each segment has a pair of biramous parapodia, each one is formed by a long stem, ending in two pointed branches (notopodial and neuropodia rami), and each is bordered by membranous expansions called pinnules (Fig. 7.13.13.3). Uschakov (1972) opined that it is not clear if these structures are homologous with the dorsal and ventral cirri. There are between 10 and 40, or more pairs of complete parapodia relatively constant in some species (Uschakov 1972). Several species have a special elongation of the pygidial region, named "tail," which bears not only reduced but also biramous parapodia (Fig. 7.13.13.1B, C). In the pinnules, there are four different types of glandular structures that are used in systematics of the species: rosette, hyaline, chromophil, and spur glands. Malaquin and Carin (1911, 1922) made a careful revision of these structures and suggested that the first two are homologous (called them hyalopigmend organs), and chromophil and spur glands are very related. Rosette and hyaline glands are small glands, which are not stained with hematoxylin; they are formed by yellow photogenic cells surrounded by a layer of transparent cells, and below them is a ganglion (Uschakov 1972). Rosette glands are situated in the parapodial trunks of the first two segments, and both pinnules are close to the apices of the rami of all parapodia (Fig. 7.13.13.3D, E). Tebble (1960, 1962) considered that spur glands are a subsidiary structure of the chromophil glands and pointed out the difficulty in the determination of the hyaline glands in fixed specimens. Orenzans and Ramírez (1973) also included the apical glands, seen in all pinnules, composed of granules enclosed in a fusiform fibrous matrix, and other unicellular glands, both without taxonomic value. Gouveneaux et al. (2017) analyzed the shape and function of the parapodial light glands in several species of *Tomopteris*, coinciding with Malaquin and Carin (1922) about the homology in their morphology, but they differ in that rosette glands must be endocrine glands and hyaline glands are typical exocrine glands.

The chromophil glands (that stain deeply with hematoxylin) are the most obvious and larger, which appear only in the ventral pinnules in most parapodia, from the third or fourth segment onward. They are formed by numerous tubules with a common opening (Figs. 7.13.13.3C and 7.13.13.6A). In some species, they are associated with the spur glands, named for its resemblance to a protruding stinger on the ventral edge of the pinnules. In some species, these structures appear alone in the first few parapodia, without chromophil glands (Day 1967).

The gut is a straight tube, in some sections undulate (Fig. 7.13.13.1C), and extends from the head to the pygidium.

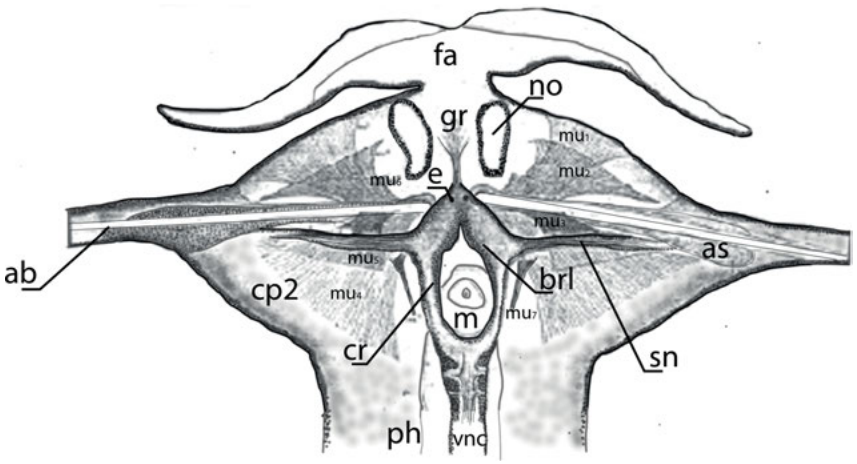


Fig. 7.13.13.4: Nervous system. Head of *Tomopteris euchaeta* (modified from Chun, 1878). ab, acicular bristle; as, acicular sac; brl, brain lobes; cp2, second cirriform appendages; cr, circumpharyngeal ring; e, eyes; fa, frontal antennae; gr, antennae nerves; m, mouth; mu1-7, muscles layers; no, nuchal orgams; ph, pharynx; sn, setigerous nerve; vnc, ventral nerve cord.

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The mouth is located between the bases of the second acicular appendages and is connected with a very short tubular, unarmed pharynx (Fig. 7.13.13.1B). Tomopterids are generally considered to be carnivores, capturing their prey from the planktonic communities as adults or oocytes of other tomopterids. Remains of fish larvae (herring fry) and fragments of Siphonophora (*Agalmopsis elegans*), Appendicularia (*Oikopleura dioica*), and Chaetognatha (*Parasagitta elegans*, *Sagitta setosa*) have been observed in their guts (McIntosh 1921, Lebour 1923, Pettibone 1963, Åkesson 1962, Rakuza-Suzczewski 1968, Uschakov 1972). According to Rakusa-Suszcewski (1968), in the Atlantic Ocean, *Tomopteris helgolandica* attacks by making holes in body of the prey, sucking their body fluids.

Nervous system. The nervous system consists of a cerebral ganglion, located between the bases of the second pair of acicular appendages, and is extended forward by nerves that go to the antennae and nuchal organs. From its posterolateral regions it gives rise to the circumpharyngeal connectives, which surround the foregut and initiate a longitudinal double nerve cord in the ventral region (Fig. 7.13.13.4). This ventral nerve cord is characterized by the absence of segmental swellings, in both, larvae and adults. Their position on the body wall is extremely superficial, covered only by a single layer of squamous epidermal cells (Åkesson 1962). Helm et al (2018) described that the ventral nerve cord in *Tomopteris helgolandica* is intraepidermal and consists of two distinct neurite bundles. Immunohistochemistry analysis provides a picture of a medullary-like arrangement of somata, segmentally arranged commissures, and branching nerves. The nervous structure of the appendages of the first two segments is complex and the origin and function of their nerves are debatable (Vejdovsky 1878, Greef 1879, Meyer 1924, 1926, Åkesson 1962).

Sensory organs. The main sensory organs are as follows: (1) frontal antennae originating from the anterior dorsal margin of the brain lobes; (2) eyes, which have no vitreous body, and the light-refracting lens arises from the epidermal cells at the bottom of a central depression (Åkesson 1962, 1964) in the cerebral ganglion on a transversal line that cross between the second segment; and (3) nuchal organs, which consist of a pair of prominent ciliated structures situated laterally on the head described in the literature as the epaulettes (Åkesson 1962) innervated by a pair of nerves that come from the brain (Figs. 7.13.13.2 and 7.13.13.4).

Nephridia. The excretory system is formed by paired nephridial organs along the body, except in the first region; each excretory organ opens to the exterior ventrally by a nephridiopore located close to the frontal parapodial base (Goodrich 1900, Åkesson 1962). Bartholomaeus (1997) described the excretory organs in *Tomopteris helgolandica* as metanephridia, which bear a multiciliated solenocyte. The nephridial complex is formed by a ciliated funnel, open to the celomic cavity, a short duct, and a single multiciliated solenocyte. This study confirms that tomopterids are the only taxon in which nephridial funnels remain permanently open and have terminal solenocytes, as had been described by other authors such as Mayer (1924, 1926) and Hatchfeld (1926).

Biology and ecology

The tomopterids have a worldwide distribution in the pelagic realm of the oceans and seas of our planet (Rosa 1908, Dales 1957, Tebble 1960, Day 1967, Uschakov 1972) in the oceanic regions, from surface to abyssal waters of 5,000 m or more in depth (Tebble 1960, Day 1967, Uschakov 1972, Orensanz and Ramirez 1973). Some species have been described as cosmopolitan because they have been observed in all regions, from the polar to the tropic equatorial (Tebble 1960). These worms are common in zooplankton samples but are usually found in low abundance, although they are sometimes caught in great numbers (Southern 1911, Åkesson 1962, Ushakov 1972, Fernandez-Alamo personal observations). They must play an important role in the trophic webs of marine ecosystem; for example, Southern (1911) considered that they can be important food for fishes.

Tomopterids are considered voracious predators that feed on other animals in the planktonic community, as found in fragments of siphonophores, oocytes of tomopterids, chaetognaths, tunicates (Appendicularia), and remains of larval herring (McIntosh 1921, Lebour 1923,

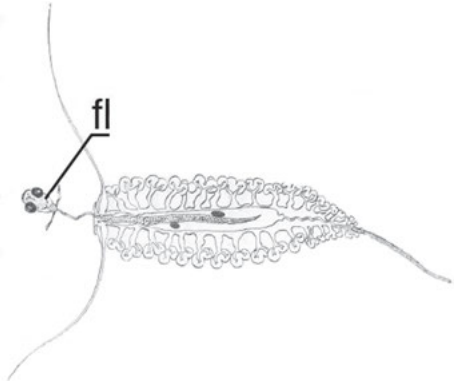


Fig. 7.13.13.5: *Tomopteris helgolandica* swallowing a herring larvae. From Lebour (1923). fl, fish larvae.

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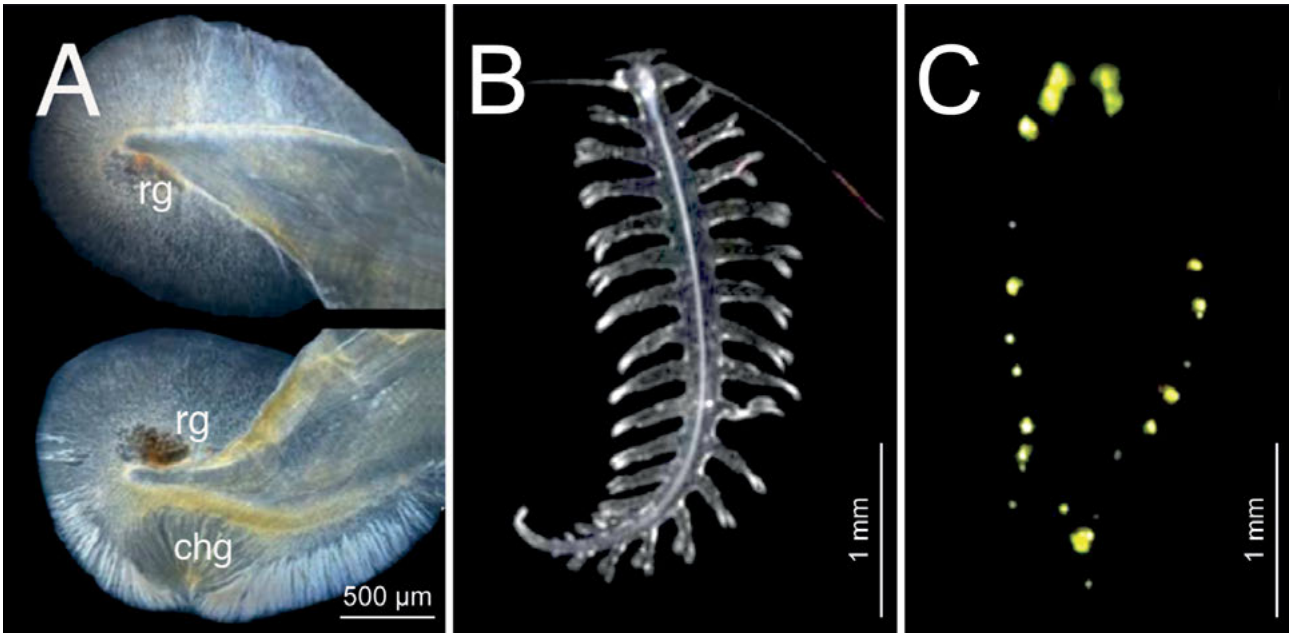


Fig. 7.13.13.6: Bioluminescence organs. A, Fresh parapod of *Tomopteris planktonis* modified from Gouveneaux et al. (2016) rights of use pending. B, C, Light emission of *Tomopteris helgolandica*. B Photo in natural light. C, KCl-induced bioluminescence, photo in dark. Modified from Gouveneaux and Malleft (2013) rights of use pending. rg, rosette gland; chg, chromophil gland.

Åkesson 1962, Pettibone 1963, Rakuza-Suzczewski 1968, Uschakov 1972). However, Lebour (1923) also mentioned the presence of microscopic unicellular food, mainly diatoms and flagellates in some specimens of *Tomopteris helgolandica*, and described specimens of *Sagitta* swallowing a fish larva (Fig. 7.13.13.5). On the other hand, if animal food is absent, Phlyllodocidae also feed on plants (Ushakov 1972).

Thuesen and Childress (1993) studied some physiology and biochemistry aspects (oxygen consumption, enzymatic activities, and chemical composition) of *Tomopteris nisseni* Rosa, 1908, *Tomopteris pacifica* Izuka, 1914, and *Tomopteris* sp., observing that, in general, they presented higher metabolic values than other animals of the meso- and bathypelagic zones, as chaetognaths and crustaceans.

Gouveneaux et al. (2018) observed the locomotion of *Tomopteris helgolandica* and described that not only the parapods are involved but also the undulate bending of the body produced by the antagonistic action of longitudinal muscles and probably the participation of the coelomic liquid acting as a hydrostatic skeleton. The second pair of cirriform appendages are not used in the locomotion but rather function as a prominent sensory organ acting mainly as a balancing and floating organ of the animal (Åkesson, 1962). Parapodia of the trunk have bilobed podial processes that bear special fins or pinnules, but it is not clear whether these fins are homologous with the dorsal and ventral cirri (Ushakov 1972).

Bioluminescence

This interesting phenomenon was recorded in tomopterids by Greeff (1882, 1885), who observed that the glands located in the pinnules emit bright light. Apstein (1900, 1916) described the rosettes glands as lighting organs. Meyer (1926, 1930) showed that the origin of the rosettes are the coelomoducts, which have nerves. Harvey (1952) observed yellowish light emitted by *Tomopteris helgolandica*. Terio (1960, 1964) described luminescence in the hyaline glands and the rosettes of the rami of the first two pairs of parapods that possibly produce yellow or yellow-greenish light, confirming the suggestion that both glands are photogenic organs. Dales (1971) briefly provided information of photogenic organs in Tomopteridae, and Ushakov (1972) described these organs formed by yellow photogenic cells surrounded by a layer of highly transparent cells related with a ganglion, assuming that the function of bioluminescence is the attraction between males and females, which is of great importance for pelagic forms that do not form dense populations. Gouveneaux and Mallefet (2013) studied the emission pattern and control of the bioluminescence in *T. helgolandica*, and they strongly support the hypothesis that this phenomenon is under nervous control, revealing new insight into the pathways involved. The yellow light flashes are produced via the activation of nicotinic cholinergic receptors and a calcium-dependent intracellular mechanism involving L-type calcium channels (Fig. 7.13.13.6A, B). Francis et al. (2014) identified an

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anthraquinone involvement in the bioluminescence of *Tomopteris* collected in Monterey Bay, northeast Pacific. Gouveneaux et al. (2017) reported an interesting diversity in the bioluminescence color patterns in four species of Tomopteridae, analyzing its possible role in the behavior of these organisms and the possibility of using biochemical analysis in a taxonomic review of the family. Gouveneaux et al. (2018) described the histology, physiology, pharmacological, and behavioral responses of *T. helgolandica* related with their bioluminescence and its close relationship with the function of the nervous system.

Reproduction

Only sexual reproduction is known in tomopterids. They are gonochoric organisms having paired gonads in some segments, and fertilization is always external (MBARI on 1 July 2015, https://www.youtube.com/watch?v=cdr1k-WmSiiE). Åkesson (1962) recorded a sexual ratio of 1:1 in *Tomopteris helgolandica*, and Malaquin and Caren (1922) provided data on the sex ratio in some other species. Rosa (1908) indicated sexual dimorphism due to the shape and size of the tail parapods.

Gonads are simple and are located in the hollow parapodial branches, usually dorsal ones, and in several or in all segments, although in some species they are also in the ventral rami, or in both dorsal and ventral (Malaquin and Caren 1922). It is important to mention that in *Tomopteris helgolandica* the segmental subdivision of the mesoderm into hollow somites is a very transitory one and does not correspond to the conditions found in other polychaetes; consequently, the adults present a nonsegmental coelom that is prolonged in the parapodial branches (Malaquin and Caren 1922, Åkesson 1962). Støp-Bowitz (1948) included this feature in the description of the species from the north Atlantic. In *T. helgolandica*, Ushakov (1972), Fauvel (1923), and Støp-Bowitz (1948) observed the gonads in different segments, arguing that this character is probably dependent on the degree of maturity of the specimens and has no weight in the systematics. Genital ducts and orifices are in the matured individuals in the fourth and sometimes in the fifth parapodial segment (Malaquin and Caren 1922).

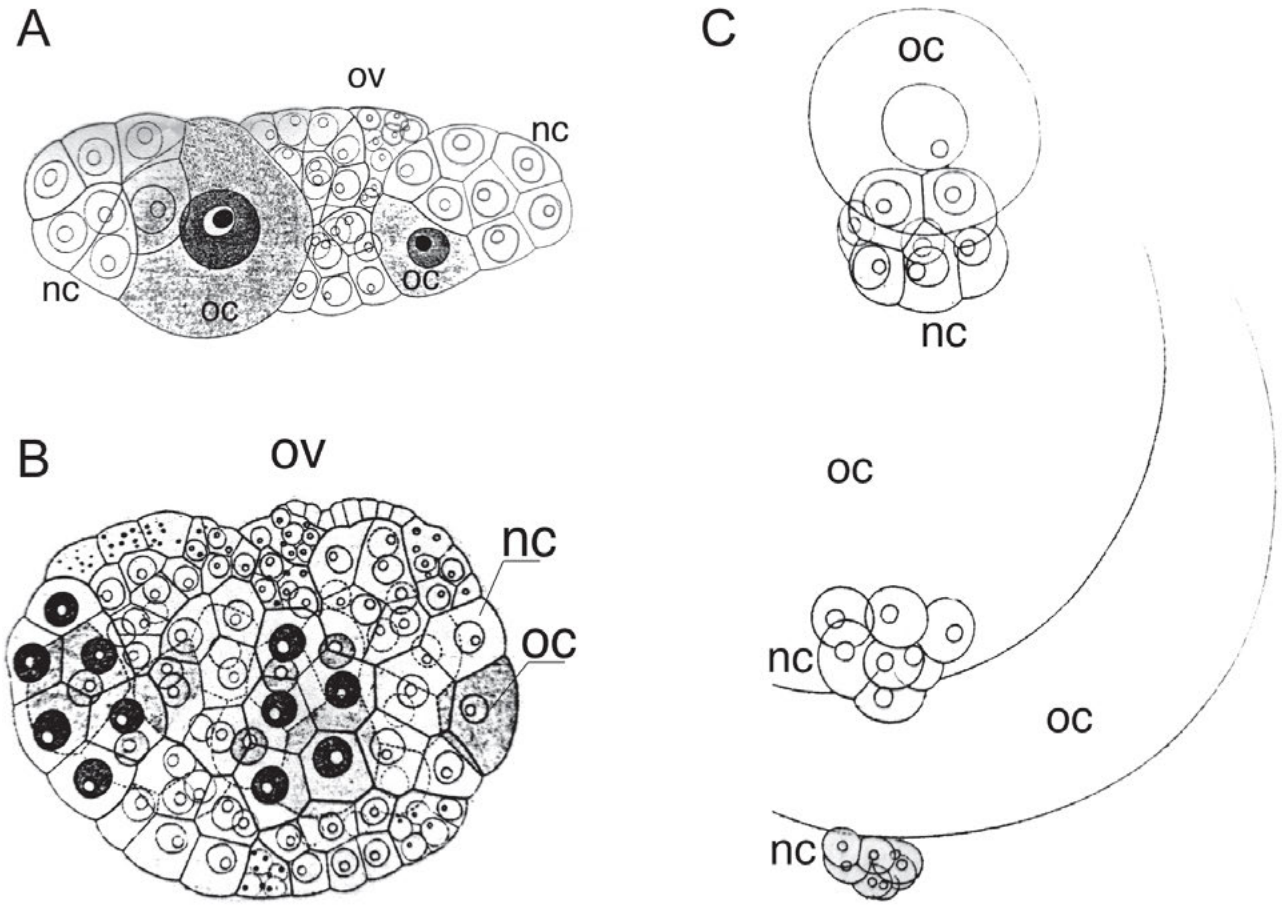


Fig. 7.13.13.7: Gonads and oogenesis, A, *Tomopteris elegans* Chun, 1887 ovary. B, *Tomopteris euchaeta* Chun, 1887 ovary. C. Growth of an oocyte of *T. euchaeta*. ov, ovary; oc, oocyte; nc, nurse cells; chrg, chromophil gland. A, B, C modified from Chun (1887).

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Information on the male gonads is scarce. Malaquin and Caren (1922) illustrated the sixth parapod of *Tomopteris helgolandica*, which show the testes in the distal zone of both rami. In *Tomopteris catharina* (Gosse, 1853) and *T. helgolandica*, the nephridia store the sperm before they are released, whereas in females, additional gonoducts with a ciliated funnel are formed (Meyer 1924, 1926).The ultrastructure of the sperm of *T. helgolandica* was described by Franzén (1982) as an aberrant type with two flagella, an axonema with different microtubular pattern (9+0) that rotates around its longitudinal axis when swimming. The ovaries are clusters of eight cells, of which the larger is the egg (Chun 1887; Fig. 7.13.13.7A, B). Oogenesis is extraovarian; the clusters of previtellogenic oocytes are released into the coelom where they remain floating and maturing (Fig. 7.13.13.7C); nurse cell-oocyte associations have been described by Carpenter and Claparède (1860), Chun (1887), Fullarton (1895), Dons (1909), Senna (1911), and Åkesson (1962).

In *Tomopteris helgolandica,* spawning probably occurs throughout the year as mature females are observed in all seasons, with different stages of oocyte maturity. Yolky eggs are fertilizable when the last remains of the nutrition cells have disappeared (Åkesson 1962). Fertilization in the natural environment is unknown; however, it could be observed by some videos (2015 MBARI, Weir and wonderful Deep-sea worms, 3.03 min) where females constructed a spherical mass of mucus where it is possible to observe some larvae. Both larvae and juveniles of Tomopteridae are part of the zooplankton community and are frequently recorded in net samples, as described and illustrated (Meyer 1890, Malaquin 1899, Apstein 1900, 1916, Malaquin and Carin 1922). The larvae have five segments in tomopterids and seven segments in phyllodocids (Ushakov 1972).

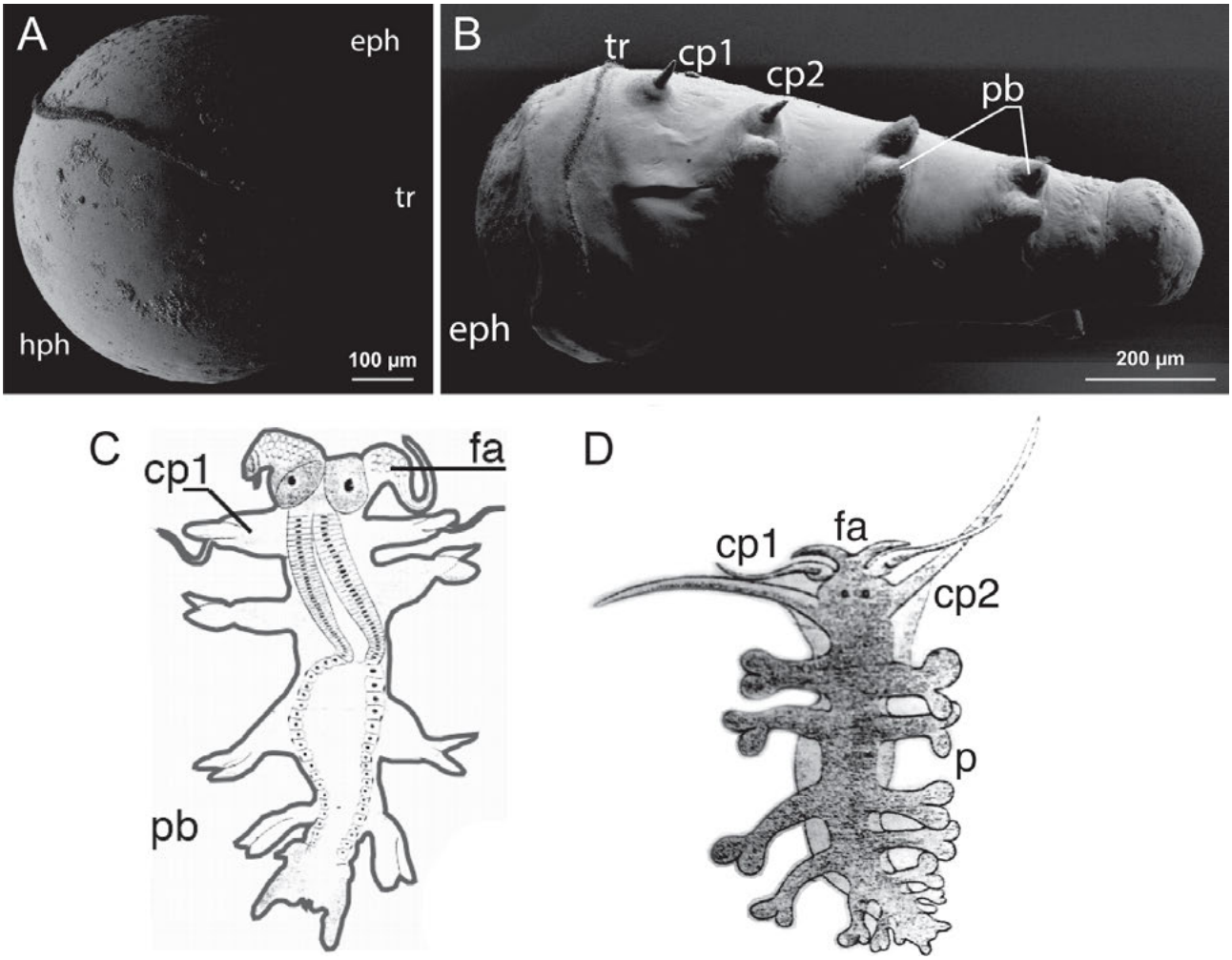


Fig. 7.13.13.8: Reproduction and development. A, Trochophora. B, Larvae of *Tomopteris helgolandica*, lateral side (courtesy of Conrad Helm, Georg-August-University Göttingen, Germany). C, Larvae. D, Juvenile of *T. helgolandica* modified from Apstein, 1900. eph, episphere; hph, hyposphere; tr, prototroch; cp1, first cirriform appendage; cp2, second cirriform appendage; pb, parapodia bulbs; p, parapodia.

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Åkesson (1962) collected adult females and males of *Tomopteris helgolandica* to study the reproduction process *in vitro*, describing their early ontogenetic stages. Åkesson and Melander (1967) provided a detailed description of oocytes, their fertilization and first cleavages, in the same species. The trochophora larva has a spherical shape (Fig. 7.13.13.8A) or with a form of two cones separated by the prototroch (Åkesson 1962), and its shape differs from the trochophores of Phyllodocidae and other polychaetes. The histologic differentiation of the trochophore and the morphologic changes to the first larval stages were described by Åkesson (1962). At the end of the fourth day, the embryo has become differentiated into a metatrochophore, which develops into four segments during the next few hours. The first larval stages occur in 3 days, and at the end of the fourth day, the embryo has transformed into a metatrochophore with four segments and the primordia of its appendages (Fig. 7.13.13.8B). On the fifth day, the appendages of the first two segments form bristles (two and a pair, respectively), which are transitory structures that will be replaced in the second segment by the definitive acicula in juveniles and adults (Fig. 7.13.13.8C, D). At about the same time, the first rudiments of the rosette organ are discernible at the base of the third parapodia, the rudiment of the fifth segment appears, and the embryo starts the differentiation of the prepygidial and pygydial zones that develop the postlarval segments (Åkesson 1962).

During the later part of embryonic development, important changes in the head and anterior part of the trunk occur. The first segment and their appendages move in an anterior position until they are preoral and precerebral structures; between their bases the first rudiments of the frontal antennae appear. In larvae with 9–10 segments, both structures are similar in size, and the appendices of the second segment begin a rapid growth (Fig. 7.13.13.8C), reaching a length similar to that of the body in adults. They also develop a prominent musculature and complexity of the nerves, which function as a floating organ (Åkesson 1962).

Invagination during the development of the nervous system of *Tomopteris* may be considered as a primitive character, indicating the great age of the family Tomopteridae (Åkesson 1962), which coincides with the findings of Briggs and Clarkson (1987) who recorded fossils defined as tomopterids (*Eotomopteris aldridgei* Briggs and Clarkson, 1987) from the Lower Carboniferous of Edinburg, Scotland.

Parasites

Støp-Bowitz (1948) described two specimens of *Tomopteris nisseni* of different localities in the North Atlantic with ectoparasitical Crustacea on a parapodium and on the dorsum. Damas (1936) recorded larval stages of *Cunina lativentris* (Narcomedusae) in the body cavity of *T. nisseni*, causing its castration. Dales (1957) recorded parasites in *Tomopteris septentrionalis* and *Tomopteris elegans* Chun, 1887 from the northeast Pacific but did not provide more details. Numerous specimens of *Tomopteris* present internal parasites, possibly corresponding to larval stages of trematod flatworms (personal observation).

Phylogeny and taxonomy

The systematic position of the family Tomopteridae has been uncertain from the beginning, since Grube (1850) created a defined order (at the same level of the polychaetes) called Gymnocopa with the only family Tomopteridae to include these organisms that present corporal parapods without chaetae (his position was supported by Apstein 1900). Their phylogenetic affinities are doubtful and enigmatic, and they have been considered an aberrant group (Bergström 1914, Støp-Bowitz 1948, Tebble 1960, Day 1967, Ushakov 1972, Rouse and Pleijel 2003, Eklöf et al. 2007). Most authors related them to Phyllodocida (Ehlers 1917, Bersgström 1914, Meyer 1926, Støp-Bowitz 1948, Dales 1962, Fauchald 1977, Fauchald and Rouse 1997, Rouse and Fauchald 1997), although little actual evidence is available (Rouse and Pleijel, 2003). Struck et al. (2007) placed tomopterids as sister to the Glyceridae/Goniadidae clade, that is, in turn, sister to a phyllodocid/alciopid clade. Struck (2011) and Purschke (2016) considered Tomopteridae close to Glyceridae within Phyllodocida in Errantia and forming part of monophyletic group Pleistoannelida.

Evidence of monophyly is the presence of chaetae, as aciculae, only in the appendages of first two segments (Fauchald and Rouse 1997). Struck et al. (2007) and Zrzavý et al. (2009) placed Tomopteridae as sister to Glyceridae and Goniadidae. Ushakov (1972) assumed that Tomopteridae evidently became separated very early and their adaptations to pelagic life originated a different line.

Rouse and Pleijel (2003) have suggested that relationships of this family must include molecular evidences based on a wide sampling of this taxon, which guarantee and provide the possibility of considered Tomopteridae outside of Phyllodocida or even outside Aciculata.

Tomopteridae Grube, 1850: 343.
Synonyms: Order Gymnocopa, Grube, 1850: 343
Type genus: *Tomopteris* Eschscholtz, 1825: 736
Diagnosis: Pelagic polychaetes with transparent and flattened bodies, with a variable number segments (12–40), and chaetae limited to the first two segments. Body divided in head, trunk, and sometimes an elongated tail

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(Figs. 7.13.13.1A–C, 7.13.13.2A, B, and 7.13.13.3A). Cephalic lobe with a pair of divergent and ribboned frontal antennae, which form the anterior border of the head a pair of small eyes, and a pair of nuchal organs, covered with ciliary epithelium. Pharynx is short and unarmed. Cephalic lobe fused with the two first segments, which bear two pairs of cirriform appendages with an internal acicula; the first pair is located anterior to the mouth, and during development the aciculae or even the whole appendage may be lost; the second pair is very large and is always retained in adults and may grow as long as the body. Trunk with biramous parapodia lack chaetae, with a long stern, ending in two pointed branches of about the same size, which are bordered by a membranous fin or pinnule. The main types of glands in the parapods are rosettes and hyaline glands that are small, formed by photogenic cells the first can be found in the parapodial trunks of the first two segments and in all pinnules, both dorsal and ventral, the last located only in the ventral pinnules of all parapods; chromophil glands present in the ventral pinnules of all parapods, except the first 2–4, in some species associated with the spur glands. The posterior region of the body diminishes; parapods reduced in size in several species; this region is modified into a tail that carries reduced parapods. Gonads are present usually in the dorsal ramus, some times in the ventral, and less frequently on both.

Remarks: The relative homogeneity in the morphology of the members of family has caused serious problems in their taxonomy, presenting numerous synonyms at the levels of genera and species. Rosa (1908) placed the genera *Briaraea* Quoy & Gaimard, 1827; *Johnstonella* Gosse, 1851; and *Escholtzia* Quatrefages, 1865 into synonymy with *Tomopteris* Eschoscholtz, 1825. Rosa (1908) also described *Enapteris* as a new genus for *Tomopteris euchaeta* Chun, 1887 and, therefore, considered the family integrated by two genera *Tomopteris* and *Enapteris*, a position that has been followed by most works on these worms. Day (1967) considered that the specimens studied by Rosa (1908) on which he based the description of his new genus were juveniles of *T. euchaeta*, and consequently *Enapteris* is a synonym of *Tomopteris*; hence, the family is left with a single genus. Day (1967) described "the parapodial rami expanded with broad pinnules each divided into an outer frilly area bearing the glands and an inner clear area which simulates a flattened extension of the ramus." Is interesting that in Chun's (1887) original description, these were not mentioned, but Apstein (1900) included a key and a scheme (Fig. 7.13.13.3F) of them in which the parapodial branch is rectangular and the pinnule is only in their external part, showing the main feature used by Rosa (1908) to erect the new genus, using only the same illustration of Apstein (1900). Fernández-Álamo (2000) observed the structure of the parapodia, agreeing with Day's opinion that Tomopteridae only has the genus *Tomopteris* (Fig. 7.13.13.3B, C).

In this regard, it is important to draw attention to the fact that actually in the WoRMS database Tomopteridae has the status of an accepted taxon but still maintains the validity of five genera (Read and Fauchald 2021), although three of them (*Briaraea* Quoy & Gaimard, 1827; *Escholtzia* Quatrefages, 1865; and *Johnstonella* Gosse, 1853) are placed in synonymy since 1908 by Rosa, which was accepted by Hartman (1959) and Dales and Peter (1972). Regarding the fourth genus, *Enapteris* (Chun, 1888) was placed in synonymy by Day (1967), arguing that the original description was based on juvenile specimens and an erroneous observation of the main character, which is the structure of the pinnule. Later this was corroborated by Fernández-Álamo (1983, 2000). Thus, Tomopteridae is a monogeneric family with *Tomopteris* Eschscholtz, 1825 as unique genus. Also, in WoRMS (Read and Fauchald 2021), the position of dividing the genus *Tomopteris* into two subgenera is maintained on the basis of the presence of hyaline glands or rosette glands and other characters that change during the ontogeny of organisms, for which Tebble (1960, p. 171) rejected this division because it does not represent a practical method in the taxonomy of the Tomopteridae family.

Tomopteris Eschscholtz, 1825: 744

Type species: *Tomopteris onisciformis* Eschscholtz, 1825
Synonyms: *Briaraea* Quoy & Gaimard, 1827: 235
Enapteris Rosa, 1908: 30
Johnstonella Gosse, 1853: 356
Escholtzia Quatrefages, 1865: 224
This genus has the characters of the family.
54 species (Read and Fauchald 2021)

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7.13.14 Sphaerodoridae Malmgren, 1867

Introduction

The family Sphaerodoridae is a well-defined group of annelids characterized by the presence of spherical tubercles over their surface, an epithelium protected by a thick cuticle without collagen filaments, segments poorly delineated, small and short prostomial appendages, and simple or compound chaetae (Ruderman 1911, Reimers 1933, Fauchald and Rouse 1997, Pleijel and Dahlgren 1998, Hausen 2005, Filippova et al. 2010, Capa et al. 2014, 2016a, 2019, Capa and Bakken 2015). Species described in the family are of relatively small size, generally ellipsoid in shape and with certain exceptions measuring between 0.5 and 5 mm in length.

The monophyly of the family has only being assessed recently (Capa et al. 2016a, 2019), but it was generally assumed before due to their characteristic external morphology, i.e., the presence of inflated capsules and tubercles present in two or more longitudinal rows on the dorsum (Ruderman 1911, Fauchald and Rouse 1997, Pleijel and Dahlgren 1998, Figs. 7.13.14.1A–D, 7.13.14.2A–H, and 7.13.14.3A–D, G–J). Sphaerodorids were earlier regarded as an aberrant family (Pettibone 1982) but is now commonly considered as belonging to Phyllodocida although sister-group relationships are still far from being understood (Rouse and Fauchald 1997, Pleijel and Dahlgren 1998, Worsaae et al. 2005, Aguado and Rouse 2006, Zrzavý et al. 2009). A relationship to Syllidae has been discussed based on the interpretation of the sphaerodorid pharynx being synapomorphic with the proventricle characteristic of syllids (see Fauchald and Rouse 1997, Aguado and San Martin 2009), but further studies indicated these structures were not homologous (Filippova et al. 2010, Helm and Capa 2015). Unfortunately, Sphaerodoridae have been neglected in latest phylogenomic analyses of Annelida (e.g., Weigert et al. 2014, Andrade et al. 2015, Struck et al. 2015).

Sphaerodoridae has recently experience a deep systematic restructure. In a previous version of the present review (Capa et al. 2014), the family contained 10 genera, delineated based on the number of longitudinal rows of large epithelial tubercles, the number and arrangement of additional smaller epithelial papillae, the chaetal morphology, and the relative length of antennae. After some partial revisions of the group, Sphaerodoridae at present includes 131 species classified in eight genera, one of the them newly erected and three being synonymized (Capa and Bakken 2015, Capa and Rouse 2015, Capa et al. 2016a, b, 2018, 2019). After the currently accepted classification, the most speciose genus is *Sphaerephesia* Fauchald, 1972, with 36 species; followed by *Sphaerodorum* Örsted, 1843 and *Sphaerodoridium* Lützen, 1961 (each with 24 species); and *Geminofilum* Capa et al. 2019 (19 species) (Capa and Bakken 2015, Capa et al. 2019). Sphaerodorids mainly live in muddy sediments from the intertidal to deep-sea environments and have a worldwide distribution. With the exception of the monotypic genus *Commensodorum* Fauchald, 1974, genera have been reported from wide geographic distribution and bathymetries. Species have generally been reported with narrower environmental requirements and show constricted geographical distributions. Besides their moderate diversity and radiation along the marine benthos, they are neither common nor abundant (e.g., Fauchald 1974, Sardá-Borroy 1987, Schaff et al. 1992, Blake and Grassle 1994, Kudenov 1994, Pleijel 2001, Böggemann 2009). From examinations of samples collected with epibenthic dredges, there are indications that sphaerodorids may also have a patchy distribution (Capa et al. 2019).

Morphology

External morphology

Body shape. Sphaerodorids are characterized by the presence of spherical glandular tubercles and papillae on their body surface, arranged in more or less obvious longitudinal and transverse rows (Ruderman 1911, Reimers 1933, Pleijel and Dahlgren 1998, Fauchald and Rouse 1997, Wilson 2000, Pleijel 2001, Hausen 2005, Filippova et al. 2010, Capa et al. 2014, 2016a, 2019, Capa and Bakken 2015; Figs. 7.13.14.1A–D, 7.13.14.2A–H, 7.13.14.3A–D, G–J, 7.13.14.6A–F, 7.13.14.8A, B, and 7.13.14.14D, G, J, and 7.13.14.15A, D, G).

Although most sphaerodorids are strongly convex dorsally and have maggotlike short, compact and ellipsoid bodies, and rounded anterior and posterior ends (Figs. 7.13.14.1C, D, 7.13.14.2B–H, and 7.13.14.14C, D,G, J), there are also some longer forms, with abrupt anterior ends, posterior segments tapering toward the pygidium, and slightly flattened dorsoventrally (Fig. 7.13.14.1A, B, E, F, 7.13.14.15D). Living individuals tend to roll up when extracted from the sediment. Because of their usual small parapodia and short appendages, their habitus diverges greatly from that of other Phyllodocida.

Prostomium. The prostomium is very small and fused with the peristomium (contrary to the interpretation of Rouse and Fauchald 1997) and is not clearly distinguishable from the rest of the body (Figs. 7.13.14.4A–E, 7.13.14.6A, D,

https://doi.org/10.1515/9783110647167-020

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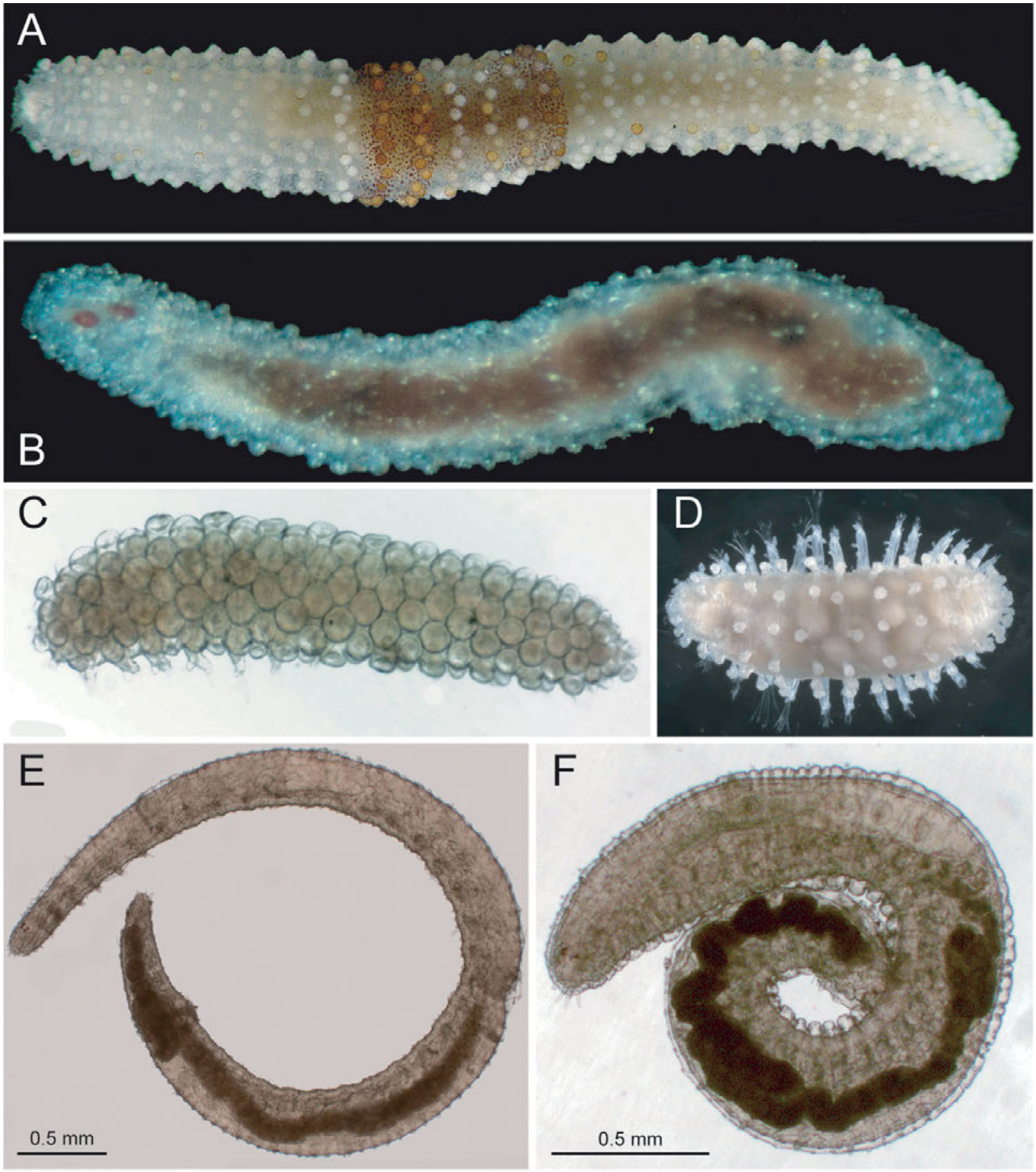


Fig. 7.13.14.1: External morphology of Sphaerodoridae. A, *Sphaerodoridium* sp. from Fiji, dorsal view. B, *Geminofilum* sp. from Guam, dorsal view, note the pigmented spots in the anterior end which are likely to represent the nuchal organs. C, Holotype of *Geminofilum macrotubercula* (Böggemann, 2009), dorsal view, off Namibia. D, *Clavodorum* sp. filled with mature eggs, dorsal view. E, *Sphaerodorum* cf. *abyssorum* Hansen, 1878 from Roscoff, France, dorsolateral view. F, *Sphaerodorum* sp. from Roscoff, France, specimen slightly squeezed to show thick transparent cuticle. A, B, E, F, living specimens. A, B, photos by Leslie Harris.

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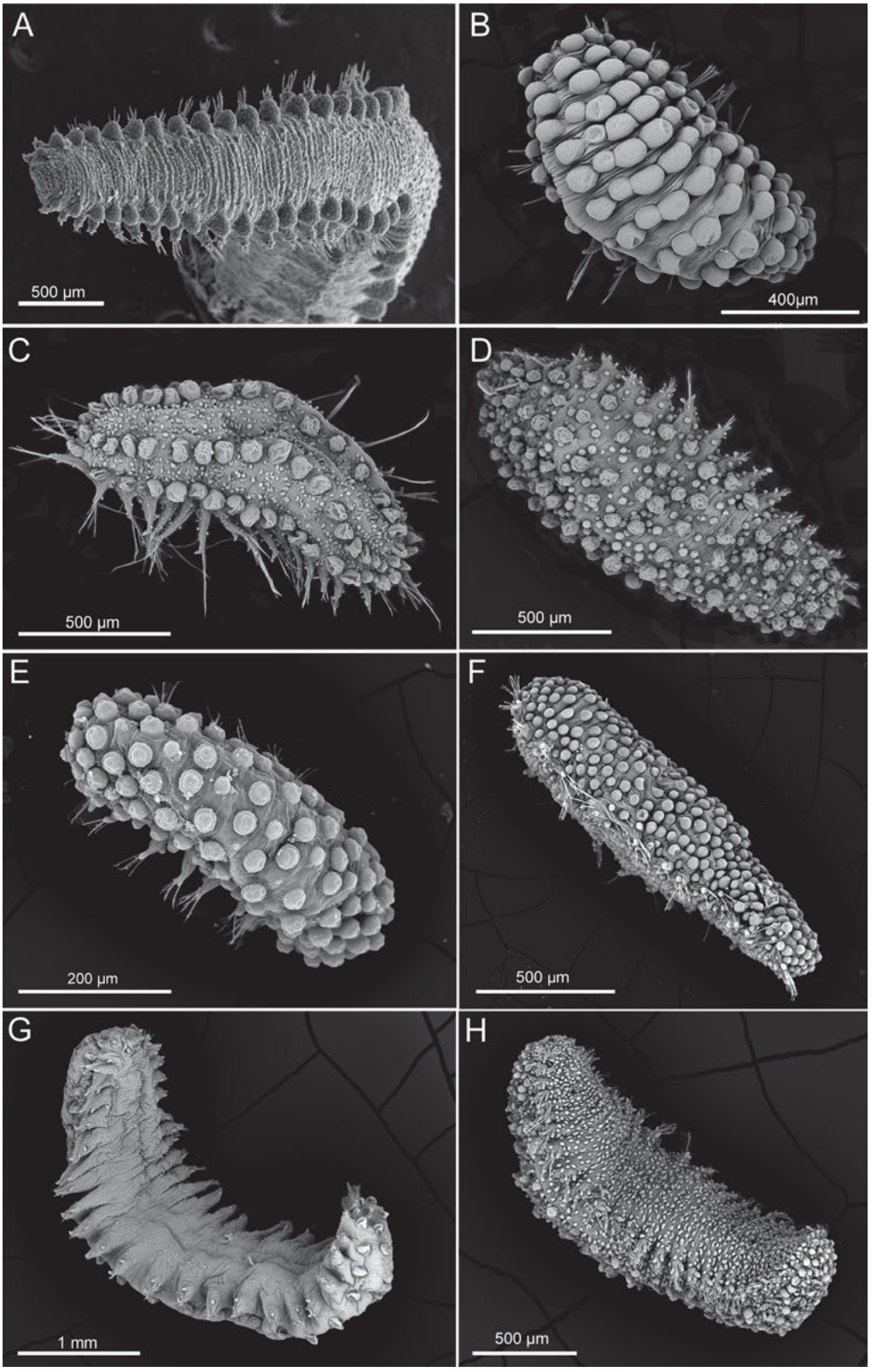


Fig. 7.13.14.2: Comparison of general external morphology and surface tubercles in Sphaerodoridae. In all images, head is at left side. A, *Sphaerodorum* cf. *flavum* Ørsted, 1843 from Norway, anterior end dorsal view. B, *Geminofilum gudmunduri* (Moreira & Parapar, 2012) from Norway, dorsal view. C, *Sphaerephesia* sp. from Norway, dorsal view. D, *Clavodorum* sp. from Norway, dorsal view. E, *Geminofilum* sp. from Australia, dorsal view. F, *Geminofilum fauchaldi* (Hartmann-Schröder, 1979) from Australia, lateral view. G, *Sphaerephesia* cf. *laureci* (Desbruyères, 1980) from Norway, ventral view. H, *Sphaerodoridium* cf. *minutum* (Webster & Benedict, 1887) from Norway, ventral view; SEM micrographs.

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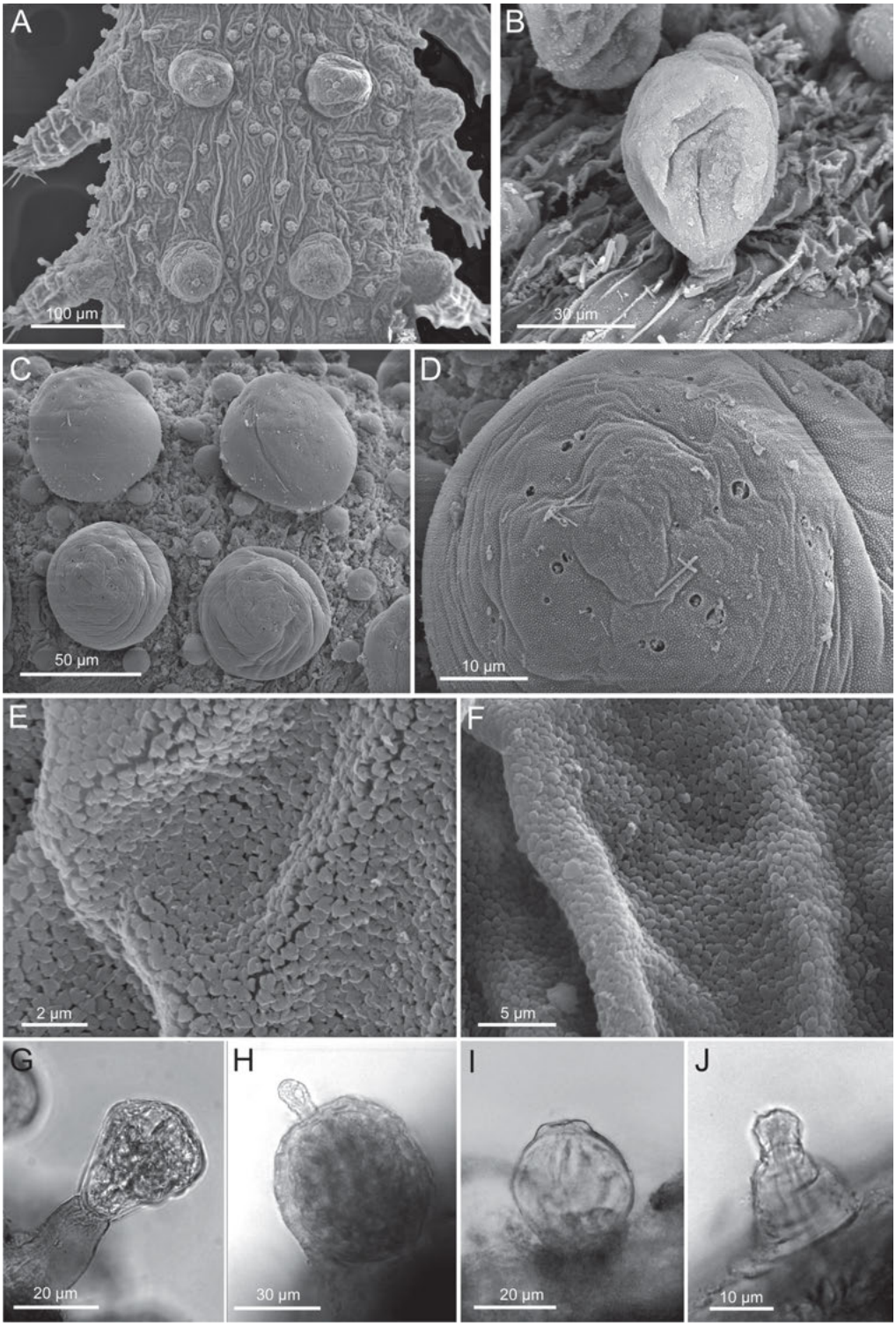


Fig. 7.13.14.3: Dorsal tubercles, papillae, and epithelial granules in Sphaerodoridae. A, *Sphaerephesia brevicapitis* (Moore, 1909) from California, USA, macrotubercles with terminal papillae. B, *Sphaerodoridium* sp. from Norway, stalked and smooth macrotubercle. C, D, *Sphaerodoropsis* sp. from Australia: C, sessile and smooth macrotubercles; D, detail of pores on macrotubercle. E, *Sphaerodoropsis* sp. from Australia, detail of cuticular surface with heart-shaped granules. F, *Sphaerodoropsis* sp. from Australia, different species than in E, cuticular surface with elliptical granules. G, *Clavodorum antarcticum* Hartmann-Schröder & Rosenfeldt, 1990 from Antarctica, stalked macrotubercle. H, *Sphaerodorum muhlenhardtae* (Hartmann-Schröder & Rosenfeldt, 1988) from Antarctica, sessile macrotubercle with terminal papillae. I, *Geminofilum fauchaldi* from Australia, sessile macrotubercle with large distal invagination. J, *Sphaerodorum australiensis* (Hartmann-Schröder, 1981) from Australia, microtubercle with collar and terminal papilla. A–F, Scanning electron microscopic micrographs; G–J, light microscopic micrographs.

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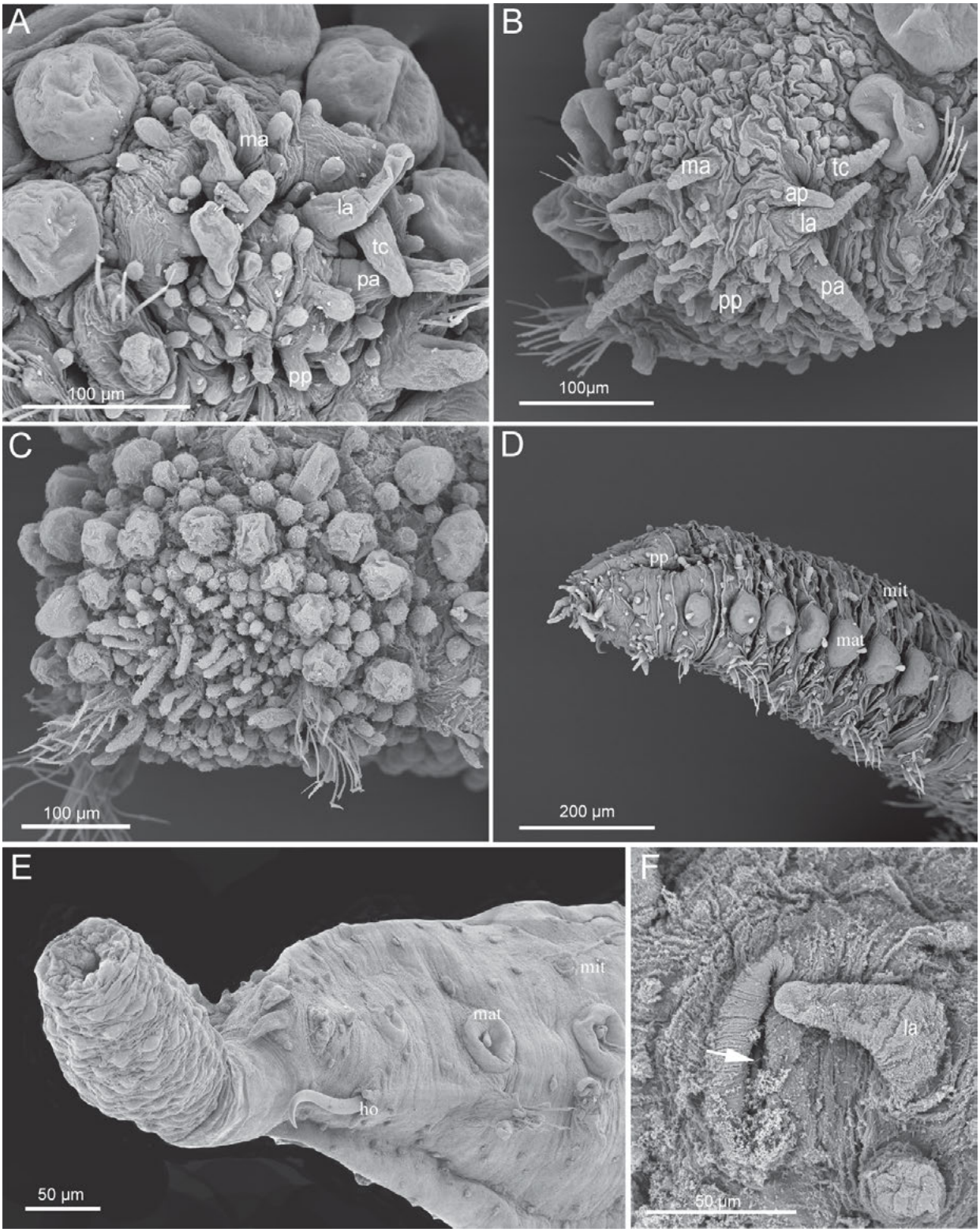


Fig. 7.13.14.4: Anterior ends. A, *Geminofilum gudmunduri*, prostomial and peristomial appendages and papillae. B, *Sphaerephesia parva* (Ehlers, 1913) wrinkled prostomial and peristomial appendages, an anterior pair of papilliform papillae (pp) is present. C, *Clavodorum* sp. with head appendages and papillae similar in form and shape. D, *Sphaerodorum* cf. *flavum* distinct head appendages and different types of tubercles on the body surface. E, *Sphaerodorum* cf. *abyssorum* with papillated everted pharynx and hooks (ho) on chaetiger 1. F, *Sphaerephesia* sp. with nuchal organ pit (arrow) behind lateral antennae. ho, hook; la, lateral antenna; ma, median antenna; mit, microtubercle; mat, macrotubercle; pa, palp; pp, papilla; tc, tentacular cirrus; SEM micrographs.

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7.13.14.14D, G, J, K, and 7.13.14.15A, G). As a consequence, the brain is dislocated into the peristomium and first chaetiger, and the nuchal organs are internalized. Similarly, cerebral eyes, if present, are visible in the same region (Figs. 7.13.14.1E–F, 7.13.14.6A, E, and 7.13.14.10). The anterior end can be retracted inside the body (Ruderman 1911). The segments are poorly delineated externally in most species (Figs. 7.13.14.1A–F, 7.13.14.2A–H, 7.13.14.6A–F, 7.13.14.14C, D, G, and 7.13.14.15A, D, G). The prostomial appendages are located in the anterior end projecting forward (Figs. 7.13.14.4A–E, 7.13.14.6A, D, E, 7.13.14.14A, and 7.13.14.15A, G). The assortment of terms referring to these structures in the literature reflects the lack of information about their nature, hindering homology statements of these with the appendices found in other Phyllodocida. All sphaerodorids bear two pairs of anterior prostomial appendages often similar in shape and size and a single appendage dorsal to the posterior pair of appendages, which in some cases differs in shape and size from the rest (Figs. 7.13.14.4A–D, 7.13.14.6A, D, E, 7.13.14.14A, and 7.13.14.15A, G). Recent studies mostly coincide in naming the ventralmost pair of appendages as palps, the dorsal pair lateral antennae, and the unpaired appendage median antenna (e.g., Rouse and Fauchald 1997, Pleijel and Dahlgren 1998, Wilson 2000, Pleijel 2001, Worsaae et al. 2005, Aguado and Rouse 2006, Böggemann 2009, Filippova et al. 2010, Moreira and Parapar 2011, Reuscher and Fiege 2011, Moreira 2012, Magalhães et al. 2011; Figs. 7.13.14.4A–E, 7.13.14.6A, D, E). This would be the most conclusive and parsimonious interpretation of these appendages, especially when considering the presence and arrangements of prostomial appendages in other related annelids (Aguado and Rouse 2006). Although there are some exceptions in the morphology of the anterior end in other representatives of Phyllodocida, as for instance in glycerids and goniadids (Orrhage 1999), no anatomical study or comparison has been performed to date. However, in members of Glyceriformia, palps, antennae and the elongated prostomium are fused forming the typical annulated anterior end characteristic of this taxon (Orrhage 1990). Thus, these structures form a single anterior sensory appendage terminating in four fingerlike projections of equal size. A detailed investigation of their innervation pattern still allows identifying the ventralmost appendages as palps (palpostyles) in Glyceridae (Koldehoff and Purschke unpublished observation). In Sphaerodoridae, the prostomial appendages are made up of epidermal supportive cells, gland cells, and various types of receptor cells (Fig. 7.13.14.9A–C).

After misinterpretations on an earlier paper that dealt with the nervous system of other polychaetes (Orrhage 1966) resulting in some confusion on this matter (e.g., Glasby 1993, Aguado and Rouse 2006, Reuscher and Fiege 2011), there is no new published information about the innervation of anterior appendages in Sphaerodoridae (Orrhage 1990, Orrhage and Müller 2005). As it has been done formerly in eunicidans, several authors termed all five prostomial appendages as antennae because of their similar appearance (e.g., Claparède 1863, Fauchald 1974, Kudenov 1987a, b, Borowski 1994, Moreira et al. 2004, Moreira 2012, Aguirrezabalaga and Cebeiro 2005, Moreira and Parapar 2007). Some authors have also named a pair of appendages located behind the lateral antennae as antenniform papillae (Aguado and Rouse 2006, Moreira and Parapar 2011, Moreira 2012; Fig. 7.13.14.4B) or the third pair of antennae (Fauchald 1977), but their nature also needs investigation. In addition, the situation becomes even more complicated because of the presence of additional often smaller prostomial papillae, which are common in certain representatives. These papillae can be very similar to the prostomial appendages, impeding their recognition and distinction from each other (e.g., Ruderman 1911; Fig. 7.13.14.4A–D). They can protrude at the base of the prostomial appendages, consequently referred to as spurs (Kudenov 1987b, Böggemann 2009, Moreira et al. 2011), giving the appendages a furcate appearance.

Peristomium. The peristomium bears a pair of appendages, referred to as tentacular cirri and, in some cases, also some additional papillae (Fig. 7.13.14.4A–C).

Tubercles and papillae. Although superficially similar to certain syllids (e.g., *Sphaerosyllis*, see chapter 7.13.2; Figs. 7.13.2.23 and 7.13.2.24), the tubercles of sphaerodorids (Figs. 7.13.14.1A–D, 7.13.14.2A–H, 7.13.14.3A–D, G–J, 7.13.14.6B, C, D, F, 7.13.14.8A–B, 7.13.14.14A, D, G, J, and 7.13.14.15A, D, G) are not considered as homologous to the epidermal papillae present in other polychaetes (Rouse and Fauchald 1997). The terminology referring to the protuberances of the body was randomly used until Fauchald (1974) proposed to classify them according to their size, shape, position, and in some cases function. Thereby, he proposed the term macrotubercles, microtubercles, and papillae following the criteria in Tab. 7.13.14.1.

The number of dorsal longitudinal and transverse rows of protuberances, particularly the macrotubercles (Figs. 7.13.14.3A–D, G–I, 7.13.14.14A, C, D, G, J, and 7.13.14.15A, D, G), and their arrangement have been considered as key diagnostic features at the generic level. Members of *Euritmia* Sardá-Borroy, 1987 typically lack macrotubercles and microtubercles (only papillae are present; Fig. 7.13.14.13A), and *Sphaerodorum* Ørsted, 1843 has two longitudinal rows of macrotubercles and two of microtubercles

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Tab. 7.13.14.1: Classification of the body protuberances according to Fauchald (1974).

		Shape				
Tubercle terminology	**Size**	**General shape**	**Peduncle**	**Collar**	**Terminal papillae**	**Position**
Macrotubercles	Large	Spherical	Absent/ present	Absent	Absent/present	Dorsal/ventral
Microtubercles	Small	Ellipsoid	Absent	Present	absent	Dorsal
Papillae	Medium/ small	Hemispherical, spherical, or conical	Absent	Absent	Absent	Dorsal, ventral, parapodial, prostomial

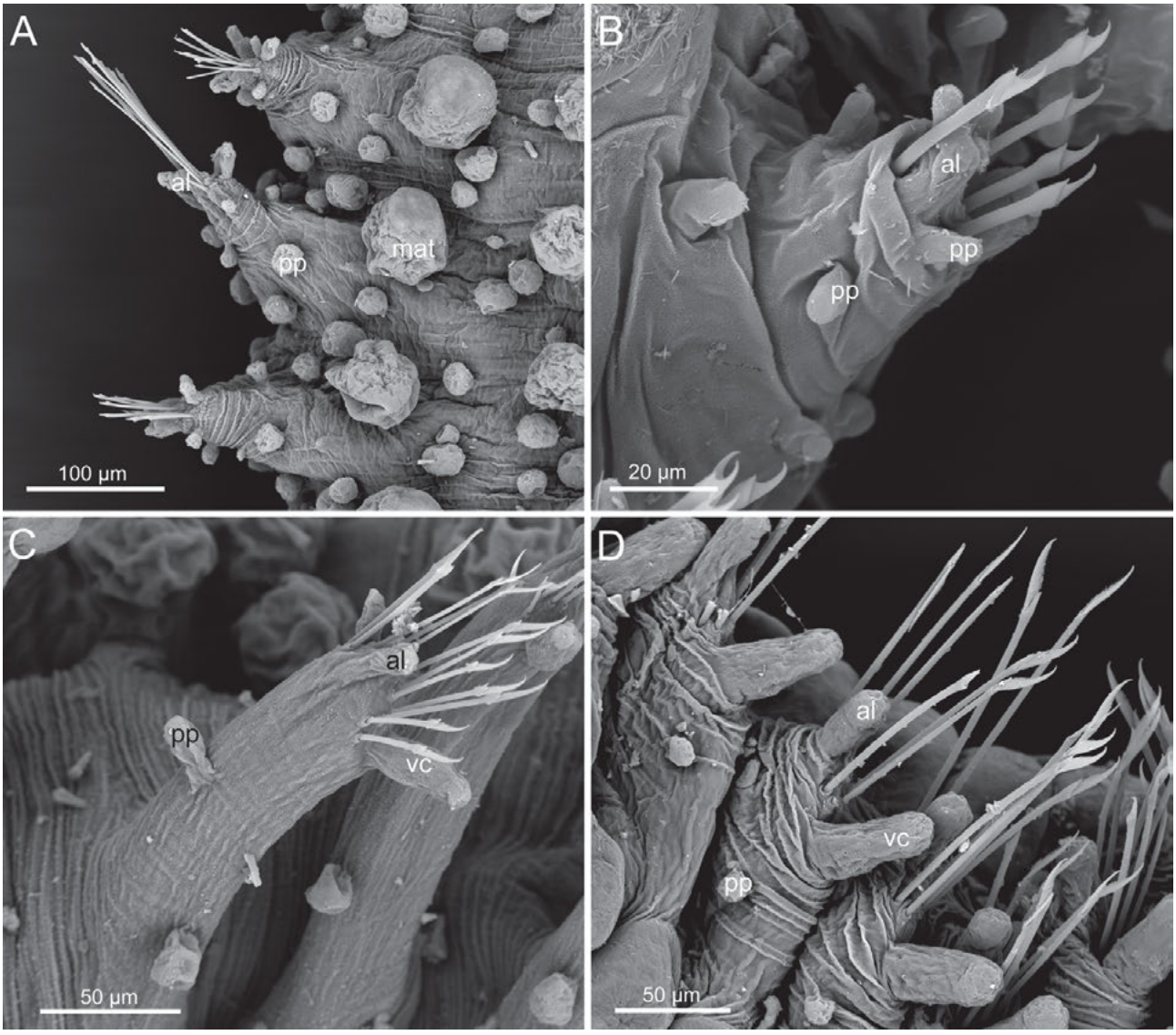


Fig. 7.13.14.5: Diversity of parapodia within Sphaerodoridae. A, *Sphaerodoridium* sp. from Norway, dorsal view. B, *Sphaerodorum* sp. from Australia, dorsal view. C, *Sphaerodoridium* sp. from Norway, anterior view. E, *Geminofilum gudmunduri* from Norway, ventral view. al, acicular lobe; mat, macrotubercle; vc, ventral cirrus; pp, papilla. SEM micrographs.

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(Figs. 7.13.14.2A, 7.13.14.4D, E, and 7.13.14.15G). *Commensodorum* Fauchald, 1974 and *Sphaerephesia* have four longitudinal rows of sessile macrotubercles in a single transverse row per segment (Figs. 7.13.14.2C and 7.13.14 A3). *Clavodorum* Hartman & Fauchald, 1971 bear six and *Sphaerodoridium* Lützen, 1961 have more than six rows of macrotubercles in a single transverse row per segment (Figs. 7.13.14.1D, 7.13.14.2D, 7.13.14.3B, G, and 7.13.14.15A). Macrotubercles of the recently erected *Geminofilum* Capa et al., 2019 are arranged in double transverse rows while members of *Sphaerodoropsis* Hartman & Fauchald, 1984 have macrotubercles arranged in three transverse rows per segment (Figs. 7.13.14.1A–C, 7.13.14.2B, E, F, 7.13.14.3C, 7.13.14.4C, and 7.13.14.15D).

It has been speculated that the epithelial tubercles could be ovaries (Ørsted 1844), respiratory organs (Johnston 1845), secretory glands (Claparède 1863), or sensory glands (Kölliker 1864, Ruderman 1911). Recent studies have shown that these capsules, especially the macrotubercles, have a number of pores on their surface with circular actin staining (Fig. 7.13.14.3D); the cuticle is thinner than that on the rest of the body; and they are well innervated (Fig. 7.13.14.9D–F), indicating that at least macrotubercles have in fact a dual function: they are primarily glandular structures comprising several types of gland cells and are sensory as well possessing a number of different receptor cells (Helm and Capa 2015; Fig. 7.13.14.9D, F). The larger pores measuring about 1 µm in diameter visible in the SEM (Fig. 7.13.14.3D) most likely are the openings of these gland cells (Fig. 7.13.14.9D). Other pores belong to collar receptors sending their single cilium through smaller openings being less than 0.5 µm wide (Fig. 7.13.14.9A, B).

Parapodia. Sphaerodorids typically have uniramous parapodia supported by a single straight acicula and equipped with protuberances (Figs. 7.13.14.5A–D, 7.13.14.14H, and 7.13.14.15H). The common digitiform appendages located

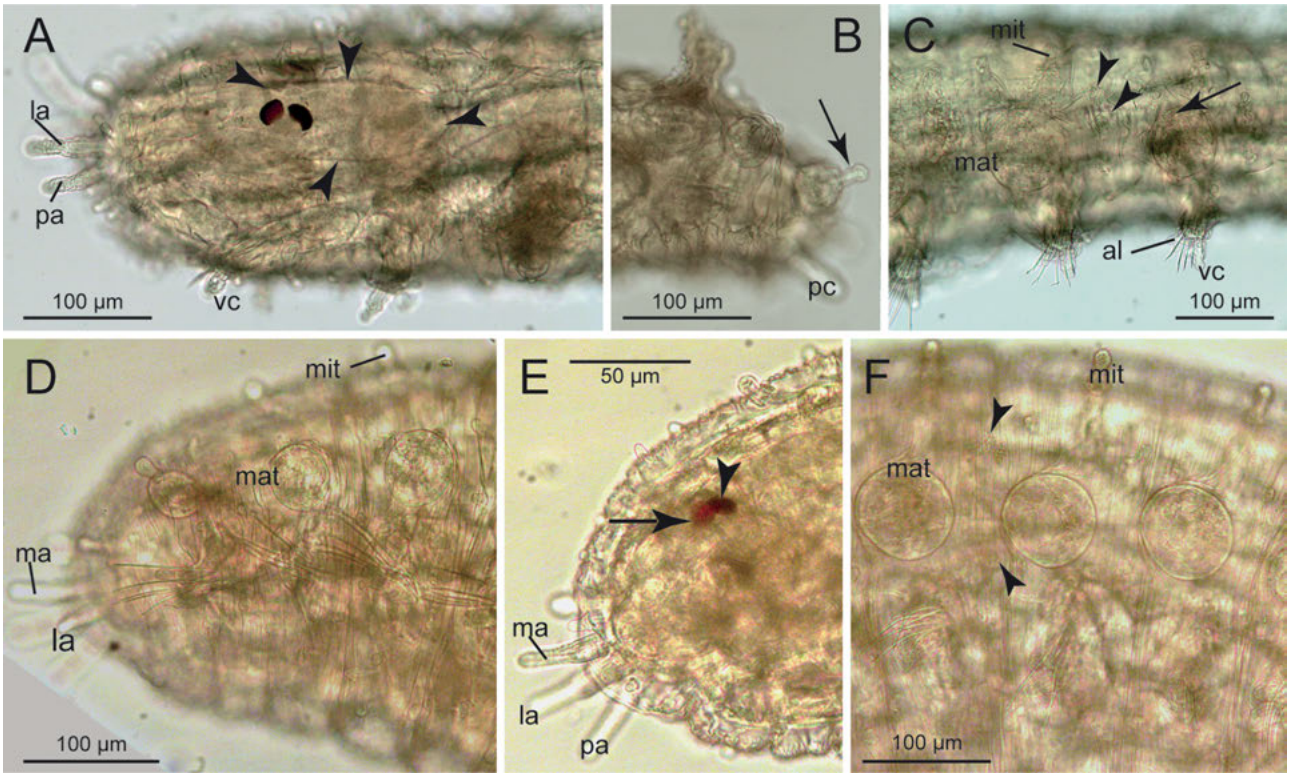


Fig. 7.13.14.6: A–C, *Sphaerodorum* cf. *abyssorum* from Roscoff, France. A, Anterior end with two pairs of eyes and brain outline marked by arrowheads. B, Lateral view of pygidium with pygidial cirrus (pc) and macrotubercle with terminal papilla. C, Three mid body segments with parapodia, macro- (mat) and microtubercles (mit); note the papillae between tubercles (arrowheads), arrow points to papilla on macrotubercle. D–F, *Sphaerodorum* sp., from Roscoff, France. D, Anterior end in peripheral view showing median and lateral antennae (ma, la), palps (pa), macrotubercles (mat), and parapodia. E, The same specimen, plane of focus somewhat deeper showing single eye with stalked lens (arrow), arrowhead points to pigment cup, impeding presence of two closely associated eyes. Note the different colors of lens and pigment cell. F, Parapodia, macrotubercles (mat) and microtubercles (mit) in midbody region, arrowheads point to papillae; al, acicular lobe; la, lateral antenna; mat, macrotubercle; mit, microtubercle; pa, palp; pc, pygidial cirrus; vc, ventral cirrus. Micrographs from living specimens.

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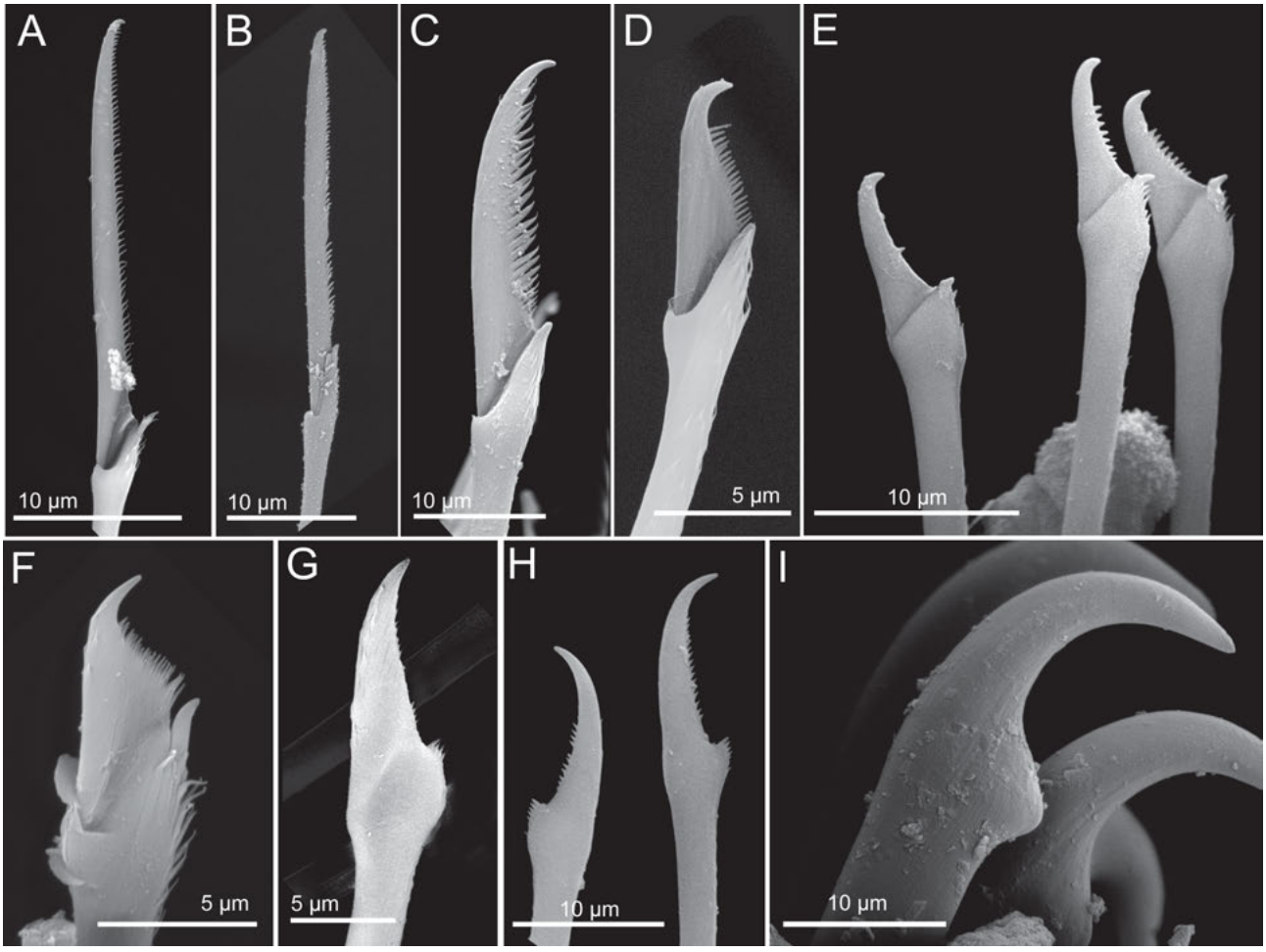


Fig. 7.13.14.7: Chaetae in Sphaerodoridae. A, B, Compound chaetae with long blades. A, *Sphaerephesia amphorata* Capa et al., 2016 from Massachusetts, USA. B, *Sphaerephesia* cf. *philippi* (Fauvel, 1911) from Norway. C, D, Compound chaetae with short blades. C, *Geminofilum gudmunduri* from Norway. D, *Geminofilum fauchaldi* from Australia. E, Compound chaetae showing intraparapodial variability of serration of blades, *Sphaerodorum* sp. from Antarctica. F, Compound chaetae with wide and short blades, *Sphaerephesia* sp. from Australia. G, Pseudocompound chaeta, *Sphaerodorum olgae* Moreira & Parapar, 2011 from Antarctica. H, I, Simple chaetae, variability along the body axis, *Sphaerodorum* cf. *flavum* from Norway: H, anterior chaetiger; I, midbody chaetiger. SEM micrographs.

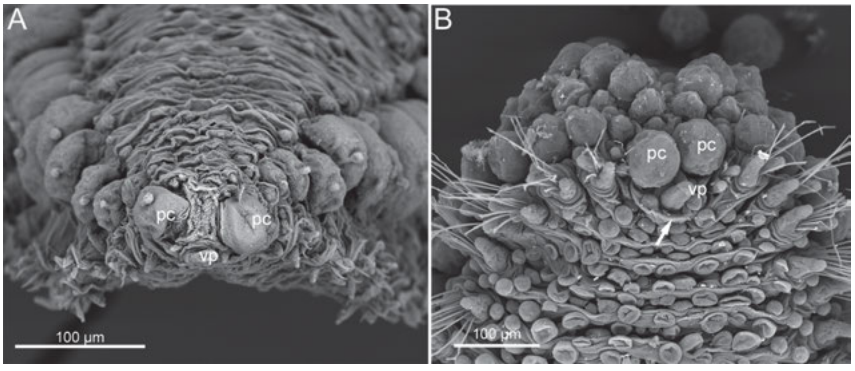


Fig. 7.13.14.8: Posterior ends and pygidium in Sphaerodoridae. A, *Sphaerodorum* cf. *flavum* from Norway, posterior view. B, *Clavodorum* sp., ventral view, arrow points to anus. pc, pygidial cirrus; vp, ventral papilla. SEM micrographs.

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on top of the parapodia in other Phyllodocida are lacking (e.g., Fig. 7.13.14.5A). Some authors have postulated the homology of some of these epithelial protuberances with the dorsal cirri of other polychaetes (Rudermann 1911, Reimers 1933) that have convergently been modified to appear alike other longitudinal rows of epithelial protuberances. However, a hypothesis that sphaerodorids have lost the dorsal cirri has also been introduced (Fauchald 1974). Because musculature is absent in the tubercles and this is also the case in dorsal cirri without a motile function in other Phyllodocida (e.g., Syllidae), homology statements of these structures are difficult to be verified (Filippova et al. 2010). However, a recent study indicates that the small and elongated dorsal tubercles, called microtubercles, only found in long-bodied members of *Sphaerodorum*, may be homologous to the dorsal cirri in other polychaetes. Evidences include the number and arrangement, with only one pair per segment located dorsally to the parapodia. They are also strongly innervated, indicating a sensory funcion and lack glandular content and pores. Both of these charcateristics differ to the remaining epithelial tubercles but conversely are shared with dorsal cirri of other polychaetes (Helm and Capa 2015).

Ventral cirri are present, and in some species parapodial lobes (pre- and postchaetal) have been described, often morphologically similar to parapodial papillae (Fauchald 1972; Fig. 7.13.14.5C, D). The chaetae protrude from the acicular lobes in more or less obvious transverse rows (Fig. 7.13.14.5A–D). Pre- and postchaetal lobes can be present, but they have often been mistaken with parapodial papillae, as they share a similar morphology.

Chaetae. Chaetae can be simple (*Commensodorum* and *Euritmia*) or compound falcigers, with a blade and a unidentate shaft with variable length and width (*Clavodorum*, *Geminofilum*, *Sphaerephesia*, *Sphaerodoridium*, and *Sphaerodoropsis*; Fig.7.13.14.7A–D, F). Members of *Sphaerodorum* bear chaetae with a wide range of morphological variation from simple (Fig.7.13.14.7H, I) to compound (previously included in *Ephesiella*; Fig.7.13.14.7E) and also bearing both types on each chaetiger (previously gathered in *Ephesiopsis*) (see Capa et al. 2018). In addition, some members of *Sphaerodorum* are often provided with stout simple hooks in both parapodia of the first chaetigers (Fig. 7.13.14.4D, E).

Pygidium. Posterior segments are in general smaller and bear a lower number of tubercles and papillae. The pygidium is usually provided with a pair of pygidial cirri resembling those macrotubercles displayed above the parapodia and a ventral digitiform single cirrus, similar in length to paired structures.

Anatomy

Epidermis and cuticle. Sphaerodorids have been characterized by having a thick cuticle (Ruderman 1911), but actual data of the width of this layer are only known for *Sphaerodorum abyssorum*, *Sphaerodorum flavum* Ørsted, 1843, and *Sphaerodoridium minutum* (Webster & Benedict, 1887), measuring up to 85 µm in thickness (Kuper and Purschke 2001, Purschke unpublished observation; Figs. 7.13.14.9A–D and 7.13.14.10). This cuticle is formed by an electron-dense epicuticle and a basal cuticle lacking collagen fibers on the trunk (Kuper and Purschke 2001), unlike most polychaetes where the cuticle comprises layers of parallel collagen fibers crossing at about 90° (e.g., Hausen 2005). Irregularly arranged collagen fibers have been observed only in the protuberances (Purschke unpublished observation). Surprisingly, the basal cuticle only comprises little material in the species investigated. This material is of fine fibrillar structure leaving empty spaces, and thus the entire cuticle has a spongy appearance (Fig. 7.13.14.9D). In certain species, the cuticle is masked with detritus (Fig. 7.13.14.9D). For these reasons, the cuticle in sphaerodorids superficially resembles the so-called tunic found in Flabelligeridae (see chapter 7.3.1.6, Vol. 1). The epicuticle is covered by a layer of small disklike or stalklike projections about 0.4 by 0.4 µm being only 40–60 nm apart (Fig. 7.13.14.9A–D). These electron-dense projections are very likely responsible for the granulated appearance of the body surface if viewed by SEM (Fig. 7.13.14.3E, F) and TEM (Fig. 7.13.14.9A–D). The epidermis lying beneath the cuticle is a thin monolayer, separated from the underlying muscles by a thin extracellular matrix (Kuper and Purschke 2001; Fig. 7.13.14.9D).

The gland cells in the epidermis, in connection with tubercles and papillae, have been regarded to have a sensory role (Ruderman 1911). However, this is likely to be a misinterpretation because these gland cells are always associated with receptor cells in the tubercles and in the papillae (Fig. 7.13.14.9A–F). There are additional gland cells located in the ventral edge of the parapodia, in relation to the ventral cirri and in the dorsal edge that could have a secretory function because it is filled with mucous (Ruderman 1911, Helm and Capa 2015). The epidermis on the trunk may also comprise gland cells in addition to epidermal supportive cells.

Musculature. The musculature apparatus in sphaerodorids is very complex, especially at the anterior end, compared with the apparently simple external morphology. *Sphaerodoropsis* sp. and *Sphaerodoridium balticum* (Reimers, 1933) are provided with longitudinal muscles forming four pairs of discrete bands that run along the

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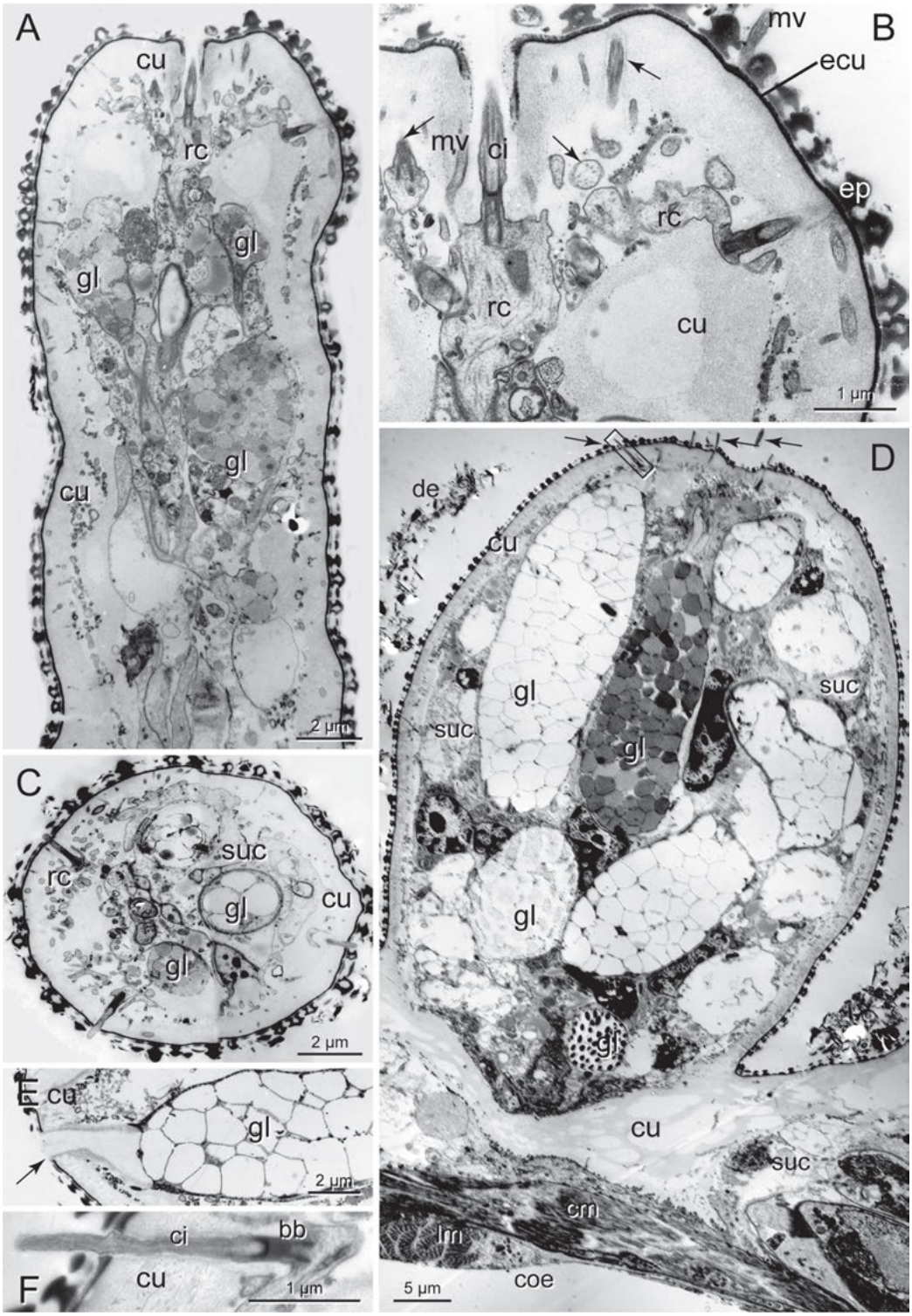


Fig. 7.13.14.9: *Sphaerodoridium minutum*, Antennae and macrotubercles. A, Antenna in longitudinal section. B, Enlargement of A showing apical parts of receptor cells, arrows point to penetrative and nonpenetrative sensory cilia, part of sensory cilia (ci) project through pores in the cuticle. C, Cross section of antenna showing supportive cell (suc), monociliary receptor cells (rc), and gland cell processes (gl). D, Stalked macrotubercle in longitudinal section, appendage primarily composed of different types of gland cells (gl) enwrapped by a few epidermal supportive cells (suc); note the cilia of receptor cells (arrows), cuticle of the body wall with empty spaces, body wall comparatively thin. E, Opening of gland cell through pore in the cuticle (arrow). F, Enlargement of boxed area in D showing short penetrative cilium of receptor cell. bb, basal body; ci, cilium; cm, circular muscle fiber; coe, coelom; cu, cuticle; de, detritus; ecu, epicuticle; ep, epicuticlur projections; gl, gland cell; lm, longitudinal muscle fiber; mv, microvillus; rc, receptor cell; suc, epidermal supportive cell. TEM micrographs.

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whole body length, the ventralmost pair being the most prominent, the dorsalmost, and two pairs of lateral and laterodorsal bands being considerably smaller in dimension (Reimers 1933, Kuper and Purschke 2001, Filippova et al. 2010, Helm and Capa 2015; Fig. 7.13.14.11A, B). By contrast, in *Sphaerodorum* spp., there are only three pairs of longitudinal bundles and the dorsal and dorsolateral bundles being either fused or closely apposed (Ruderman 1911, Kuper and Purschke 2001, Helm and Capa 2015). These bands are formed by large flattened cells lying in single rows and with the nuclei located on the distal part facing the coelomic cavity. These fibers are not covered by a coelomic epithelium (Tzetlin 1987, Kuper and Purschke 2001, Tzetlin and Filippova 2005). Small bands of transverse muscle fibers encircle the body between the epidermis and the longitudinal muscles except for a narrow gap in the midventral line (Ruderman 1911, Reimers 1933, Kuper and Purschke 2001, Filippova et al. 2010, Helm and Capa 2015; Fig. 7.13.14.11C). This transverse musculature is represented by a few and distinctly separated bands in each segment (e.g., Fig. 5B, C in Filippova et al. 2010). Based on confocal laser scanning microscope observations, Filippova et al. (2010) concluded an unusual position of the transverse fibers above the longitudinal fibers in short-bodied members of the family (Filippova et al. 2010, Helm and Capa 2015). This is in contrast to previous observations and what is generally found in annelids and should be confirmed by TEM observations (Ruderman 1911, Reimers 1933; see Fig. 1A in Kuper and Purschke 2001; Fig. 7.13.14.9D). Helm and Capa (2015) regarded this unusual appearance of transverse fibers in short-bodied species as a derived character having evolved within sphaerodorids. Moreover, two pairs of bracing muscles are present in each segment, located between the longitudinal and the transverse fibers. They extend from the dorsal longitudinal muscle bands to the ventral longitudinal band, running either in an anterior or posterior direction and crossing over themselves on both sides of each segment (Filippova et al. 2010, Helm and Capa 2015).

The neuropodia contain chaetal pro- and retractor muscles. Oblique muscles extend from the midventral line toward the parapodia, forming an "'inverse double-V," separated by large fiber-free areas (Filippova et al. 2010, Helm and Capa 2015; Fig. 7.13.14.11C).

Alimentary canal. The gut in sphaerodorids is a straight tube (Ruderman 1911, Reimers 1933) sometimes coiled in the anterior part of the body (personal observation). It is provided with an axial muscular pharynx, typical for Phyllodocida (Rouse and Fauchald 1997, Pleijel 2001, Tzetlin and Purschke 2005, Filippova et al. 2010; Fig. 7.13.14.11A). In the short-bodied forms, a structure superficially similar to the proventricle present in Syllidae was described (Ruderman 1911, Reimers 1913, Rouse and Fauchald 1997, Pleijel and Dahlgren, 1998, Pleijel 2001, Worsaae et al. 2005, Aguado and Rouse 2006). Recently, a less-developed bulbous pharyngeal region was also described in the long-bodied sphaerodorids (Helm and Capa 2015). However, in sphaerodorids, this pharyngeal structure does not exhibit a clear distinction between the eversible, strawlike, muscular pharyngeal tube followed by a noneversible sucking bulblike proventricle with highly specialized musculature (Tzetlin and Purschke 2005). Thus, the term proventricle should be avoided in this group. The gut musculature in short-bodied sphaerodorids is most likely exclusively made up of a dense grid layer of outer circular and inner longitudinal fibers (Filippova et al. 2010), whereas the long-bodied forms present a similar outer layer, but the inner layer is formed by radial fibers (Helm and Capa 2015).

The mouth opening is surrounded by circular muscles (Ruderman 1911, Reimers 1933, Filippova et al. 2010). It leads into a short so-called buccal cavity forming a pair of small folds at the tip of the muscular axial pharynx (Ruderman 1911, Reimers 1933). Some authors have indicated that this pharynx is eversible (Ruderman 1911, Reimers 1933, Pettibone 1963, 1982, Fauchald 1974, 1977, Rouse and Fauchald 1997, Wilson 2000, Helm and Capa 2015) and that it is provided with terminal papillae (Rathke 1843, Ruderman 1911, Fauvel 1911, Wilson 2000, Helm and Capa 2015; Fig. 7.13.14.4E). In *Sphaerodoridium balticum*, *Sphaerodoridium minutum*, and *Sphaerodorum flavum*, the muscular pharynx ends in two paired epithelial lips with a more or less smooth surface and distinct papillae on the tip of the pharynx are not present (Ruderman 1911, Reimers 1933, Purschke and Thomas unpublished observation). These lips can be protruded and positioned directly on the substratum for the uptake of food. Buccal cavity and muscular pharynx are lined by a cuticle, which successively becomes thinner with depth in the muscular region. Jaws are absent.

Coelom. The coelom comprises a single cavity taking a large sace inside the body. It is lined by a thin peritoneum that also surrounds the nerve cord, the gut, and the dorsal and ventral blood vessels. Septa are absent in all sphaerodorids investigated so far, and mesenteries are incomplete. A small mesentery is usually present connecting the ventral nerve cord with the body wall and forming the subneural vessel (e.g., fig. 35 in Ruderman 1991, fig. 1A, B in Kuper and Purschke 2001). As a result, the body cavity forms a more or less continuous cavity in which the brain,

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gut, developing gametes, etc., are moveable to some extent. The coelom is filled with fluid and a few coelomocytes, granulocytes, and developing and mature gametes (Ruderman 1911, Reimers 1933, Kuper and Purschke 2001; Figs. 7.13.14.1D and 7.13.14.10).

Blood vascular system. Sphaerodorids have a well-developed blood vascular system consisting of a ventral and a dorsal longitudinal vessel, numerous subepidermal vessels that surround the whole body, and nephridial vessels (Kuper and Purschke 2001). The ventral vessel, located below the ventral nerve cord, is wider than the dorsal vessel and is partially branched into a few lacunae (Kuper and Purschke 2001). In *Sphaerodorum flavum*, the epidermal macro- and microtubercles are irrigated with larger subepidermal vessels that in the rest of the body that may also form distinct lacunae (Kuper and Purschke 2001).

Nephridia. *Sphaerodorum flavum* has a pair of protonephridia in each body segment with two terminal monociliated cells called solenocytes. A nephridioduct is formed by two multiciliated cells that enclose the extracellular nephridial canal (Kuper and Purschke 2001). This canal opens to the nephridiopore without penetrating the cuticle. Because protonephridia have also been described by Ruderman (1911), this pattern has been generalized for all sphaerodorids (Bartolomaeus and Quast 2005). The protonephridia are in close association with the blood vascular system (Kuper and Purschke 2001, Bartolomaeus and Quast 2005). On the other hand, the absence of nephridia as stated by Reimers (1933) is obviously an erroneous interpretation. The same applies to the assessment of Goodrich (1945) interpreting the excretory organs of Sphaerodoridae as metanephridia.

The presence of a well-developed blood vascular system together with protonephridia as the type of excretory organs is unusual among metazoans (Ruppert and Smith 1988, Kuper and Purschke 2001) and is only shared with members of Phyllodocidae, Alciopidae, Goniadidae, Glyceridae, and Nephtyidae as well as Pisionidae in Phyllodocida (Ruppert and Smith 1988, Kuper and Purschke 2001). However, the absence of a filtration barrier (extracellular matrix) at the weir formed by the solenocytes (see, e.g., Fig. 2C in Kuper and Purschke 2001) might be explained by the presence of blood vessels and coelom, and it can be hypothesized that such filtration structures in the form of podocytes may be found somewhere at the blood vessels.

Nervous system. The brain occupies a large portion of the anterior end, and it may extend into the second chaetiger in the resting condition, with the prostomium not withdrawn (Figs. 7.13.14.6A and 7.13.14.10). Because there is a lack of septa and mesenteries, it can move far backward if the anterior end is retracted into the body (Ruderman 1911). The brain is only anteriorly connected to the body wall and where the nuchal organs open to the outside. Thus, it projects as a large free bulgelike structure posteriorly into the body cavity. The ventral nerve cord is subepidermal

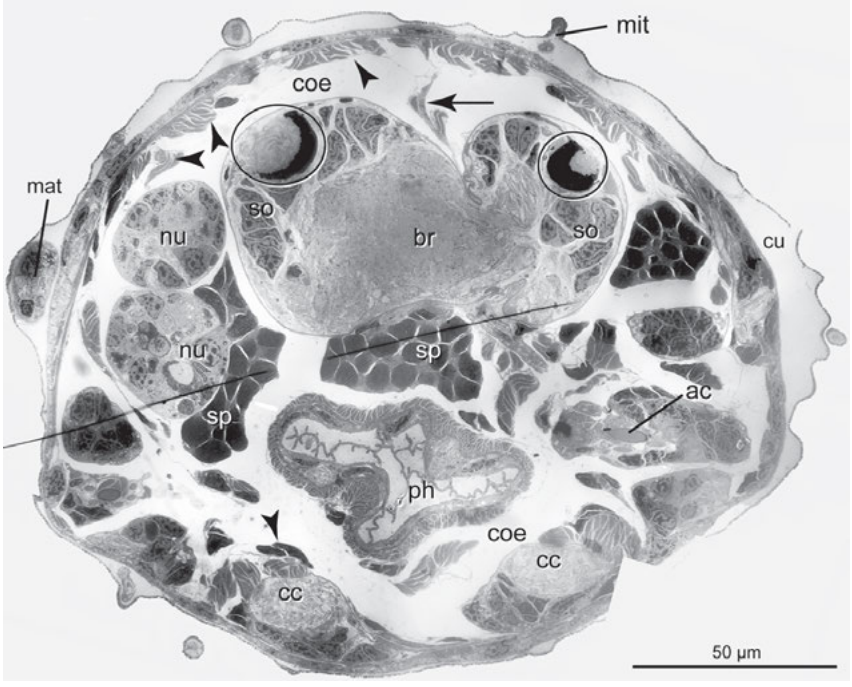


Fig. 7.13.14.10: *Sphaerodorum* cf. *abyssorum* from Roscoff, France; TEM cross section through anterior end showing internal brain with pigmented eyes (encircled) embed in somata of neurons (so), left nuchal organ (nu), pharynx (ph), parapodia, micro- (mit) and macroubercle (mat), groups of spermatids (sp), and longitudinal muscle bands (arrowheads); note the reduced mesenterium and muscle band fastening the brain to dorsal body wall (arrow), circumesophageal connectives (cc) in basiepthelial position. ac, acicula; br, neuropil of brain; cc, circumesophageal connective; coe, coelom; cu, cuticle; mat, macrotubercle; mit, microtubercle; nu, nuchal organ; ph, pharynx; so, somata of brain neurons; sp, spermatid. Photomontage of 16 micrographs; original photo J. Spannagel, Osnabrueck.

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and consists of two contiguous but distinctly separated connectives. It is attached to the body wall by a delicate ventral mesenterium (see above). In the ganglia, two large packages of perikarya are found besides the connectives (Ruderman 1911, Reimers 1933, Kuper and Purschke, 2001).

Sense organs. Several sensory organs have been described in Sphaerodoridae, including nuchal organs, eyes, antennae, and palps. Lateral organs have not been observed so far (Fauchald and Rouse 1997). Moreover, sensory cells have also been reported, which are especially abundant on the antennae, palps, and protuberances (Fig. 7.13.14.9A–F). Nuchal organs are internalized and present as large paired ciliated structures (Ruderman 1911, Reimers 1933) each located at the bottom of two dorsolateral pits opening between prostomium and peristomium with the slitlike aperture often found behind the lateral antennae (Figs. 7.13.14.1B and 7.13.14.4F). They have been studied in *Sphaerodorum flavum* and *Sphaerodoridium balticum* (Ruderman 1911, Reimers 1933). The organs can be protruded to the exterior by the animal (Ruderman 1911). These longitudinal apertures have also been seen in most other genera (Capa and Bakken 2015, Capa et al. 2016; Fig. 7.13.14.4F). Preliminary electron microscopic observations indicate that their structure follows the general pattern of polychaete nuchal organs comprising ciliated supportive cells forming the swollen ends and monociliated receptor cells interspersed between them terminating in an olfactory chamber at the bottom of the nuchal pit (Purschke 1997, unpublished observation). These organs project as posterior prolongations into the body cavity beside the brain (Fig. 7.13.14.10). They are the most conspicuous sensory organs in sphaerodorids, although being almost invisible due to their aberrant position.

Certain species possess one or two pairs of pigmented eyes, whereas other species are apparently eyeless. These eyes are typically two pairs of brown or red subepidermal spots in a trapezoidal arrangement (e.g., in *Ephesiella abyssorum* Hansen, 1878, *Sphaerodorum flavum*, Fig. 7.13.14.6A). Both eyes from each side may be in close contact, sometimes appearing as a single pair of crescent-shaped eyes often erroneously described in the literature (see, e.g., Fauchald 1974, Pettibone 1982). However, certain species such as *Sphaerodorum* sp. and *Sphaerodoridium balticum* definitely possess only one pair of eyes confirming earlier observations (e.g., Reimers 1933, Hartmann-Schröder 1996; Fig. 7.13.14.6E). The eyes are located dorsolateral in the brain, implanted inside two cerebral lobes of ganglionic cells, which are generally observed in the peristomium (Ruderman 1911, Reimers 1933; Fig. 7.13.14.10). However, because the brain is slightly mobile and can be dislocated toward posterior segments, the eyes may be found in the second or third segment and sometimes also asymmetrically arranged (Fig. 7.13.14.6A). Although comparatively large, eyes are composed of only a limited number of cells. Arrangement and occurrence of cell types and cell ultrastructure is as usually reported for

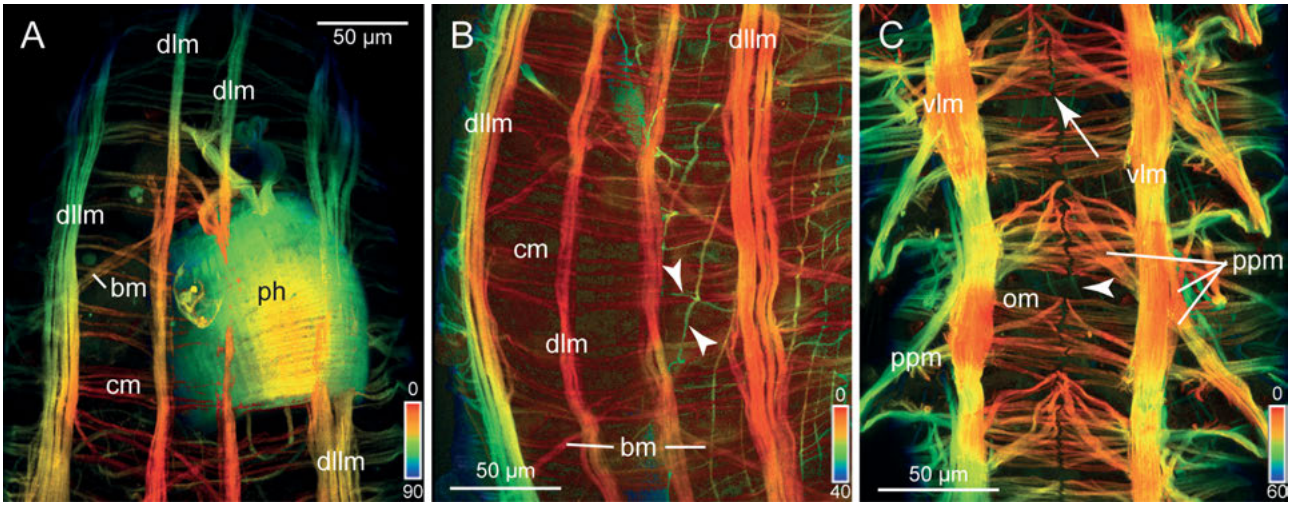


Fig. 7.13.14.11: Musculature in *Sphaerephesia* sp. (as *Sphaerodoropsis* sp.). LSM micrographs after labeling with FITC-conjugated phalloidin. A, Dorsal view with pharynx, in the pharynx longitudinal and transverse peripheral fibers are visible. B, Dorsal view showing dorsolateral longitudinal muscles (dllm), dorsal longitudinal muscle band (dlm), thin circular fibers (cm), bracing muscles (bm), in deeper layers longitudinal and circular fibers of the gut are visible (arrowheads). C, Ventral view; note the gap in the musculature in the ventral midline (arrow), ventral longitudinal (vlm), transverse and oblique fibers (om), and muscles of the parapodia (ppm) end at the ventral midline. bm, bracing muscle; cm, circular muscle; dllm, dorsolateral longitudinal muscle; dlm, dorsal longitudinal muscle; om, oblique muscle; ph, pharynx; ppm, parapodial muscle; vlm, ventral longitudinal muscle. Original photos from A. Filippova.

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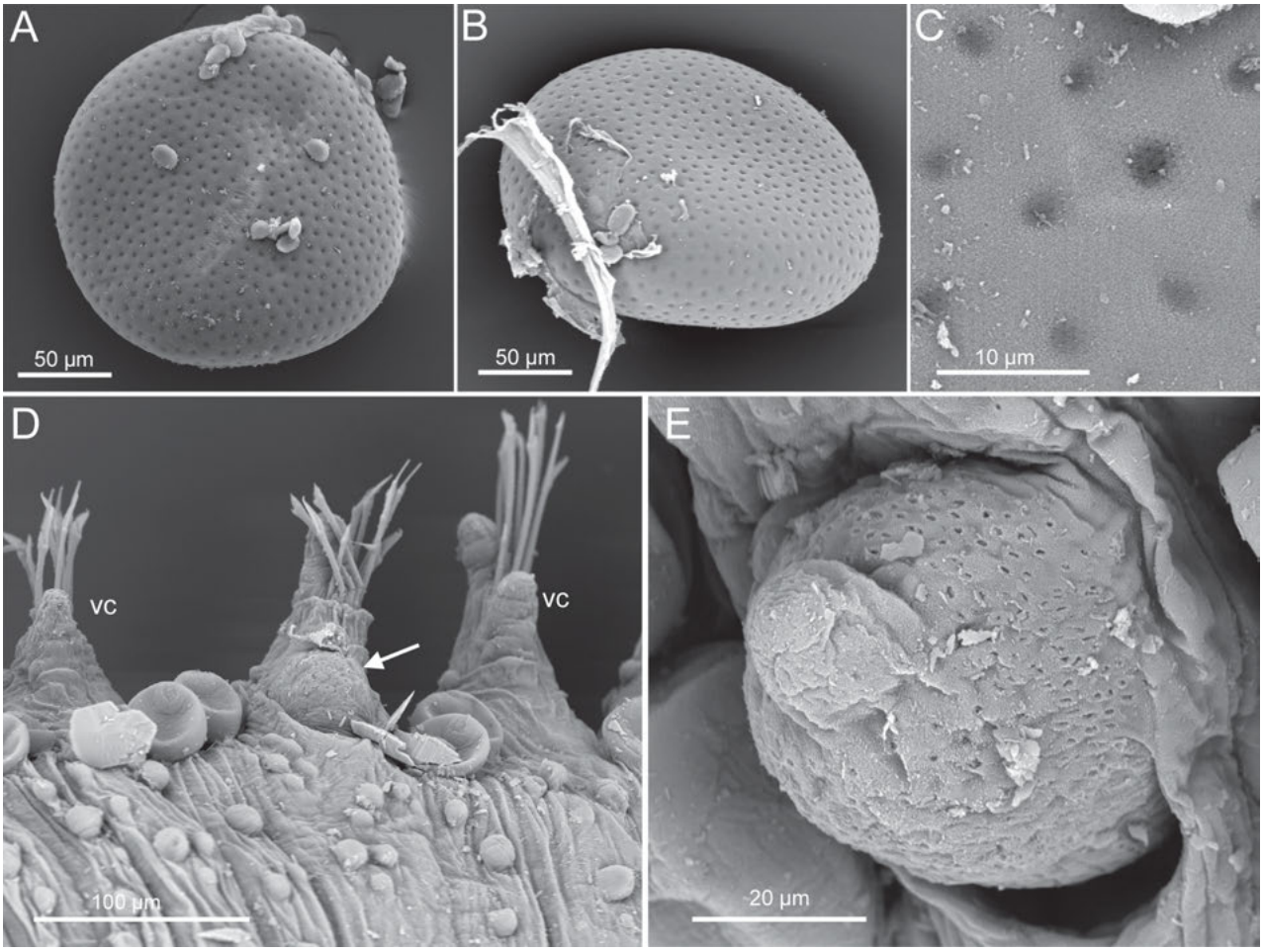


Fig. 7.13.14.12: A–C, Oocytes of *Sphaerodorum* sp. from Brazil. C, Detail of sculpture in the surface. D, E, *Geminofilum fauchaldi* (Hartmann-Schröder, 1979) from Australia, male with copulatory organs only in chaetiger 6: D, ventral view showing copulatory organ (arrow) and normal flanking ventral cirri (vc); E, detail of copulatory organ, same specimen. A–E, SEM micrographs.

adult eyes in other errant polychaetes (Purschke unpublished observation, see Suschenko and Purschke 2009). In *Sphaerodorum* sp. and *Sphaerodoridium balticum*, the eyes are equipped with a lens that is absent in the eyes of *Sphaerodorum abyssorum* and *Sphaerodorum flavum* (Ruderman 1911, Hartmann-Schröder 1996, Purschke unpublished observation; Fig. 7.13.14.6A, E). In addition, unpigmented rhabdomeric and ciliary photoreceptor-like sense organs are present in the brain; these have been mistaken as statocysts by Reimers (1933). In summary, sphaerodorids possess the entire set of cerebral sense organs as generally described to occur in Phyllodocida (Purschke 2005).

Uniciliate penetrative primary sensory cells have been reported in Sphaerodoridae, occurring in various places on the body including the protuberances (see above). They are provided with stiff cilia and probably have a mechanoreceptive function (Purschke 2005). These are either so-called collar receptors or may occur without a collar of microvilli. In addition, nonpenetrative multiciliary sensory cells of unknown function were found as well (Fig. 7.13.14.9A–D, F).

Gonads and gametes. Sphaerodorids are gonochoristic. The gonads of both sexes in *Sphaerodorum flavum* (as *Sphaerodorum gracilis*) are of a "dispersed" type occurring in all but the anterior segments (Christie 1984) instead of discrete organs. The gametocytes are therefore proliferated from groups of cells originating from a still unknown tissue (Dorresteijn 2005). There are no follicle or nurse cells associated with the gametocytes. The spermatocytes are proliferated from greatly flattened plates of cells of variable size that in later stages of spermiogenesis break away from the plate and become solitary and float freely in the coelomic fluid (Christie 1984). Five stages of spermatogenesis were described for *Sphaerodorum flavum* occurring for 5–7 months and finishing in October, when spawning takes place and spermatozoa measure around 2 µm (Christie 1984). Sperm is of the so-called

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"primitive" type with small, round, and distinctly set off heads (Franzen 1956, 1958), indicative of external fertilization. Oogenesis (previtellogenic and vitellogenic development) also takes place in the body cavity and lasts about 7 months in females of this species ending with disc-shaped mature oocytes as large as 200–700 μm depending on the species (Fig. 7.13.14.12A, B). Oocytes may occupy most of the coelomic cavity (Reimers 1933, Hartman 1961, Christie 1984; Fig. 7.13.14.1D). These eggs contain mainly large quantities of lipid and yolk granules in their cytoplasm (Christie 1984). The vitelline envelope is a thick membranelike structure of about 10 μm in several species (Rathke 1843, Thorson 1946, Christie 1984, Fauchald 1974), which could be the general pattern for the family. The egg envelope is composed of six layers and provided with fine radial striations, which appear to pass to the external surface of the oocyte in *Sphaerodorum flavum* (Christie 1984). In the other *Sphaerodorum* species examined, there is no sign for such striations, but instead the egg envelope is provided with small pits and some minute structures of uncertain significance (Capa unpublished observation; Fig. 7.13.14.12C).

External fertilization (Christie 1984) is thought to be the general reproductive strategy, but "copulatory structures" have recently been described in over 25 species mainly belonging to *Euritmia*, *Clavodorum*, *Gemonifilum*, *Sphaerephesia*, *Sphaerodoropsis*, and *Sphaerodoridium* (Moreira et al. 2004, Böggemann 2009, Reuscher and Fiege 2011, Moreira and Parapar 2012, Capa and Bakken 2015, Capa and Rouse 2015, Capa et al. 2019). Males were described as presenting one to four pairs of modified, inflated, and distally opened ventral cirri between parapodia of chaetigers 4–8 (varying between species), whereas females presented one or two pairs of oval, distally opened tuberclelike structures, located ventrolaterally between parapodia generally in the same segments as the "copulatory organs" of the males (Fig. 7.13.14.12D–E) or else modified, inflated ventral cirri with pores (Capa et al. 2019). The nature of these structures needs to be studied in detail and their function corroborated. However, the presence of sexual dimorphism could indicate a role in the transfer of gametes. Moreover, nephridia of males in *Sphaerodoropsis arctowskyensis* Hartmann-Schröder & Rosenfeldt, 1988 were described as opening into the inflated ventral cirri of the sixth chaetiger (Reuscher and Fiege 2011).

Distribution, biology, and ecology

Distribution

Sphaerodoridae is a group of annelids associated mainly with marine sediments from the intertidal to deep sea environments from worldwide localities, but it is also found in hard substrates associated with algae (e.g., Fauchald 1974, Hartmann-Schröder 1981, Sardá-Borroy 1987, Moreira 2012) or coral reefs (e.g., Hartmann-Schröder 1974, 1979). They are generally not abundant in benthic samples (Pleijel 2001), and due to the generally small size, they have been considered to be one of the groups of polychaetes present in the sediment-inhabiting meiofauna (Villora-Moreno 1997, Worsaae and Kristensen 2005).

Some early publications extended the idea that sphaerodorids are most common on soft sediments from either boreal or antiboreal regions and from deep water (e.g., Fauchald 1974). Earlier, Borowski (1994) presented some figures, indicating that of the 79 nominal species of sphaerodorids known at that time, 39 of them were found in shelf sediments, 23 in bathyal or abyssal depths, and 13 showed a broad bathymetric range. Sphaerodorids have been reported from intertidal environments (e.g., Fauchald 1974, Christie 1984, Sardá-Borroy 1987) to abyssal depths (e.g., Hartman and Fauchald 1971, Fauchald 1974, Desbruyères 1980, Borowski 1994, Kirkegaard 2001, Aguado and Rouse 2006, Böggemann 2009. An updated revision showed that the continental shelf, specially the shallower waters, holds most species richness, with 61 species, while 48 species have been described from the bathyal zone, 11 species from the abyssal zone and 59 from the deep sea species (Martin et al. 2021). However, since more scientific efforts have been devoted to shallow than deeper habitats these figures may not reflect the real scenario and more deepwater species are awaiting to be discovered. The number of records in temperate and tropical waters has increased dramatically over the last three decades (e.g., Hartmann-Schröder 1979, 1981, 1984, 1989, Kudenov 1987b, Sardá-Borroy 1987, Bakken 2002, Moreira et al. 2004, Moreira and Parapar 2007, Rizzo 2009, Magalhães et al. 2011, Martin et al. 2021).

Sphaerodorid genera have, in most cases, a broad distribution. The species are however restricted to more specific environmental conditions. The reproductive characteristics such as the production of large eggs and a direct development without planktonic larvae could also be a reason for a more restricted geographical distribution of species (Mileikovsky 1960). It may still be premature to determine the degree of endemicity of sphaerodorid species with accuracy because most of them urgently require taxonomic revision. There are numerous cases in the literature of species having been described from one or a few specimens and never reported again, such as *Clavodorum rosehipiformis* Böggemann, 2009; *Geminofilum pycnos* (Fauchald, 1974); *Sphaerephesia elegans* Hartman & Fauchald, 1971; *Sphaerephesia fauchaldi* Kudenov, 1987; *Sphaerephesia sibuetae*, Desbruyères,

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1980; *Sphaerephesia solis* Reuscher & Fiege, 2011; *Sphaerephesia stellifer* Aguirrezabalaga & Cebeiro, 2005; *Sphaerephesia triplicata* Fauchald, 1974; *Sphaerodoridium bengalorum* (Fauchald, 1974); *Sphaerodorum bipapillata* Kudenov, 1987; *Sphaerodorum indutum* Fauchald, 1974; *Sphaerodorum mixtum* Hartman & Fauchald, 1971; *Sphaerodorum pallida* Fauchald, 1974; *Sphaerodorum ramosae* Desbruyères, 1980; *Sphaerodorum shivae* Rizzo, 2009; *Sphaerodorum recurvatum* Fauchald, 1974; and *Sphaerodorum vietnamense* Fauchald, 1974, among others. This may be an indication of the paucity of these taxa, the low sampling effort in certain areas or inadequate collecting methods used to date. For instance, individuals of many species may pass through a 1 mm sieve or those occurring in coarse sands may have been overlooked so far. Alternatively, it could indicate that the definition of the morphospecies have been in some cases too narrow.

Opposite examples are also present in the literature with a few species that have a worldwide or cosmopolitan distribution, and these also need revision. This is the case for *Sphaerodorum flavum* reported from the Arctic, sub-Antarctic, Atlantic, and Pacific Oceans as well as from 0 to 1500 m depth (see references in Fauchald 1974 or Moreira 2012). *Sphaerodoridium minutum* is also considered as broadly distributed in the Arctic, East, and West Atlantic and West Pacific (Fauvel 1923, Fauchald 1974, Moreira 2012). Because of the limited amount of morphological characters known to date, molecular taxonomic studies might help to clarify whether such nominal species are complexes of sibling species.

Feeding biology

Feeding biology of free-living sphaerodorids is unknown, but after finding some organic matter and sand on the gut of *Sphaerodoridium balticum* (Reimers, 1933), it has been postulated that they are deposit feeders or else they may feed pumping fluids from prey or hosts or on organic detritus (Fauchald and Jumars 1979, Jumars et al. 2015). Commensalism and symbiosis have also been reported in the family: *Commensodorum commensalis* (Lützen, 1961) was reported as a commensal on the tentacular cirri of the trichobranchid polychaete *Terebellides stroemii* Sars, 1835 in Sweden (Lützen 1961). Up to six individuals were found per host with a prevalence of 3.5% of all known populations of the species (Lützen 1961, Martin and Britayev 1998). *Sphaerodorum ophiurophoretos* Martin & Alvà, 1988 was described from the arms of the brittle star *Amphipholis squamata* (Delle Chiaje, 1828), laying perpendicular to the longitudinal arms axis, with the head positioned near the ventral side of the arms but with no signs of being attached to it, and there are some suggestions that a previously reported sphaerodorid found on this ophiuroid refers to this species (Giard 1880, Fauvel 1923, Fauchald 1974, Barel and Kramers 1977). The prevalence of *S. ophiurophoretos* in populations of *A. squamata* at the English Channel coast of France was up to 12% and had a seasonal effect (Alvà and Jangoux 1989). *Sphaerodorum flavum* has also been reported as parasitic of three host brittle star species feeding on the epithelium of their hosts (Martin and Britayev 1998).

Reproduction

Studies dealing with the reproductive biology of Sphaerodoridae are scarce. Some publications refer to casual observations on the presence and size of the gametes (Thorson 1946, Hartman 1961, Capa et al. 2014) and a few deal with early development of selected species (Mileikovsky 1967, Hartman and Fauchald 1971) or gametogenesis (Christie 1984). At least some species are polytelic (discrete, iteroparic), implying they have multiple, not continuous, reproductive cycles over the course of their lifetime. Females with oocytes at early stage of maturation have been observed after spawning in at least *Sphaerodorum flavum* (see Christie 1984). In *Sphaerodoropsis pluritubercula*ta Capa & Rouse, 2015 sperm develops in cluster attached to a large central cytophore until elongate heads are about 35 μm long and they develop a flagellum of similar length (Capa and Rouse 2015). Free sperm at various stages of development is dispersed in the coelom, giving adult male coelomic content a whitish appearance. Females of this species were found with bluish-gray oocytes at various stages of development, with largest eggs observed being about 150 μm in diameter, suggesting development is lecithotrophic (Capa and Rouse 2015).

Fertilization in Sphaerodoridae was assumed to be external due to the shape of the sperm, with apparent round and small heads of some studied species (Franzen 1956, 1958, Christie 1984), but structures attributed to be copulatory or pseudocopulatory organs recently described for several species changed that view (Moreira et al. 2004, Böggemann 2009, Reuscher and Fiege 2011, Moreira and Parapar 2012, Capa and Bakken 2015, Capa and Rouse 2015, Capa et al. 2019). In addition, males of *Sphaerodoropsis pluritubercula*ta kept in aquaria were observed pseudocopulating and producing spermatophores that attached to the body surfaces of females and other males (Capa and Rouse 2015).

A case of a self-fertilizing hermaphrodite, *Sphaerodorum mixtum* (Hartman & Fauchald, 1971), was reported after observation of embryos of 16–32 cells being retained in the coelom of median segments of the body (Hartman and Fauchald 1971), an attribute that deserves further investigation.

The size of the mature eggs and the quantity of lipid droplets and yolk granules contained within them suggest that development in at least *Sphaerodorum flavum*,

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Sphaerodoridium minutum, and *Sphaerephesia philippi* (Fauvel, 1911) is direct, nonpelagic, and lecithotrophic (Mileikovsky 1967, Christie 1984). Juveniles of *S. minutum* and *S. philippi* found at bathopelagic level showed no adaptations for planktonic life (Mileikovsky 1967).

Taxonomy and phylogeny

In 1867, Malmgren erected the family Sphaerodoridae for a distinct polychaete with large spherical capsules on the dorsum. The history of the family did however start in 1843 where both, Ørsted and Rathke, described species that later were claimed to be the same: *Sphaerodorum flavum* Ørsted, 1843 from Denmark and *Ephesia gracilis* Rathke, 1843 from Norway (Leuckart 1847, Malmgren 1867). The problems concerning which name to be given priority has been discussed in the literature (e.g., Lützen 1961, Fauchald 1974, Wolff and Petersen 1991), and it is currently accepted that *S. flavum* was the first sphaerodorid described in the literature (Capa et al. 2019).

Most taxonomic studies of sphaerodorids to date have been descriptive. *Ephesia* Rathke, 1843 and *Sphaerodorum* Ørsted, 1843 were the only two genera used until the sixties of the past century, when Lützen (1961) erected *Sphaerodoridium* and Pettibone (1963) reerected *Ephesiella*. Body lengths, type of chaetae, or number of rows of macrotubercles were morphological features used for classification purposes. Fauchald (1974) reviewed the family and outlined and discussed morphological features as taxonomic characters. Nevertheless, it has only been recently that phylogenetic hypothesis have been formulated and implications have resulted in the assessment of the homology and polarization of characters used in sphaerodorid classification and the systematic restructure of the group (Capa et al. 2016a, b, 2018, 2019).

It is generally accepted that Sphaerodoridae is part of Phyllodocida, but there are no conclusive studies on its position within that group (Pleijel 2001, Capa et al. 2016a). The monophyly of Sphaerodoridae relies on the presence of tubercles on the dorsum (Fauchald and Rouse 1997, Pleijel and Dahlgren 1998). The type of nephridia has also been suggested as a character supporting the monophyly of the group, but specific studies of the homology of nephridial types are required (Rouse and Fauchald 1997). However, in case the occurrence of protonephridia with solenocytes can be confirmed as a character of the entire family, Sphaerodoridae could in fact be part of a clade within Phyllodocida with these cells being its autapomorphic character as indicated by the results of phylogenetic analyses of Pleijel and Dahlgren (1998). In that study, Sphaerodoridae was part of a clade comprising Phyllodocidae, Lacydoniidae, Paralacydoniidae, Nephtyidae, Goniadidae, and Glyceridae.

Syllidae was early suggested as sister group to Sphaerodoridae based on the development of parapodia, type of chaetae, lacking branchiae, and poorly developed circulation system (Claparède 1863) and, most important, based on the presence of a seemingly similar muscular structure of the pharynx, called proventricle (Ruderman 1911, Glasby 1993, Pleijel 2001, Aguado and Rouse 2006). Also, a combined study using morphological and molecular data placed the sphaerodorid representative as sister to syllids (Zrzavý et al. 2009). However, molecular studies (Aguado et al. 2007) and detailed comparison of the muscular fibers forming this structure in members of both families (Filippova et al. 2010) indicate that sphaerodorids and syllids are not closely related (i.e., not sister groups), and similarities shared by the "proventricles" are only superficial (see discussion above).

A sister group relationship to Phyllodocidae based on a muscular axial pharynx with terminal papillae (Fauvel 1911) and possession of excretory organs being protonephridia with solenocytes and a well-developed blood vascular system has been suggested (Kuper and Purschke 2001). A similar phylogenetic position after analyses of morphological data has also been suggested (Pleijel and Dahlgren 1998) but did not have support in consensus trees. In a morphological phylogeny of all polychaetes (Rouse and Fauchald 1997), a sister group relationship between Sphaerodoridae and Pilargidae was proposed, based on shared nephridial structures, but at that time, both groups have not been studied in enough detail to support such a relationship (Kuper and Purschke 2001). Other phylogenetic studies suggest a sister-group relationship between Sphaerodoridae, Glyceridae, and Goniadidae based on either molecular data (Böggemann 2009) or combined morphological and molecular data analyses (Worsaae et al. 2005). However, in the latter, the clade containing the goniadid and the sphaerodorid did not have morphological synapomorphies. Interestingly, early works also discussed the systematic position close to goniadids (Rathke 1843, Grube 1850), but the suggested relationship was not justified based on specific characters. Grube (1850) rather argued why sphaerodorids were not in the same groups as goniadids and glycerids because of the lack of jaws and the presence of tubercles, indirectly indicating that sphaerodorids should be a separate group. Similarities of the

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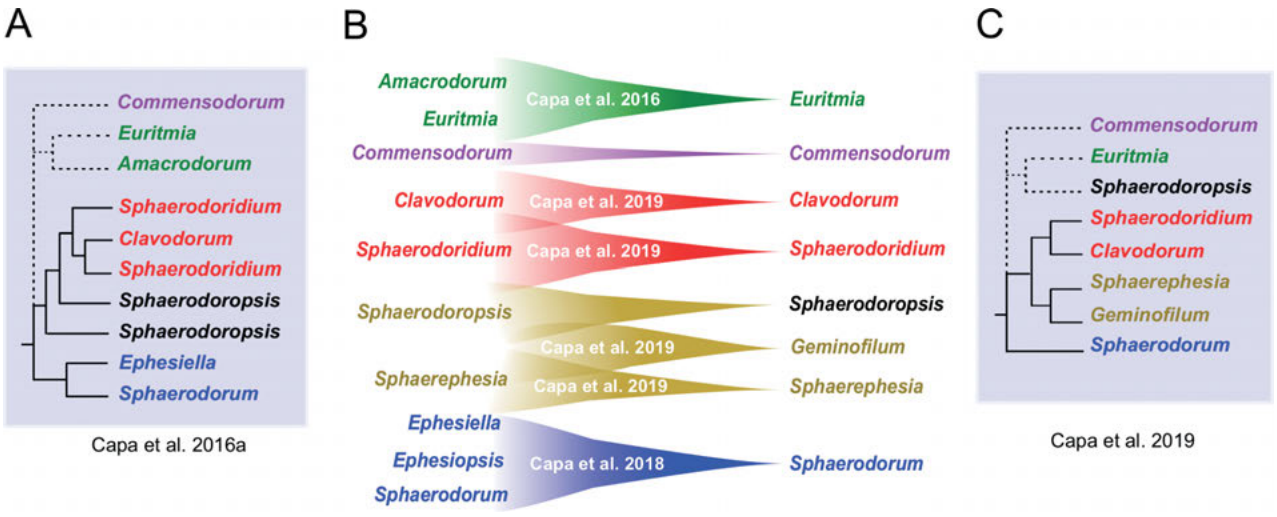


Fig. 7.13.14.13: A, Phylogenetic hypothesis (Capa et al. 2016a) after analyses of morphological characters and DNA sequence data of a variety of sphaerodorids (solid line in the tree). Relationships of some genera were not tested as data were unavailable (dotted line). B, Systematic restructure after analyses of morphological and/or molecular data of sphaerodorids in several studies. C, Current systematic classification and relationships of members of Spherodoridae (*sensu* Capa et al. 2019).

larvae of sphaerodorids and glycerids have also been pointed out (Mileikovsky 1967).

Several early studies included sphaerodorid species in phylogenetic analyses, but usually only as an outgroup or as part of the in-group of large data sets but with only one or two terminals included (e.g., Worsaae et al. 2005, Aguado et al. 2007, Böggemann 2009, Aguado and Bleidorn 2010), resulting in variable positions within Phyllodocida. A recent study included a more comprehensive representation of the sphaerodorid diversity and several mitochondrial and nuclear DNA markers in addition to morphological data. Results support the monophyly of the family, but sister-group relationships with other Phyllodocida remained poorly supported (Capa et al. 2016a). Latest phylogenomic studies have not included Sphaerodoridae representatives (e.g., Struck et al. 2011, 2015, Weigert et al. 2014, Andrade et al. 2015). All in all, the position of Sphaerodoridae remains unresolved.

Until recently, the family was divided into 10 accepted genera (see Capa et al. 2014). Several of these were revised, and the generic structure has been reorganized from pylogenetic studies (Capa et al. 2016b, 2018, 2019). These revisions reclassified Sphaerodoridae in eight genera, one being newly erected, and three synonymized with existing ones, all in all comprising 131 species (Capa and Bakken 2015, Capa and Rouse 2015, Capa et al. 2016a, 2016b, 2018, 2019, Martin et al. 2021). There are still a number of species that need taxonomic revision and some genera (i.e., *Euritmia* or *Sphaerodoropsis*) that require assessment of the monophyly and relationships with other members of the family (Fig. 7.13.14.13).

Some of the major changes in the systematics of Sphaerodoridae include the following (see Fig. 7.13.14.13):

- *Levidorum* Hartman, 1967, was originally considered as a sphaerodorid genus, until it was moved to a separate family (Perkins 1987), and later included in Syllidae (Glasby 1993).
- Before the recent generic restructure (Capa et al. 2019), *Sphaerodoropsis* contained 50% of the described species (see Capa et al. 2014). The genus showed to be a heterogeneous assemblage of species showing a wide range of attributes and organized in four informal groups based on the number and distribution of the dorsal macrotubercles (Borowski 1994). *Sphaerodoropsis* is now reduced to hold species previously considered as *Sphaerodoropsis* group 4 (Borowski 1994, Capa & Bakken 2015, Capa et al. 2016b) after phylogenetic analyses and restructure of the family (Capa et al. 2019), but it is in need of a thorough revision to assess relationships with other sphaerodorids.
- Some of the previously considered species in *Sphaerodoropsis* (those with spherical or semispherical macrotubercles arranged in four longitudinal rows) were moved to *Sphaerephesia* together with species with similar macrotubercle arrangement but with macrotubercles being pear-shaped, or bearing a terminal papilla (Capa et al. 2019).
- Long-bodied sphaerodorids were initially allocated in three genera based on chaetal morphology.

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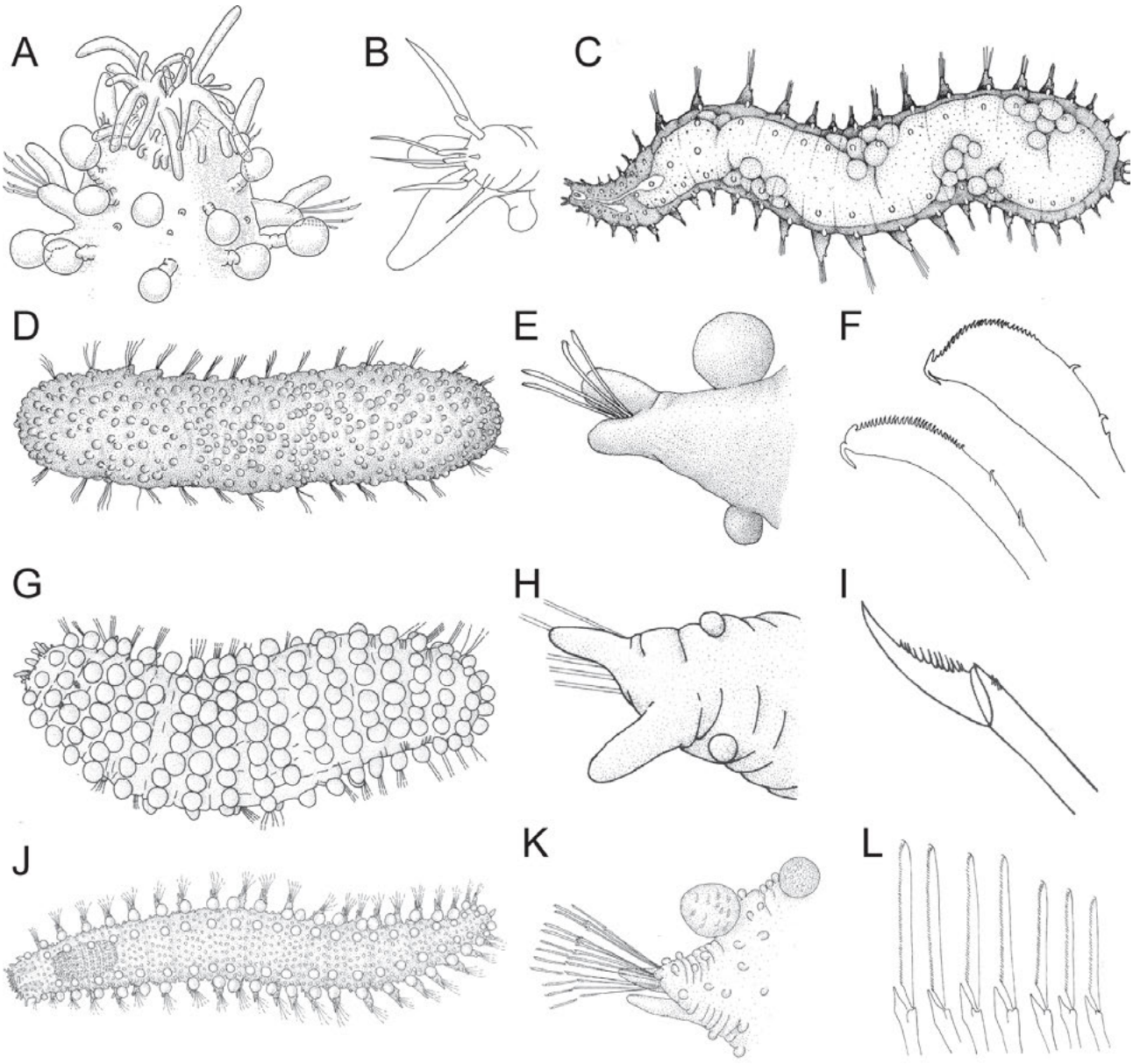


Fig. 7.13.14.14: A, B, *Clavodorum fauchaldi*: A, anterior end, dorsal view; B, parapodium from chaetiger 18 (posterior segments) (redrawn from Desbruyères 1980). C, *Commensodorum commensalis*, entire specimen (from Lützen 1961). D–F, *Euritmia hamulisetosa*: D, entire specimen; E, midbody parapodium; F, simple chaetae (from Moreira 2012). G–I, *Geminofilum gudmunduri*: G, entire specimen; H, parapodium from chaetiger 12 (midbody parapodium); I, compound chaeta (position not indicated in the description) (from Moreira and Parapar 2012). J–L, *Sphaerephesia anae* (Aguado & Rouse, 2006): J, entire specimen; K, parapodium from midbody chaetigers; L, compound chaetae from midbody chaetigers (from Aguado and Rouse 2006).

Phylogenetic analyses recovered *Ephesiella* and *Sphaerodorum* paraphyletic, and synonymization of *Ephesiella* and *Ephesiopsis* to *Sphaerodorum* was proposed (Capa et al. 2018).

– *Amacrodorum* Kudenov, 1987 was recently synonymized with *Euritmia* (Capa et al. 2016b) because their members shared main diagnostic features. Both genera were erected the same year, after encountering undescribed species in distant world localities (Kudenov 1987, Sardá-Borroy 1987).

– *Clavodorum* and *Sphaerodoridium* were only distinguished by the relative length of antennae, which raised the question if this character alone was sufficient for separating genera (Hartmann-Schröder and Rosenfeldt 1990, Bakken 2002). Phylogenetic studies delineated two genera among these species and some previously

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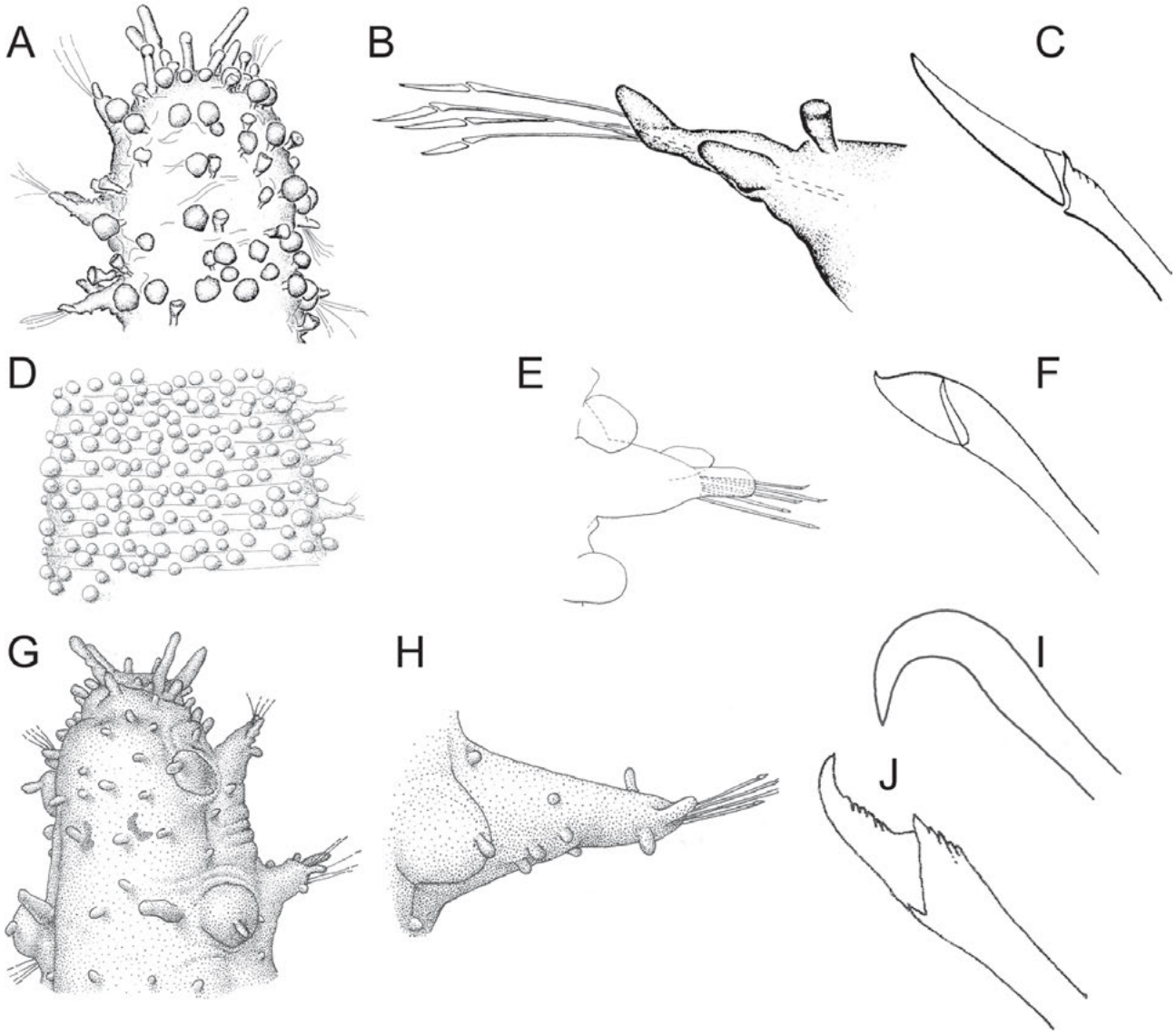


Fig. 7.13.14.15: A–C. *Sphaerodoridium campanulata* Borowski, 1994: A, anterior end; B, parapodium from chaetiger 8 (posterior parapodium); C, compound chaeta from chaetiger 2 (anterior parapodia) (from Borowski 1994). D–F, *Sphaerodoropsis multipapillata* Hartmann-Schröder, 1974: D, chaetigers from midbody; E, parapodium from midbody chaetigers; F, compound chaeta (position not given in description) (from Hartmann-Schröder 1974). G–I, *Sphaerodorum abyssorum*: G, anterior end, dorsal view; H, midbody parapodium, dorsal view; I, compound chaeata (from Moreira 2012). J, *Sphaerodorum guayanae*, recurved hook from first chaetiger (from Hartman and Fauchald 1971).

considered as *Sphaerodoropsis*. Distinction of members of both genera is now based on the number of longitudinal rows of macrotubercles (Capa et al. 2019).

Classification

Sphaerodoridae Malmgren, 1867

Diagnosis: Most species with inflated, ellipsoid bodies, others elongated. Epithelium covered with papillae of varying sizes. Segmentation not conspicuous (Fig. 7.13.14.1A–F). Prostomium fused to peristomium (Fig. 7.13.14.4A–E). Paired palps, paired lateral, and a median antennae present, not articulated (Fig. 7.13.14.4A–E). Tentacular cirri present, not articulated (Fig. 7.13.14.4A–E). Parapodia uniramous, with well-developed neuropodia (Fig. 7.13.14.5A–D). Dorsal cirri inconspicuous, in some species as a modified tubercle. Ventral cirri present (Fig. 7.13.14.5C–D). Branchiae absent. Single straight acicula per parapodium supporting parapodial lobe. Simple or compound chaetae (Fig. 7.13.14.14F, I, L, 7.13.14.15C, F, H, I, J). Paired pygidial cirri and single ventral appendage (Fig. 7.13.14.8A–B).

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***Clavodorum* Hartman & Fauchald, 1971**

Type species: *Clavodorum atlanticum* Hartman & Fauchald, 1971

10 species, from shallow areas to the deep sea (to 5000 m), worldwide including Adriatic Sea, North of France, North Sea, California, Gulf of Mexico, Bermuda, and off Mozambique.

Diagnosis: Body generally short and ellipsoid. Up to six longitudinal rows of macrotubercles on dorsum, forming one transversal row per segment. Macrotubercles stalked and smooth, without terminal papillae. Smaller and also stalked tubercles on ventrum. Microtubercles absent. Papillae all over body surface and parapodia. Prostomial and peristomial appendages digitiform of different relative lengths. Parapodia with only compound chaetae; hooks absent (Figs. 7.13.14.1D, 7.13.14.2D, 7.13.14.3G, and 7.13.14.14A, B).

***Commensodorum* Fauchald, 1974**

Type species: *Sphaerodoridium commensalis* Lützen, 1961

1 species, originally described as a commensal on the feeding tentacles of *Terebellides stroemii* from the Kattegat and the Skagerrak, Sweden, but later found in sediments.

Diagnosis: Body short and ellipsoid. Four longitudinal rows of macrotubercles, in one transverse row per segment. Macrotubercles sessile and smooth, without terminal papillae. Microtubercles absent. Papillae inconspicuous. Prostomial and peristomial appendages short, spherical. Parapodia with only simple chaetae enlarged subdistally; hooks absent (Fig. 7.13.14.14C).

***Euritmia* Sardá-Borroy, 1987**

Type species: *Euritmia hamulisetosa* Sardá-Borroy, 1987

5 species, from southern Spain, Greenland, Norway, Alaska, South Carolina (USA), and South Africa, from 0 to 800 m depth.

Diagnosis: Body short and ellipsoid. Macro- and microtubercles absent; papillae all over body surface and parapodia. Prostomial and peristomial appendages short, spherical, or digitiform. Parapodia with simple chaetae, enlarged subdistally, with serrated edge; hooks absent (Fig. 7.13.14.14D–F).

***Geminofilum* Capa et al., 2019**

Type species: *Sphaerodorum distichum* Eliason, 1962

36 species, from Norway, Iceland, Spain, California (USA), Thailand, Peru Basin, Namibia, Tanzania, South Africa, Western and Southern Australia, Tasman Sea, Southern Ocean, and Antarctica. Most species were described above 200 m, but others were found in deeper waters, to 4100 m at the Peru Basin.

Diagnosis: Body short and ellipsoid. Macrotubercles sessile, spherical, or hemispherical, arranged in two transverse rows per segment; additional smaller papillae on dorsum (or absent) and ventrum. Prostomial and peristomial appendages short, spherical, or digitiform. Parapodia with compound chaetae, unidentate, with serrated edge; hooks absent (Figs. 7.13.14.2B, E, F and 7.11.14G–I).

***Sphaerephesia* Fauchald, 1972**

Type species: *Sphaerephesia longisetis* Fauchald, 1972

37 species, described worldwide areas a wide range of depths (from 0 to 5400 m depth).

Diagnosis: Body mainly short and ellipsoid, some species slender. Four longitudinal rows of macrotubercles. Macrotubercles sessile, spherical, or hemispherical, pear shaped, or with terminal papilla. Microtubercles absent. Papillae over body surface and parapodia. Prostomial and peristomial appendages short. Parapodia with compound chaetae; hooks absent (Figs. 7.13.14.2C, G, 7.13.14.7A, B, F, 3A, and 7.13.14.14J–L).

***Sphaerodoridium* Lützen, 1961**

Type species: *Sphaerodorum claparedii* Greeff, 1866

22 species, from worldwide areas and from shelf to abyssal depths (to 5500 m).

Diagnosis: Body short and ellipsoid. More than six longitudinal rows of macrotubercles on dorsum, in one transversal row per segment. Macrotubercles sessile or stalked; smooth, without terminal papillae. Microtubercles absent. Additional papillae over body surface and parapodia. Prostomial and peristomial appendages spherical or digitiform, median antenna shorter that or as long as lateral. Parapodia with only compound chaetae; hooks absent (Figs. 7.13.14.1A, 7.13.14.3B, 7.13.14.5A, C, 7.13.14.9, and 7.13.14.15A–C).

***Sphaerodoropsis* Hartman & Fauchald, 1971**

Type species: *Sphaerodorum sphaerulifer* Moore, 1909

3 species described from shallow waters (0–20 m) in Tanzania and Australia.

Diagnosis: Body generally short and ellipsoid. Epithelial tubercles in several longitudinal rows and three or more clear transverse lines per segment. Macrotubercles sessile and smooth, without terminal papillae. Microtubercles absent. Prostomial and peristomial appendages short, spherical, or digitiform. Parapodia with semicompound chaetae; hooks absent (Fig. 7.13.14.15D–F).

***Sphaerodorum* Ørsted, 1843**

Type species: *Sphaerodorum flavum* Ørsted, 1843

27 species, from worldwide areas, from intertidal to abyssal depths.

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Diagnosis: Body long and slender. Two longitudinal rows of macrotubercles, one pair per segment, may be absent in first chaetiger. Macrotubercles sessile, with terminal papillae. Two longitudinal rows of microtubercles, one pair per segment, running parallel between macrotubercles. Additionally, papillae arranged in four to five transverse rows on dorsum and ventrum. Prostomial and peristomial appendages short, spherical, or digitiform. Parapodia from chaetiger 2 with simple, pseudocompound or compound chaetae; hooks absent or present (Figs. 7.13.14.1E, F, 7.13.14.2A, 7.13.14.3H, J, 7.13.14.4D, E, 7.13.14.5B, 7.13.14.6A–F, 7.13.14.7G, H, I, and 7.13.14.15G–J).

Acknowledgments

We would like to thank curators, collection managers, and colleagues that assisted MC during the revision of the collections in Museum Nacional de Ciencias Naturals, Madrid; Museum National d'Histoire Naturelle, Paris; University Museum, Bergen; Los Angeles County Museum, Los Angeles; Smithsonian Institution National Museum of Natural History, Washington; Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main; and Zoological Museum Hamburg. Specimens were also loaned from other institutions such as Australian Museum, Sydney; Museum Victoria, Melbourne; Museum and Art Gallery of the Northern Territory, Darwin; and Museo de Zoologia, Universidade de São Paulo. Most SEMs were taken during MC visits to some of these museum collections, in part funded (ES-TAF-3520, ES-TAF-2839, FR-TAF-2644) by the European Commission Taxonomic Initiative SYNTHESYS.

Leslie Harris kindly provided us with some photographs and images for this chapter. MC is funded by the Ramón y Cajal programme (RYC-2016-20799) by the Spanish Ministerio de Asuntos Económicos y Transformación Digital, the Agencia Estatal de Investigación, the Comunidad Autónoma de las Islas Baleares, and the European Social Fund.

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Supplement

Sedentaria incertae sedis

Günter Purschke

Aphanoneura Veydovsky, 1884: Aeolosomatidae Levinsen, 1884 and Potamodrilidae Bunke, 1967

Introduction

Aphanoneura Veydovsky, 1884 comprises a small group of aberrant minute meiofaunal annelids. These somewhat oligochaete-like annelids mostly occur in freshwater habitats, and thus far, only one marine species has been described, *Aeolosoma maritimum* Westheide & Bunke, 1970. Usually, aphanoneurans are free living except for *Hystricosoma* species, which live epizoically on crayfish, including *Hystricosoma chappuisi* Michaelsen, 1926, occurring on *Astacus astacus* (Linnaeus, 1758) (Bunke 1988). All species comprise only a few segments and range between 0.3 and 10 mm in length, although most species are at the smaller end of this range (Bunke 1967, Giere 2009, Gil et al. 2019, Timm 2020). Aphanoneurans do not bear any appendages, including parapodia, which are reduced to dorsal and ventral bundles of chaetae (Fig. 1A–D). The *Aeolosoma* species are readily recognized by the presence of colored epidermal glands, which are usually distributed across the entire body (Figs. 1A and 2A, B) (Bunke 1988, Giere 2009). The *Aeolosoma* species primarily reproduce asexually by paratomy, and sexually mature individuals are rarely found (Bunke 1967, Timm 2020). Irrespective of their small size, the first species, *Aeolosoma hemprichi* Ehrenberg, 1828, was described almost 200 years ago (Ehrenberg 1828). Principally, the *Aeolosoma* species are frequently identified in surveys and studies on aquatic oligochaetes, and thus numerous records have been published from most parts of the world (e.g., Rota and de Jong 2015, Gil et al. 2019, Timm 2020, Spiller 2020).

Aphanoneura is a species-poor group currently comprising two families, Aeolosomatidae Levinsen, 1884 and the monotypic Potamodrilidae Bunke, 1967. Aeolosomatidae consists of approximately 30 species in three genera (*Aeolosoma* Ehrenberg, 1928; *Rheomorpha* Ruttner-Kolisko, 1955; and *Hystricosoma* Michaelsen, 1926), whereas in Potamodrilidae, there is the single species *Potamodrilus fluviatilis* (Lastochkin, 1935) (Fig. 1A–D; Read and Fauchald 2020). Because of their delicate body, specimens become opaque after fixation, making preserved material hardly suitable for correct species identification. It also creates a challenge for type storage, which might be the main reason for the high number of uncertain species (Gil et al. 2019, Read and Fauchald 2020, Timm 2020). The most comprehensive morphological and systematic study on aphanoneurans to date is that of Bunke (1967), and most morphological studies date from the 1980s to the early 2000s (e.g., Bunke 1985, Purschke and Hessling 2002, Marotta et al. 2003). More recent work

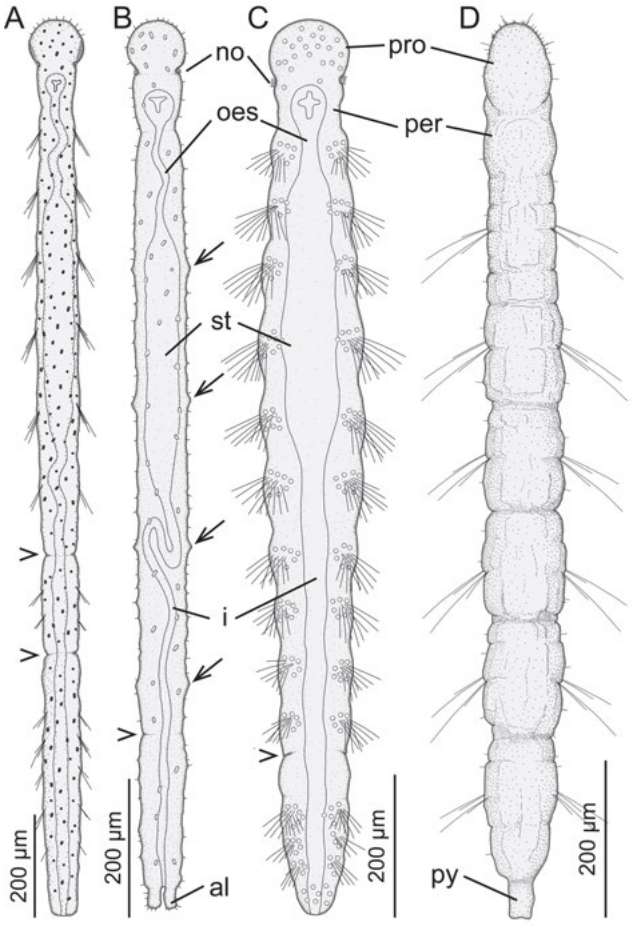


Fig. 1: Morphology and habitus of Aphanoneura. Schematic representations. Borders of zooids marked by arrowheads. A–C, Aeolosomatidae. A, *Aeolosoma hemprichi* Ehrenberg, 1828; individual comprising three zooids. B, *Rheomorpha neizvestnovae* (Lastochkin, 1935) made up of two zooids: note adhesive papillae (arrows) and adhesive pygidial lobes (al). C, *Hystricosoma chappuisi* Michaelsen, 1928; two zooids. D, *Potamodrilus fluviatilis* (Lastochkin, 1935). al, adhesive lobe; I, intestine; no, nuchal organ; oes, esophagus; per, peristomium; pro, prostomium; py, pygidium; st, stomach. A, B, D, redrawn and modified from (Bunke 1967); C, redrawn and modified from (Pop 1975).

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mainly focuses on asexual reproduction and regeneration (e.g., Falconi et al. 2015, Chen et al. 2020) or is concerned with faunistic issues (e.g., Glasby et al. 2009, Rota and de Jong 2015, Gil et al. 2019, Timm 2020).

Traditionally, these annelids were classified as oligochaetes (e.g., Michaelsen 1928, Avel 1959), but the absence of any clitellate key character or synapomorphy finally led to their exclusion from Clitellata. Bunke (1967) raised the first doubts on their affiliation as oligochaetes and erected a separate family, Potamodrilidae, for *Potamodrilus fluviatilis*. They were finally excluded from Clitellata in the early 1970s (Brinkhurst and Jamieson 1971). However, Timm (1981) placed Aeolosomatidae and Potamodrilidae in the single taxon Aphanoneura but outside Clitellata. This view was confirmed by several morphological and the first molecular studies addressing this question that, nevertheless, could not unambiguously clarify their position (Rota et al. 2001, Struck et al. 2002, Struck and Purschke 2005, Rousset et al. 2007). However, Zrzavý et al. (2009) were the first to reveal a sister group relationship of the clade *Hrabeiella*/Aphanoneura with Clitellata with strong statistical support. This placement was further confirmed by a recent phylogenomic study focusing on clitellate phylogeny (Erséus et al. 2020). Thus, the old view of a closer relationship with Clitellata has again received strong support and is currently under discussion.

Morphology

External morphology

Size. Aphaneurans have a short cylindrical body with no appendages and thus somewhat resemble oligochaetes if viewed superficially (Figs. 1A–D and 2A). Their body comprises a prostomium, a peristomium, a limited number of segments, and a pygidium (Bunke 1967, 1988, Rouse and Pleijel 2001). In Aeolosomatidae, the trunk is usually represented by a series of zooids, and thus the total number of segments varies (Fig. 1A, B). However, their number in the first zooid is constant and species specific; in the *Aeolosoma* species, it varies between 5 and 17. *Potamodrilus fluviatilis* does not reproduce by paratomy, and adults always have six chaetigers (Fig. 1D).

Prostomium. In contrast to oligochaetes, the prostomium is comparatively large, rounded, wider than the rest of the body, and somewhat flattened in Aeolosomatidae. Moreover, ventrally it is usually supplied with densely arranged motile cilia, which serve as the main locomotory device. The only exception is *Hystericosoma*, which moves by contractions of its body wall musculature (Bunke 1988). In the *Aeolosoma* species, this ciliary field is connected to two ciliary grooves situated laterally at the border between the prostomium and the peristomium (Fig. 1A). These grooves are also present in the other two genera but are not connected to the ventral ciliary field (Fig. 1B, C). Rouse and Fauchald (1997) regarded these ciliated structures to represent nuchal organs, which was confirmed in a subsequent ultrastructural analysis (Hessling and Purschke 2000). Although the prostomium is not flattened and the ciliated field ends in front of the mouth in *Potamodrilus*, it continues into the foregut in *Aeolosoma*. Additional cilia are distributed all over the body and are denser at the anterior end (Fig. 1A–D); these cilia are immotile, vary in length, and belong to various receptor cells (Bunke 1967, Hessling and Purschke 2000, Purschke and Hessling 2002). From the peristomium onward, the body appears more or less circular in cross section.

Pygidium. The body tapers toward the posterior end and terminates in the pygidium, bilobed in *Rheomorpha neizvestnovae* (Lastochkin, 1935), and distinctly set off and somehow funnel-like in *Potamodrilus*. It has an adhesive function in both species.

Parapodia and chaetae. Except in *Rheomorpha*, each segment following the achaetigerous peristomium bears chaetae arranged in two pairs of bundles representing the highly reduced neuro- and notopodia (Bunke 1967, 1988, Rouse and Pleijel 2001). In *Rheomorpha*, chaetae are lacking, but the trunk's epidermis is equipped with segmentally arranged adhesive glands (Fig. 1B, arrows). Arising directly from the body wall are simple hair chaetae or capillaries (e.g., *Aeolosoma hemprichi*), but occasionally a few additional sigmoid serrated chaetae may be present as well (e.g., *Aeolosoma psammophilum* Bunke, 1967; Figs. 2B and 3A–D). The capillaries may be equipped with a series of fine hairs or a fine serration on one side (*Potamodrilus fluviatilis;* Fig. 3E). Rarely only sigmoid chaetae are present in all segments (Bunke 1988). Types, length, and number of chaetae are species specific, with a maximum of 12 per bundle and different arrangements in dorsal and ventral bundles. Within a species, the number and types of chaetae may vary individually between segments (Bunke 1967).

Epidermal glands. A characteristic feature of Aeolosomatidae is their colored epidermal glands, which are found all over their body (Figs. 1A–C and 2A, B) (Bunke 1967, 1988, Rouse and Pleijel 2001). These cells have been interpreted as pigment cells by Potswald (1971) because they possess only a single vacuole containing a colored lipid; their ultrastructure does not exhibit characteristics typical of gland cells. This may have led to their vernacular name:

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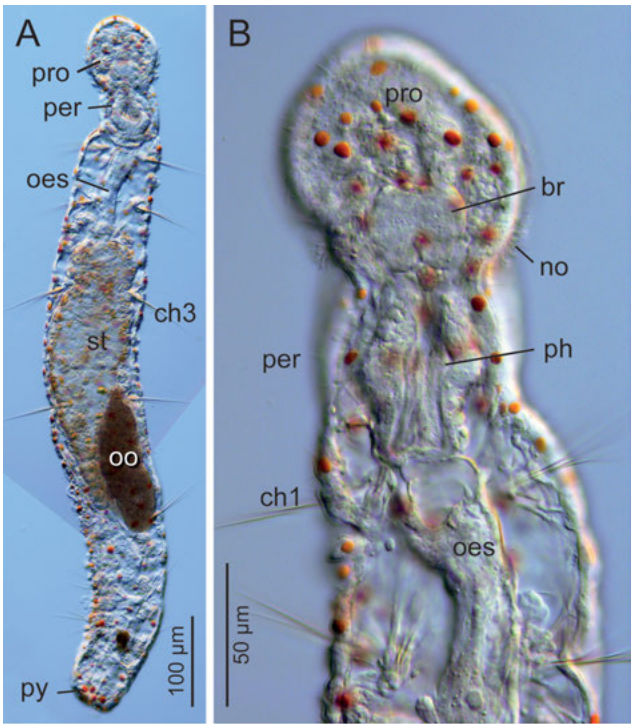


Fig. 2: Morphology and habitus of *Aeolosoma* sp. Living individual, light microscopy. A, Entire animal with mature egg. B, Enlargement of anterior end. br, brain; ch1, 3, chaetigers 1, 3; i, intestine; no, nuchal organ; oes, esophagus; oo, oocyte; per, peristomium; ph, pharynx; pro, prostomium; py, pygidium; st, stomach. Micrographs courtesy of Rüdiger Schmelz, A Corũna, Spain.

oil drop worms. Although this hypothesis likely describes them more accurately, it has not been maintained by subsequent authors who continued calling them gland cells of unknown function (Bunke 1988, Rouse and Pleijel 2001, Giere 2009). Irrespective of their disputed function, the pattern, the size, and the color of these cells are important diagnostic features in *Aeolosoma* spp. (Figs. 1A, 2A, B, and 5A, B). Each cell encloses a large vacuole filled with liquid ranging in color from yellow, red, green, or blue-green. In certain species, these gland cells are accompanied by a satellite cell. Only in very few species is the liquid colorless or these cells lacking. Because the color fades away immediately after fixation, live observations are necessary to determine species (Potswald 1971, Bunke 1988). In *Hystricosoma*, these pigment cells contain an orange-red vacuole and are arranged around the chaetae (Fig. 1C).

Anatomy

Epidermis and cuticle. The body wall consists of a delicate cuticle, epidermis, and extracellular matrix (ECM) followed by circular and longitudinal muscle fibers or a coelothelium (peritoneum). As the name Aphanoneura implies, the epidermis also includes the entire nervous system. The ECM is very delicate and sometimes appears to be absent (Potswald 1971), which likely represents an artifact in TEM preparations. The cuticle is only 0.5–0.8 µm thick and composed of scarce fine fibrils that are slightly denser arranged apically (Potswald 1971). In *Aeolosoma*, collagen fibers and an epicuticle are lacking. Very few microvilli penetrate the cuticle. This feature is in contrast to most other aquatic annelids and especially those forms with thin cuticles (Hausen 2005, Purschke et al. 2014). This paucity in microvilli somewhat resembles that found in the semiterrestrial polychaetes Parergodrilidae and *Hrabeiella* or oligochaetes, although all of these have a collagenous cuticle (Jamieson 1981, Purschke 2019, 2020). During cuticle formation and regeneration, microvilli density increases, indicating that most of them are transitory, reduced after the cuticle has been formed (Potswald 1971). The cuticle is covered by a thin, sheet-like layer of minute electron-dense prismatic particles (100 × 40 × 40 nm) or epicuticular bodies (Potswald 1971, Bunke 1994) (Fig. 4A). These are membrane-bound and have been shown to be derived from the epidermal microvilli (Potswald 1971). Although of similar thickness, the cuticular structure is different in *Potamodrilus fluviatilis*. The outermost layer is formed by typical epicuticular projections followed by a thin apical layer of electron-dense fibers comprising one to two layers and probably composed of collagen (Figs. 4B and 7A–C).

The epidermis consists of nonciliated and ciliated supportive cells, pigment cells (colored gland cells) with associated satellite cells, secretory cells, basal cells, and a few types of receptor cells (Potswald 1971, Hessling and Purschke 2000, Purschke and Hessling 2002). In *Potamodrilus*, pigment cells are absent and secretory cells are less frequent (Figs. 6A and 7A–C). In *Rheomorpha*, the epidermis also comprises adhesive glands scattered throughout the body, but most are concentrated in the pygidial adhesive lobes and the segmentally arranged adhesive papillae (Fig. 1B) (Bunke 1967). Their ultrastructure or whether they comprise a duo-gland system (see, e.g., Martin 1978) is unknown. The ciliated columnar cell described by Potswald (1971) most likely corresponds to one of the receptor cell types. Except for the ciliated supportive cells restricted to the ventral part of the prostomium, all other cell types are more or less evenly distributed all over the body. The by far most frequent cell type is the nonciliated supportive cell. At least two types of secretory cells considered to represent mucous cells have been found in *Aeolosoma bengalense* Stephenson, 1911 (Potswald 1971).

The epidermis is comparatively thin and measures less than 10 µm in most regions, except for the prostomium's

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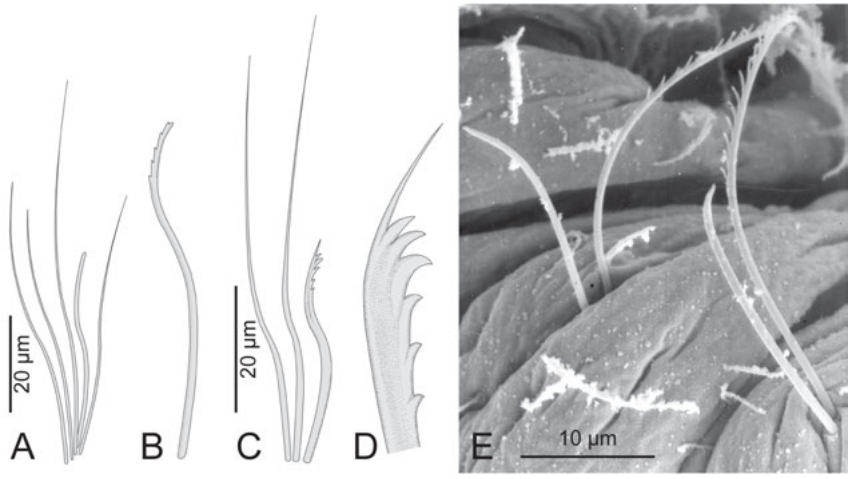


Fig. 3: Aphanoneura. Diversity of chaetae. A, B, *Aeolosoma psammophilum* Bunke, 1967. A, Bundle of chaetae from the sixth chaetiger comprising two short and two long capillaries and one sigmoid chaeta. B, Serrated sigmoid chaeta. C, D, *Aeolosoma travancorense* Aiyer, 1926. C, Bundle of chaetae from the fourth chaetiger comprising two capillaries and one heavily serrated sigmoid chaeta. D, Tip of serrated sigmoid chaeta. E, *Potamodrilus fluviatilis*. Chaetae of two consecutive segments, each bundle composed of a short and a long capillary, the latter with fine serration. SEM. A–D, redrawn and modified from Bunke (1967); E, original.

dorsal and ventral parts. The thickest cells are the ciliated cells forming the ventral region of the prostomium; their cell bodies bulge into the prostomial coelomic cavity (Fig. 4A, B). Because of their high concentration of ribosomes, mitochondria, and numerous ciliary rootles, they appear rather electron-dense. These cells are innervated by branches stemming from the stomatogastric nerves and extend anteriorly (Figs. 4B and 8A) (Hessling and Purschke 2000, Purschke and Hessling 2002). Thus, the beating activity of the ciliary field is modulated by the animals. Finally, the epidermis continues into the esophagus; the ciliated prostomial cells continue as a small median band into the dorsal wall of the buccal cavity and widen into the ciliated part of the pharyngeal lumen in Aeolosomatidae (Fig. 5A, B). In *Potamodrilus*, such a connection is absent.

Musculature. Because locomotion is mainly performed by the beating of the ciliated cells forming the ventral prostomial epidermis, body wall musculature is only weakly developed (Figs. 5A, B and 6A). It generally comprises small obliquely striated muscle fibers. The outer circular fibers are followed by longitudinal fibers; the latter are much more developed. The longitudinal fibers extend into the prostomium, below the dorsal and ventral epidermis (Fig. 4A, B). In the trunk region, they are arranged in three more or less prominent pairs of bundles, situated ventrolateral, lateral, and dorsolateral (Fig. 6A) (Bunke 1967, Purschke, unpublished observation). The ventrolateral bundle is situated at the level of the ventral cord. It forms the thickest bundle in all species investigated. In Aeolosomatidae and *Potamodrilus*, an additional small group of median longitudinal fibers is present between the widely separated connectives of the ventral nerve cord. These muscle fibers are common in annelids and have been called ventromedian longitudinal muscle (Purschke and Müller 2006, Purschke 2016, see also Lauri et al. 2014). Circular fibers are weakly developed and are separated from each other. Thus, this pattern is the same as that typical in many polychaetes and does not correspond to that present in Clitellata wherein both muscle fiber groups from a complete cylinder beneath the epidermis (Tzetlin and Filipova 2005, Purschke and Müller 2006, Purschke et al. 2014). Additional muscle fibers are, for instance, transversal fibers in the trunk and the prostomium, as well as muscles associated with the chaetae and the foregut and pharynx (Bunke 1967). The gut system is lined by a thin myoepithelium following the ECM and gastrodermis (Fig. 6B). Thus far, the musculature in Aphanoneura has not been analyzed by modern methods such as phalloidin staining followed by confocal laser scanning microscopy.

Digestive system. The alimentary canal comprises a ventral mouth opening in the peristomium, buccal cavity, pharynx, esophagus, a dilated midgut or stomach, intestine, rectum, and anus (Figs. 1A–C and 2A, B) (Bunke 1967, 1988, Rouse and Pleijel 2001). The pharynx is restricted to the peristomium, the esophagus/midgut transition is usually found in chaetiger 2 or 3, and the stomach extends for approximately two further segments. In *Potamodrilus*, the stomach starts in the first chaetiger.

In Aeolosomatidae, the pharynx is a short tube-like extension leading from the ventral mouth into the

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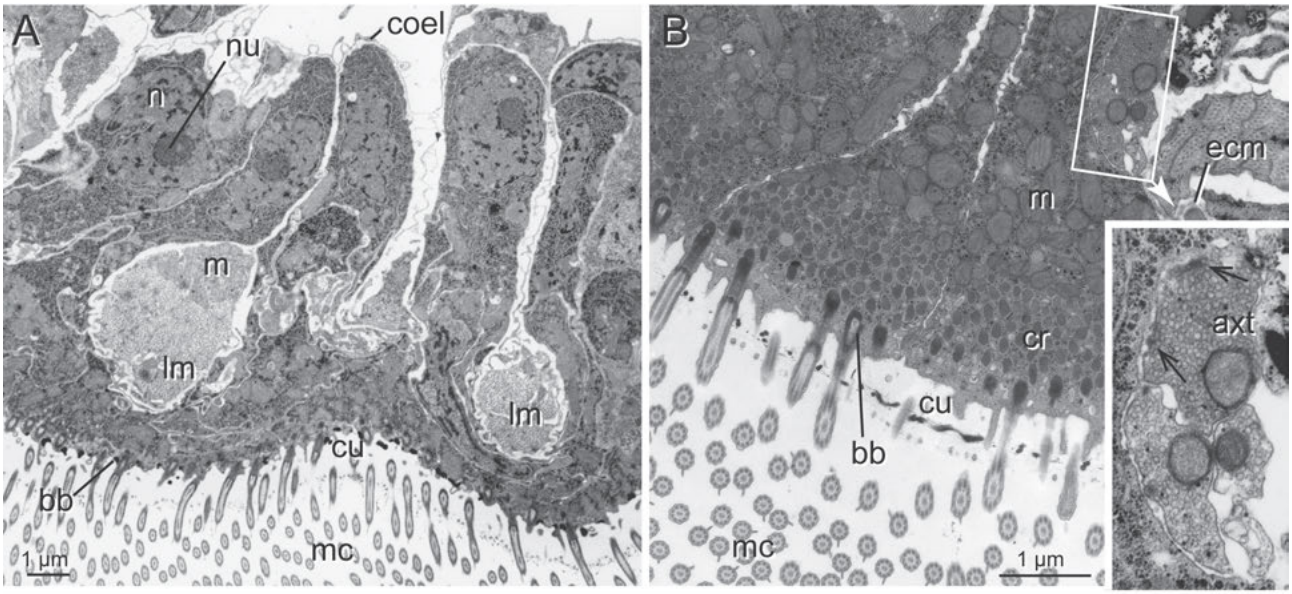
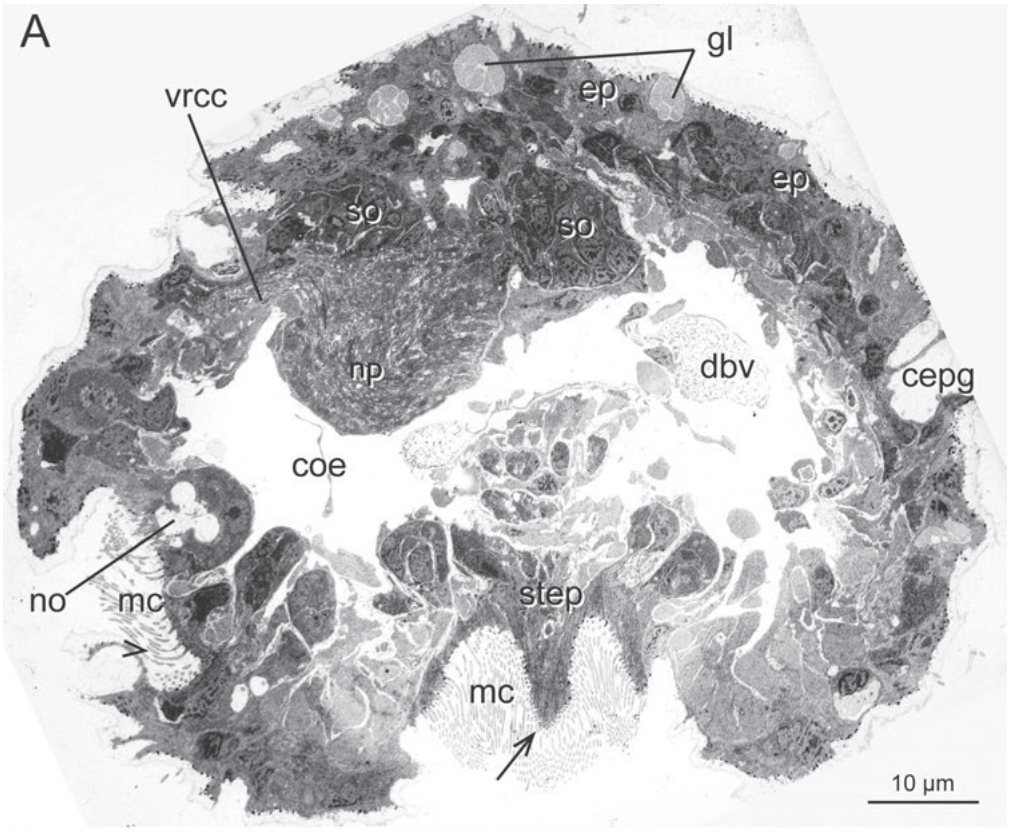


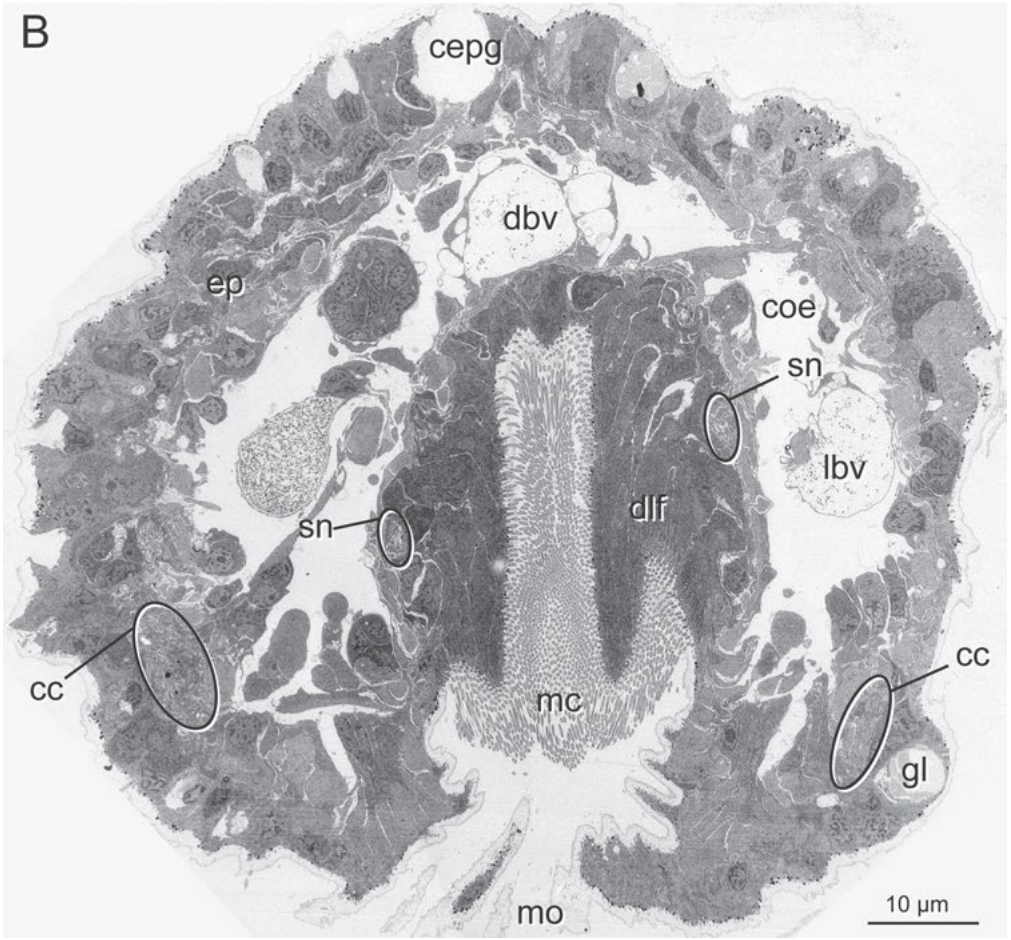
Fig. 4: Aphanoneura. Ciliated cells of the prostomium; Transmission electron microscopy (TEM). A, *Aeolosoma hemprichi*. Cell bodies bulge widely into the coelomic cavity of the prostomium, separated by small bundles of longitudinal muscle fibers (lm), and epidermal cells covered by a layer of thin coelothelial cells (coel). B, Same region in *Potamodrilus fluviatilis*. Epidermal cells exhibit three layers: an apical region with basal bodies (bb), a middle region with densely arranged ciliary rootlets (cr), followed by a region containing numerous mitochondria (m); boxed area enlarged in inset showing two axon terminals (axt) with synapses, arrow points to presynaptic membranes. axt, axon terminal; coe, coelom; coel, coelothelium; cr, ciliary rootlet; cu, cuticle; ecm, extracellular matrix; lm, longitudinal muscle fiber; m, mitochondrion; mc, motile cilium; n, nucleus; nu, nucleolus; originals.

esophagus. The dorsal and lateral epithelium of the pharynx is heavily ciliated, and the dorsal part is a direct continuation of the ventral ciliary field present on the prostomium (Figs. 5A, B). This ciliated epithelium further continues into the esophagus. Its epithelium is considerably thicker in these regions, as observed in *Aeolosoma* spp. and *Rheomorpha* (Bunke 1967, Purschke, unpublished observation). The lateral parts of the buccal cavity remain unciliated. The mouth opening is surrounded by muscle fibers that are somewhat thicker posteriorly and somewhat more distinct in *Rheomorpha* (see Bunke 1967). A somewhat thickened epithelium is also present in the ventral part of the esophagus. Compared to other annelids, the aeolosomatid foregut at most resembles the so-called dorsolateral folds predominantly occurring in smaller annelids (Purschke and Tzetlin 1996, Tzetlin and Purschke 2005). Food uptake has been described as suction feeding, and the pharynx, in conjunction with the ciliated prostomium, acts as a unit in the uptake of food particles (Singer 1978).

In *Potamodrilus*, the foregut structure differs from that of *Aeolosoma*, which was the main reason for removing *Potamodrilus* from Aeolosomatidae by Bunke (1967). In this species, the pharynx has been classified as a ventral pharynx or ventral pharyngeal bulb (Bunke 1967, 1988, Giere 2009). However, it differs from the ventral pharyngeal organs present in many other small annelids (Tzetlin and Purschke 2005). The most conspicuous structure is a tongue projecting ventrally from the pharynx's dorsal wall into the buccal cavity (Fig. 6A). It comprises a comparatively thin epithelium with a well-developed basal-apical tonofilament system, which ends in numerous strong microvilli (Fig. 6B). The cuticle is modified and stronger in this area than the cuticle on the trunk. It comprises several layers of collagen filaments, and the microvilli end at the same level; a thick epicuticle covers the entire tongue. Basally, the tonofilaments build up myoepithelial junctions with numerous muscle fibers that do not form a compact structure as observed in ventral pharyngeal organs. Instead, the single fibers are not interconnected (Fig. 6A, B). These fibers are oriented in different directions. A major portion forms an arc around the posterior part of the tongue and attaches to the epithelium of the buccal cavity and the body wall. Other fibers run dorsally and surround the esophagus, whereas others are attached to the lateral and dorsal body wall (Fig. 6A). A compact muscle bulb comprising plate-like transverse muscle fibers, typically present in ventral pharyngeal organs (Purschke and Tzetlin 1996, Tzetlin and Purschke 2005), does not exist in *Potamodrilus*. Therefore, it is problematic to classify the foregut in *Potamodrilus* as a ventral pharynx (Bunke 1967, Rouse and Pleijel 2001). Moreover, there is no correlation with the dorsal pharynx typically

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present in oligochaetous Clitellata and *Hrabeiella periglandulata*, formed by a glandular ciliated pad (Purschke 2003).

In *Potamodrilus*, the anterior epithelium of the buccal cavity is ciliated and extends dorsally, then turns posteriorly to continue into the esophagus above the tongue. The dorsal part of the esophagus is formed by two rows of large and voluminous gland cells, forming a salivary gland (Fig. 6A, C). These cells were described as "cubic cells of the dorsal wall of the foregut" by Bunke (1967). However, these salivary gland cells open into the anterior part of the esophagus, and their cell bodies lie above the comparatively thin epithelium of the esophagus (Fig. 6C). This glandular region extends behind the tongue; the esophageal lumen is triangular in cross section. In the first chaetiger, it proceeds ventrally and opens into the stomach after a short distance. The esophagus is ciliated throughout. In other Aphanoneura species, the esophagus is longer and somewhat coiled (Fig. 1C–E). The stomach (dilated midgut/intestine) usually extends for approximately two further segments, and then it is followed by the intestine that also forms a slight loop in the anterior part. The stomach and the intestine are composed of ciliated epithelium. The anus opens terminally except for *Potamodrilus*, in which it is located ventrally in the pygidium.

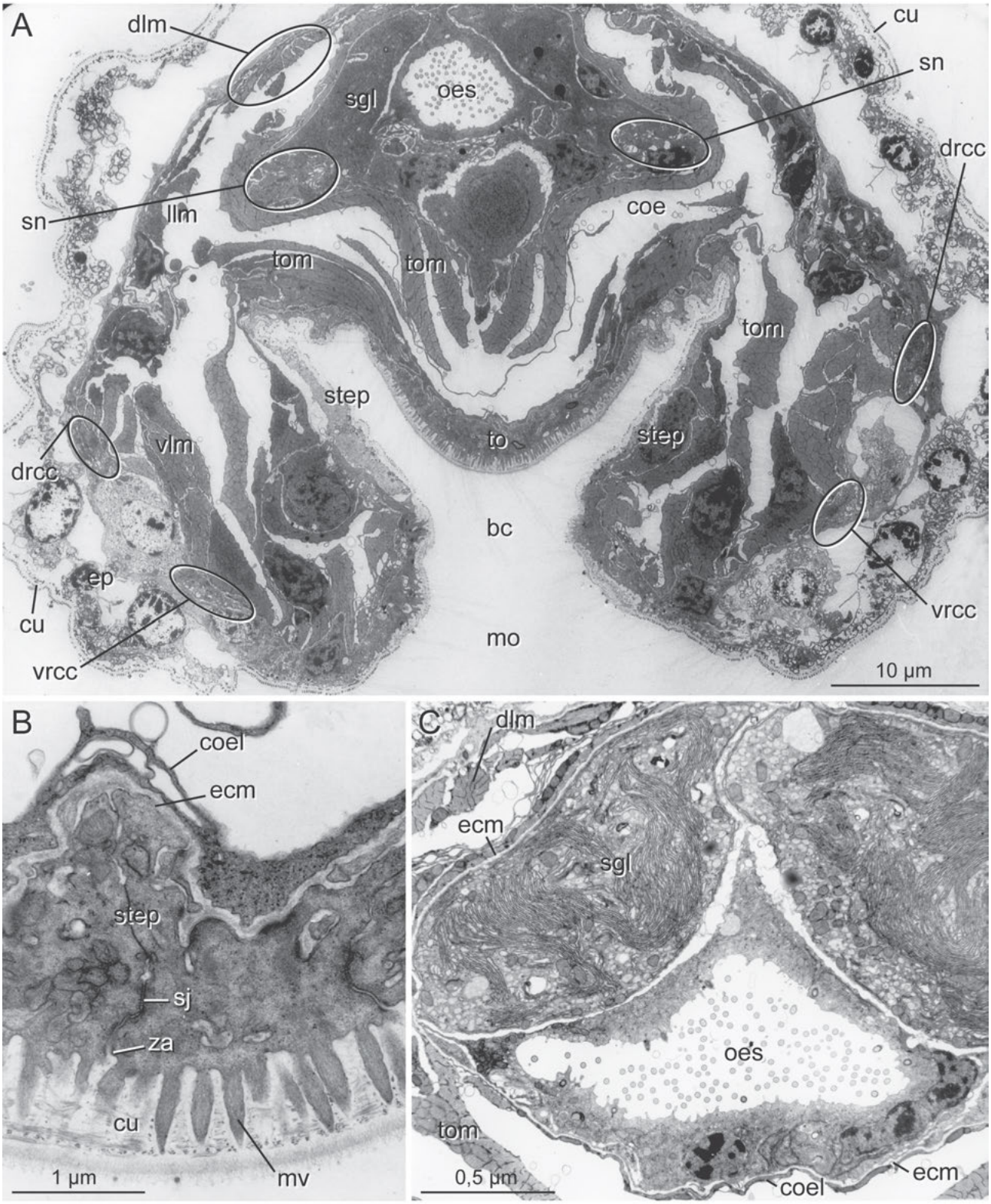
Nervous system and sensory organs. Various authors have studied the nervous system (e.g., Brace 1901, Markus 1944, Bunke 1967, Stolte 1969, Boguta 1979, Hessling and Purschke 2000, Purschke and Hessling 2002). As mentioned above, the entire nervous system, including the brain and ventral nerve cord, is intraepidermal or, more precisely, basiepidermal. Such a position is typical for several other annelids with small body sizes but is also observed in larger annelids (Purschke 2016, Helm et al. 2018). As the ventral nerve cord (and often other nervous elements) is especially difficult to distinguish in histological sections, its existence was long debated (see Stolte 1969), irrespective of the fact that Brace (1901) gave a comparatively precise description of the major components. Not until immunostaining against neuronal markers, confocal laser scanning microscopy, and transmission electron microscopy were also applied were peripheral nerves and sensory structures detected (Boguta 1979, Hessling and Purschke 2000, Purschke and Hessling 2002). Although aphanoneurans have tiny body dimensions, these investigations revealed that the nervous system is comparatively complex (Fig. 7A–D). Moreover, all derived characters (apomorphies) typical of clitellate nervous systems are absent in Aphanoneura, which was seen as additional evidence for excluding the group from Clitellata.

The central nervous system is fundamentally similar in Aeolosomatidae and *Potamodrilus*. It comprises an anterior brain situated dorsally in the posterior part of the prostomium in front of the border to the peristomium (Fig. 2B) and a chain of ventral ganglia connected by widely separated connectives (Brace 1901, Boguta 1979, Hessling and Purschke 2000, Purschke and Hessling 2002). The ventral cord connects to the brain via the circumesophageal connectives, which form a wide arc around the mouth. They are divided into long dorsal and ventral roots that unite immediately in front of the subesophageal ganglion (Fig. 7B). In each segment, two commissures have been found connecting the lateral trunks of the nerve cord except in the first chaetiger, where three commissures occur (Brace 1901, Boguta 1979, Hessling and Purschke 2000, Purschke and Hessling 2002). This anteriormost commissure is somewhat stronger or even doubled in *Potamodrilus*. Although only one commissure has been described for *Rheomorpha neiswestnovae* by Bunke (1967), it can be assumed that this nerve is present as well and has been overlooked because of its small size and intraepidermal position. The anterior commissure gives rise to a delicate median longitudinal nerve so that aphanoneurans are characterized by a trineuralian nerve cord (Fig. 7C, D) (for terminology, see Purschke 2016). The ganglia are situated at these commissures and are marked by paired serotonergic somata. They give rise to two pairs of segmental nerves, the posterior of which lies at the chaetae level and splits into two nerves each (Fig. 7C).

Another characteristic feature of the brain is that the somata are situated in paired posterior and anterior lobes in addition to the dorsal cover of somata above the bean-shaped neuropil, a character often seen in small or meiofaunal annelids possessing a comparatively complex nervous and sensory system (Schmidbaur et al. 2020). The

◂ **Fig. 5**: *Aeolosoma hemprichi*. Foregut, low power TEM micrographs from slightly oblique cross sections (on the left somewhat more anteriorly). A, Beginning of the mouth, prostomial ciliary field continues as a dorsolateral ciliary band into the mouth cavity, esophagus, and a minor branch (arrowhead) connects to the nuchal organ (no); the stomodeal epithelium forms a median ridge (arrow). B, End of the mouth (mo), cilia restricted to dorsolateral folds (dlf), ventral part of mouth cavity unciliated, positions of circumesophageal connective (cc), and stomatogastric nerve (sn) (encircled). cc, circumesophageal connective; cepg, colored epidermal gland; coe, coelomic cavity; dbv, dorsal blood vessel; dlf, dorsolateral fold, drcc, dorsal root of cc; ep, epidermis; gl, gland cell; lbv, lateral blood vessel; mc, motile cilia; no, nuchal organ; np, neuropil of the brain; sn, stomatogastric nerve; so, somata of the brain; step, stomodeal epithelium; vrcc, ventral root of cc; originals.

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brain gives rise to highly ramified anterior nerves formed by the axons of prostomial receptor cells. In addition, at least two dorsoposterior longitudinal nerves emanate from the brain in the different species. These proceed posteriorly, follow the course of the longitudinal muscle fibers, and have been shown to be motoneurons (e.g., Fig. 3B in Purschke and Hessling 2002).

The stomatogastric nerves originate from the ventral root of the circumesophageal connectives at the level of the mouth opening. Anterior branches of this nerve innervate the ventral ciliary patch of the prostomium, and posterior ones innervate the gut system, including the pharynx and tongue in *Potamodrilus*. In addition, another pair of nerves originates from the subesophageal commissure innervating the posterior mouth region (Fig. 7A, C).

At first sight, the sensory organs are poorly developed. No sense organs were observed except for the ciliated lateral pits generally present at the posterior end of the prostomium in *Aeolosoma* spp. (Figs. 1A and 2A, B). In only a few species are the ciliated pits perhaps including the entire nuchal organs absent as, for example, in *A. litorale* Bunke, 1967 and *A. maritimum* (Westheide and Bunke 1970, Westheide and Schmidt 1974). These pits have been assumed to possess a sensory function since their first description (Vejdovsky 1884, Brace 1901). More recently, these have been proven to represent typical nuchal organs (Fig. 8D) (Hessling and Purschke 2000). In *Potamodrilus fluviatilis,* such ciliated pits were not found, and these sense organs were considered absent. However, small nuchal organs are indeed present but internalized and, thus, almost impossible to detect with light microscopy (Purschke and Hessling 2002). Additionally, in a survey on sensory structures and the nervous system, the ultrastructure of several types of ciliated receptor cells was described, supplementing earlier light microscopic investigations (Fig. 8A–C) (Hessling and Purschke 2000, Purschke and Hessling 2002). These receptor cells can be distinguished by the number of cilia and whether the cilia penetrate the cuticle or remain inside or below the cuticle. Most receptor cells are multiciliated and possess cilia penetrating the cuticle (Fig. 8B, C). Groups of such cells form prominent ciliary tufts, which are especially abundant on the prostomium (Fig. 8A).

Besides nuchal organs, photoreceptor-like ciliated sense organs are also present in the prostomium (Hessling and Purschke 2000, Purschke and Hessling 2002). These are simple structures bearing cilia with modified axonemes projecting into an internal cavity (Fig. 8A). In *Potamodrilus*, four receptor cells and a few glial cells form an unpaired organ and a single extracellular cavity; in *Aeolosoma hemprichi*, four unicellular structures have been observed, each forming a phaosome (Purschke et al. 2006) (Figs. 7A and 8A). Eyes and rhabdomeric photoreceptor cells are absent. The nuchal organs are simple and consist of only a few cells; five receptor cells and four ciliated supportive cells have been counted in *A. hemprichi*, but only three sensory cells, one unciliated and two ciliated supportive cells, in *P. fluviatilis*. In both species, the organs are situated close to the ventral roots of the circumesophageal connectives. To some extent, the internal position of the nuchal organs in *P. fluviatilis* is similar to that observed in *Hrabeiella periglandulata* or the marine parergodrilid *Stygocapitella subterranea* (see Purschke 1986, 2000).

Body cavity, blood vascular system, and nephridia. The body cavity is a true coelom in Aphanoneura (Figs. 4A, 5A, B, 6A–C, 8A–D, and 9A, C). Septa and mesenteries are weakly developed and incomplete so that there is a continuous body cavity. The coelom extends into the prostomium (Figs. 4A and 5A). An ECM basally lines the epidermis followed either by muscle fibers or a thin coelothelium (9A, C). A myoepithelium surrounds the gut. Free coelomocytes are absent.

A blood vascular system is present; main vessels include a dorsal and a ventral vessel united by a prominent loop anterior and lateral to the pharynx (Fig. 5A, B). The dorsal vessel almost extends to the posterior part of the brain, and the lateral loops unite behind the pharynx (Figs. 5A, B and 9A). Although this vessel is rather close to the brain, a direct connection does not

◂ **Fig. 6**: *Potamodrilus fluviatilis*. Pharynx and esophagus, TEM micrographs from cross sections. A, Level of the mouth (mo); tongue (to) projects ventrally from the dorsal roof of the buccal cavity (bc), esophagus (oes) separated from the buccal cavity and situated dorsally; buccal cavity without cilia; the musculature of the tongue (tom) comprises several single fibers situated between the epithelium of the tongue and esophagus; dorsal and ventral roots of circumesophageal connective (drcc, vrcc) and stomatogastric nerves (sn) encircled. B, Epithelium of tongue with strong microvilli (mv) and specialized cuticle (cu). C, Esophagus (oes) composed of ciliated epithelial cells dorsolaterally accompanied by large gland cells forming the salivary gland (sgl). bc, buccal cavity; coe, coelomic cavity; coel, coelothelium; cu, cuticle; dlm, dorsal longitudinal muscle; drcc, dorsal root of circumesophageal connective; ecm, extracellular matrix; ep, epidermis; gl, gland cell; llm, lateral longitudinal muscle; mo, mouth; mv, microvillus; oes, esophagus; sgl, salivary gland; sj, septate junction; sn, stomatogastric nerve; step, stomodeal epithelium; to, tongue; tom, tongue musculature; vlm, ventral longitudinal muscle; vrcc, ventral root of circumesophageal connective; za, zonula adherens; originals.

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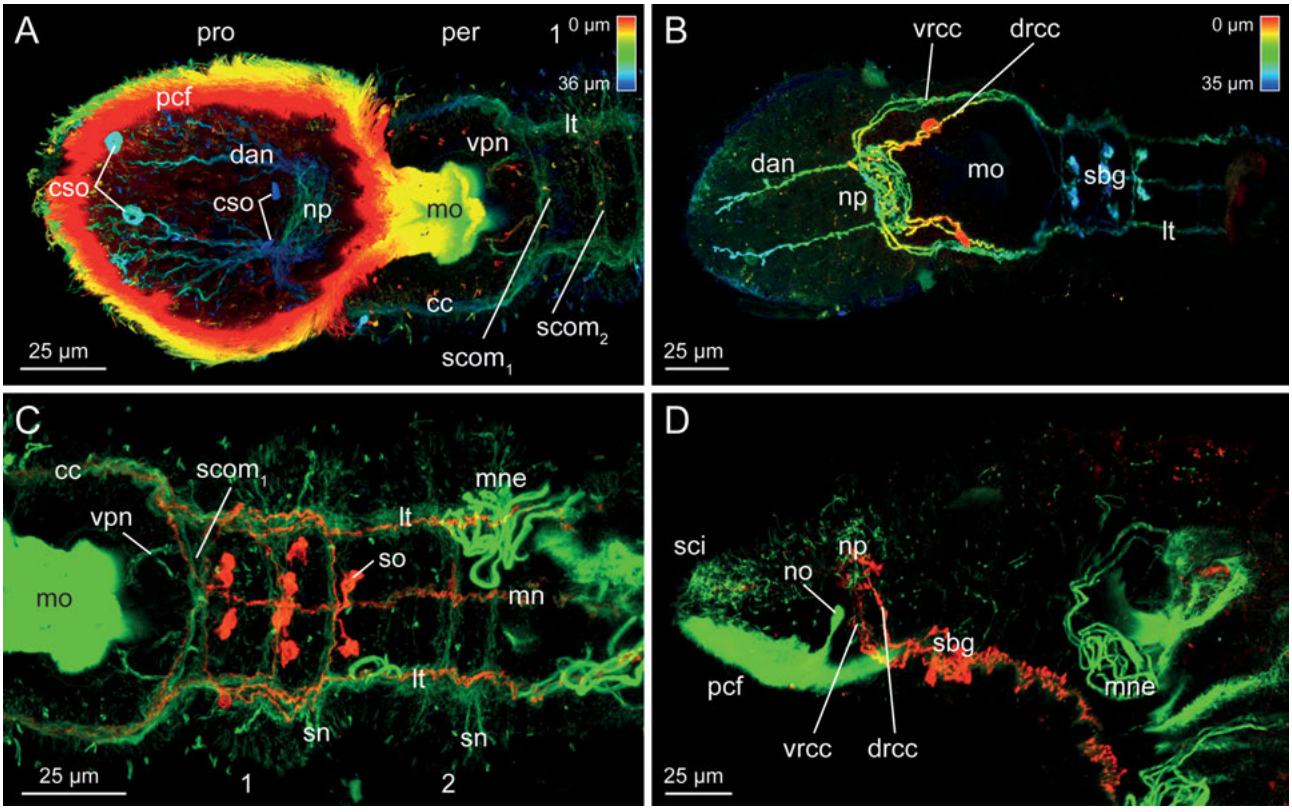


Fig. 7: Aphanoneura. *Aeolosoma hemprichi*. Nervous system after immunostaining; A, C, D, antiacetylated α-tubulin immunoreactivity; B–D, antiserotonin immunoreactivity; A, B, depth coding images; C, D, double labeling (antitubulin: green, antiserotonin: red). A, Ventral view of the anterior end. Neuropil (np) of the brain immediately in front of the mouth (mo); prostomial ciliary field (pcf) continues into the mouth (mo). In front of the neuropil, two pairs of photoreceptor-like ciliary sense organs (cso); circumesophageal connectives form a wide arc around the mouth and form the ventral nerve cord behind first subesophageal commissure (scom1), lateral tracts (lt) of ventral cord widely separated. B, Dorsal view of the anterior nervous system to show dorsal (drcc) and ventral roots (vrcc) of circumesophageal connective (cc); arrows point to serotonergic brain somata located behind the neuropil. C, Ventral nerve cord comprising three connectives (lt, mn); each commissure of the subesophageal ganglion with a pair of serotonergic somata (so). D, Nervous system in lateral view, note first two metanephridia (mne). ch1, 2, chaetigers 1, 2; cc, circumesophageal connective; cso, ciliary sense organ; dan, dorsoanterior nerve; drcc, dorsal root of cc; lt, lateral tract of the ventral nerve cord; mn, median nerve of the ventral nerve cord; mne, metanephridium; mo, mouth; no, nuchal organ; np, neuropil; pcf, prostomial ciliary field; per, peristomium; pro, prostomium; sbg, subesophageal ganglion; sci, sensory cilia; scom, subesophageal commissure; sn, segmental nerve; vpn, ventral peristomial nerve; vrcc, ventral root of cc; modified from Hessling and Purschke (2000).

exist. The dorsal and ventral vessels are accompanied by a well-developed blood sinus surrounding the gut (Fig. 2A–C in Bunke 1994). The wall of the vessels is formed by the ECM followed by peritoneal cells, less than 100 nm thick in regions without myofilaments (Fig. 9A, B) and considerably thicker where they contain small bundles of myofilaments (Bunke 1994). These thin coelothelial cells frequently form slit-like interruptions in the epithelial cover and thus are podocyte-like in certain areas (Fig. 9B). In the trunk region, segmentally arranged loops connecting the gut sinus with the ventral vessel are present. These paired loops occur at the level of the nephridial funnels and are formed by typical podocytes (Bunke 1994). A distinct heart is absent, but the dorsal and ventral vessel walls especially are contractile (Bunke 1967, 1994). At various locations, the blood vessels are in contact with the ECM of the epidermis (e.g., Fig. 9A).

As expected from the presence of a coelom and blood vascular system, the nephridia are true metanephridia (Smith and Ruppert 1988, Bartolomaeus and Ax 1992). The number and the position of nephridia vary between species and are not known for every species. In *Aeolosoma bengalense*, seven pairs are present (Bunke 1994), and two pairs each in *Rheomorpha neizvestnovae* and *Potamodrilus fluviatilis*. In the *Aeolosoma* species, the first nephridium lies in chaetiger 2 (the funnel belonging to chaetiger 1), and each consecutive chaetiger is supplied with a pair of nephridia except for the posteriormost chaetigers (in *A. bengalense*, the first zooid consisting of 8 to 10

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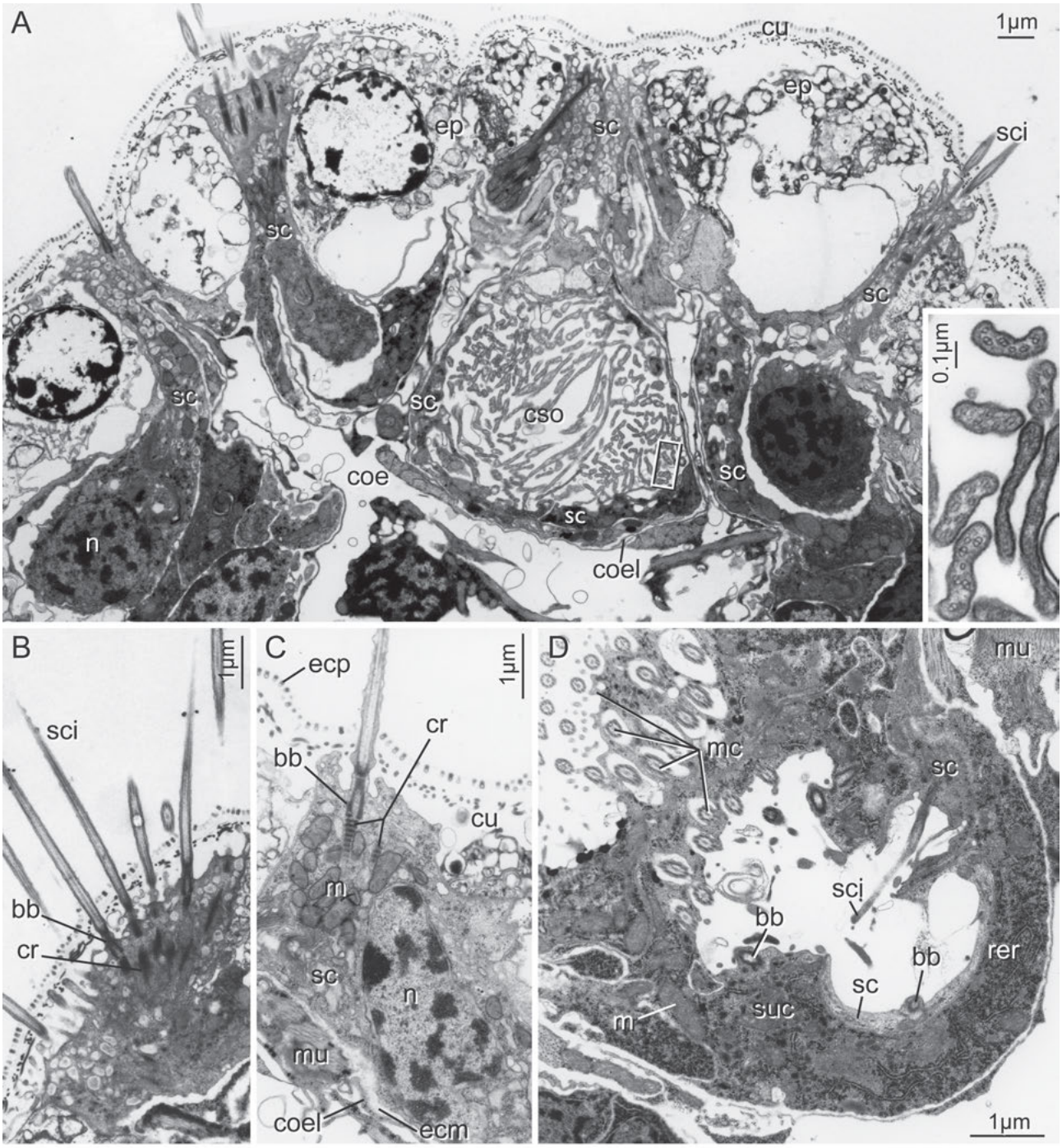


Fig. 8: Aphanoneura. Sense organs and sensory cells. TEM micrographs. A, *Potamodrilus fluviatilis*. Prostomial ciliary tufts and precerebral ciliary sense organ. Ciliary tufts comprising a few multiciliated sensory cells (sc) are situated above and around a ciliary sense organ (cso) with internalized modified cilia (inset). B, *P. fluviatilis*. Multiciliated sensory cell with numerous stiff cilia projecting from the body surface in a fanlike pattern. C, *P. fluviatilis*. Multiciliated primary sensory cell from prostomial ciliary tuft. D, *Aeolosoma hemprichi*. Nuchal organ; ciliated supportive cells (suc) form a spherical structure with a central cavity, the olfactory chamber (oc), bottom of olfactory chamber lined by a few sensory cells, each bearing one short sensory cilium (sci). bb, basal body; coe, coelomic cavity; coel, coelothelium; cr, ciliary rootlet; cso, ciliary sense organ; cu, cuticle; ecm, extracellular matrix; ecp, epicuticular projections; ep, epidermis; m, mitochondrium; mc, motile cilia; n, nucleus; rer, rough ER; sc, sensory cell; sci, sensory cilum; originals.

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chaetigers possesses seven pairs of nephridia)[1]. In *R. neizvestnovae*, the first pair lies in the first segment with adhesive papillae and the second in the following, but one segment is situated behind the stomach (Bunke 1967). In *P. fluviatilis*, the first pair lies in chaetiger 1 or 2 and the second in chaetiger 5 or 6. Only the first pair is excretory, and the second serves as spermioducts (Bunke 1967). In all species for which data are available, the nephridia possess a comparatively long and convoluted duct forming three or more loops (Fig. 2C, D) (Bunke 1967, 1994). The comparatively large size of the nephridia in aphanoneurans may be correlated to their occurrence in limnetic environments.

The ultrastructure of the excretory system is only known for *Aeolosoma bengalense* (see Bunke 1994). In this species, the nephrostome is comparatively small and consists of only two cells, an outer mantle cell and an inner cell called a terminal duct cell. The cilia of the mantle cell project into the body cavity, whereas those of the terminal cell project into the canal's lumen. The multicellular duct is ciliated throughout, and the first loops are closely associated, forming a compact structure called a nephridial body. The middle part is in intimate contact with intestinal blood spaces. In cross sections, the duct is usually formed by only one cell. The number of cilia and the length, number, and density of microvilli vary according to the duct's region.

Reproductive organs and gametes. Aphanoneura are hermaphrodites without exception (Bunke 1967, 1988, Rouse and Pleijel 2000). In Aeolosomatidae, which predominately reproduce asexually, genital organs and gametes are only known for some species and usually are only temporarily present in the populations studied (Ax and Bunke 1967, Bunke 1967, 1986, Purschke 2006). Moreover, usually, only a portion of a given population becomes sexually mature, and often sexual organs degenerate. The developing oocytes do not mature and are reabsorbed so that oviposition and development are even more poorly known. This process may indicate that sexual reproduction only occurs occasionally and is not a regular part of the life cycle in these species. By contrast, only sexual reproduction occurs in *Potamodrilus fluviatilis* (see Bunke 1967, 1985) and *Aeolosoma singulare* Semernoy, 1982 (Marotta et al. 2003, Falconi et al. 2015). Besides the latter species, genital organs or gametes have been observed elsewhere in *Rheomorpha neizvestnovae* and the following *Aeolosoma* species: *A. headleyi* Beddard, 1888; *A. hemprichi*; *A. litorale*; *A. marcusi* van der Land, 1971; *A. niveum* Leydig, 1865; *A. psammophilum* Bunke, 1967; *A. quaternarium* Ehrenberg, 1831; *A. travancorense*; and *A. variegatum* Vejdovský, 1884 (Stolc 1902, Aiyer 1929, Schäfer 1942, Marcus 1944, Ax and Bunke 1967, Bunke 1967, 1986, Gluzman 1994, 1997, Marotta et al. 2003).

Primordia of male gonads are found ventrally in all chaetigers; those of female gonads are lacking in the first and last chaetiger in *Aeolosoma litorale* (Fig. 10A) (Ax and Bunke 1967, Bunke 1967). In the latter, usually, only one pair of ovaries develops in the midbody region at the border between adjacent segments, most commonly between the third and the sixth chaetiger (Bunke 1967). As a rule, only one produces mature oocytes, and only one mature oocyte (diameter about 100–125 µm) has been found at a time (Figs. 2A and 10A–C). Female openings do not exist, but the ventral epidermis below the maturating oocyte becomes glandular, forming a clitellum-like structure with a female pore in its center. The function of this clitellum has not been clarified until recently. Additionally, one to six pairs of simple receptacula (spermathecae) are formed from chaetiger 1 onward, with three subsequent pairs the most common pattern. The receptacula are simple epidermal invaginations formed by either one or two cells except for the large species *Aeolosoma singulare*, which possess a multicellular seminal receptacle (Bunke 1967, Marotta et al. 2003). Besides the storage of sperm, there are signs of degrading sperm inside the receptacula (Marotta et al. 2003).

Paired testes develop ventrally in the same segments than the ovaries from the ventral coelomic cells (Fig. 10A) (Ax and Bunke 1967, Bunke 1967, 1988). Spermatozoa are often formed in two regions, one anterior and one posterior to the ovaries (Bunke 1967). Spermiogenesis has been described in a few *Aeolosoma* species and occurs on cytophores ultimately carrying 128 developing spermatozoa (Bunke 1967, 1986, Marotta et al. 2003). Mature spermatozoa are filiform with a long head region comprising a simple acrosomal vesicle and a cylindrical and somewhat longer nucleus. An electron-dense tubular coil surrounds the acrosome and nucleus in the periphery. The short midpiece contains a single ring-shaped mitochondrium and is followed by the flagellum possessing a typical $9 \times 2 + 2$ axoneme. The proximal centriole forms a central body in the midpiece, and the distal one gives rise to the axoneme. When the spermatozoa are discharged from the cytophores into the coelom, they still contain multiple lysosome-like vesicles at the base of the

1 Segment counts differ from Bunke (1967, 1994), who counted the peristomium as segment 1.

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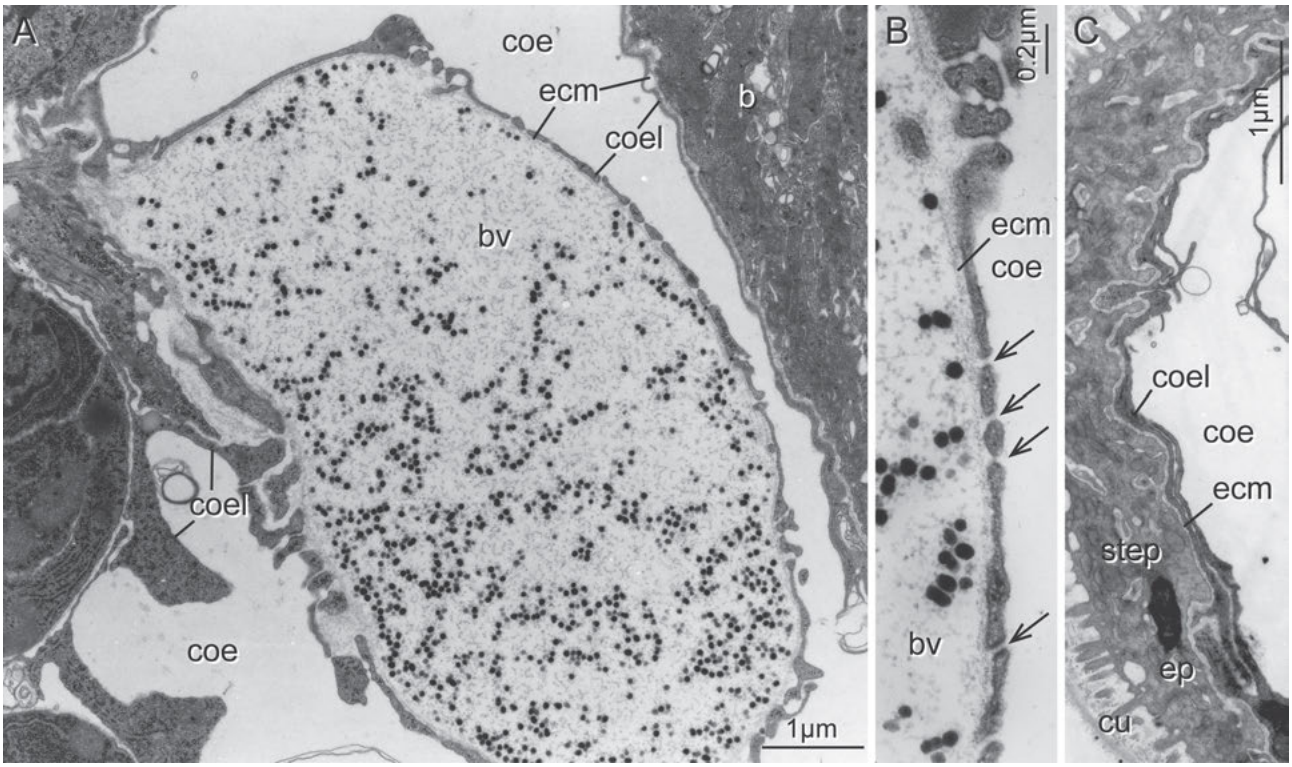


Fig. 9: Aphanoneura; coelom, coelothel (peritoneum), and blood vessels. A, B, *Aeolosoma hemprichi*. Anterior blood vessel (bv) close to the brain (b); blood vessel, brain, and epidermis lined by thin extracellular matrix (ecm) and coelomic lining (coel). B, Enlargement of a wall of a blood vessel formed by thin coelothelial cell (coel) underlain by thin extracellular matrix (ecm); arrows point to slitlike openings in the coelothelial cell. C, *Potamodrilus fluviatilis*. Thin coelomic lining (coel) above stomodeal epithelium (step). bv, blood vessel; coe, coelomic cavity; coel, coelothel; coelomic lining; cu, cuticle; ecm, extracellular matrix; ep, epidermis; step, stomodeal epithelium; originals.

nucleus and around the midpiece (Bunke 1986, Marotta et al. 2003), which may finally disappear because these are absent in spermatozoa found in the receptacles (Marotta et al. 2003). Spermatozoa are usually discharged via the posterior nephridia.

In *Potamodriuls fluviatilis*, the paired ovaries are situated in chaetiger 4, and each proliferates a single chain of maturating oocytes in the anterior-posterior direction (Bunke 1967). In the following chaetiger, only one chain with larger oocytes is present. Mature oocytes (110–130 µm) are discharged individually through the female opening situated ventrally at the border between chaetigers 5 and 6. As in *Aeolosoma* and *Reomorpha*, the female pore is surrounded by gland cells forming a clitellum-like structure. In the anterior part of the clitellum, an unpaired receptaculum is present. Male organs develop in chaetigers 3 and 4. Spermatozoa are formed on cytophores, each carrying 64 spermatids. Mature spermatozoa are filiform with a simple acrosomal vesicle followed by the nucleus and the tail region; a typical midpiece is absent or incorporated into the basal head region, where a few flattened mitochondria are situated (Bunke 1985). The flagellum is inserted obliquely to the nucleus, resulting in a hairpin-like spermatozoon. In addition, some coiled material is present around the acrosome and nucleus, and in the posterior part. The nucleus is surrounded by a single layer of small vesicles. In contrast to Bunke (1986), Marotta et al. (2003) identified a number of possible synapomorphies in the spermatozoa of *Potamodrilus* and *Aeolosoma*, but both refute any correspondence to clitellate sperm, which opposes Gluzman (1997). Sperm are discharged via the posterior pair(s) of metanephridia (Ax and Bunke 1967, Bunke 1967). They are modified to spermioducts comprising a wide funnel and a long ciliated and coiled duct. The ducts unite in the ventral midline opening in an unpaired furrow (Bunke 1967, 1988).

Reproduction and development

Except for *Potamodrilus*, sexual reproduction is a rare phenomenon in Aeolosomatidae (Ax and Bunke 1967, Bunke 1967, 1986). Sperm transfer has not been observed,

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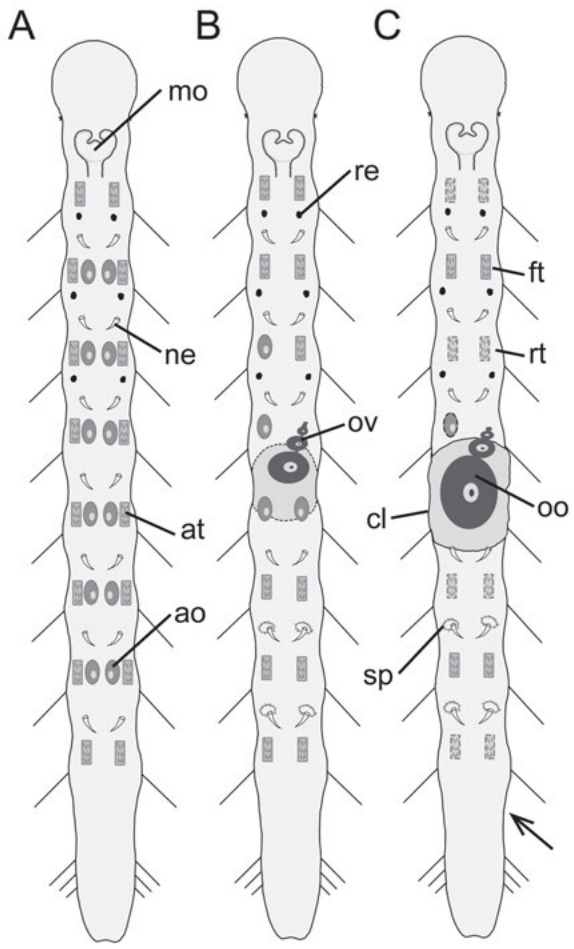


Fig. 10: *Aeolosoma litorale*. Occurrence and development of genital organs. A, Beginning of maturation, primordia of male gonads formed in all chaetigers, female gonads are only formed from the second to seventh chaetiger. B, Ongoing maturation, part of primordia disappear. C, Mature stage, only one ovary left in chaetiger 4, functional testes are present in chaetigers 2 and 7, two posterior nephridia function as spermioducts, and mature spermatozoa are gathered at the funnels. ao, anlage of the ovary; at, anlage of the testis; ft, functional testis; mo, mouth; ne, nephridium; oo, oocyte; ov, ovary; re, receptaculum; rt, residual testis; sp, spermatozoa; redrawn and modified from Ax and Bunke (1967).

but direct transfer of sperm can be assumed from the structure of the genital organs and spermatozoa. Fertilization has also not been observed. Oviposition and first development stages have only been observed in one species, *Aeolosoma quaternarium* (see Bunke 1967). Eggs are deposited individually and without cocoon formation, but inside a sticky substance probably discharged by the clitellum-like gland cells. Cleavage has only been observed until 16 blastomeres were formed and shows some correspondence to spiral cleavage. In the laboratory, juveniles hatch with six chaetigers after 3 months of development. In *Potamodrilus fluviatilis*, single eggs are deposited as well, enclosed by a voluminous sheath most likely formed by the clitellar glands (Bunke 1967). Embryonic development is unknown. Hatching juveniles possess three achaetigerous segments. Subsequently, the first pair of chaetae is formed in the second segment. New segments are then successively added from the prepygidal growth zone until the adult number of six chaetigers is achieved.

In contrast to *Potamodrilus* and *Aeolosoma singulare*, Aeolosomatidae generally reproduce asexually by paratomy (Bunke 1967, 1988, Rouse and Fauchald 2001, Falconi et al. 2006, 2015). Thus, each individual observed usually represents a chain of zooids with the main zooid carrying the prostomium (Fig. 1A–C). In a chain, the oldest secondary zooid forms the posterior end of a chain, so they are arranged in reverse order. Periodically, mature posterior zooids (possessing the same number of chaetigers as the parental zooid) detach and live independently. A new head has been formed at this stage, and often their first own secondary zooid is already visible. The number of zooids comprising a chain is species specific and generally varies between two and eight (Bunke 1967, 1988). The same applies to the number of chaetigers necessary for zooid formation.

Quantitative observations in *Aeolosoma viride* Stephenson, 1911 revealed that, on average, the main zooid lived for 66 days and produced 57 offspring (Falconi et al. 2015). In the subterminal part of the main zooid, a budding area at its posterior part produces a chaetiger representing the origin of a secondary zooid (Falconi et al. 2015). In other words, after a new zooid is formed, cell proliferation then proceeds in the opposite direction. Thus, each zooid originates in the form of a chaetiger produced by the budding zone of the main zooid. This newly formed chaetiger contains a growth zone that produces chaetigers in the anterior direction. After seven to nine chaetigers have been formed in *A. viride*, the secondary zooid completes prostomium formation and detaches from the parental chain. In this species, fission of the last zooid occurs approximately once a day. An adaptive advantage of this mode of reproduction is seen in the rapid exploitation of environmental resources under favorable conditions (Christensen 1984, Falconi et al. 2015). Generation times reported in *Aeolosoma* spp. under controlled conditions are of the same order of magnitude but hard to compare because of different experimental methods (Kuwahara and Yamamoto 1981, Zaccanti and Falconi 2002, Falconi et al. 2006, 2015). Effects of various substances on the growth rate and reproductive cycle have been studied by

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multiple authors (Kamemoto and Goodnight 1956, Parker and Kamemoto 1959, Suzuki and Kurihara 1981, Stagni et al. 1997, Wei et al. 2003). Because of this rapid life cycle, *Aeolosoma* spp. are suggested to be suitable experimental organisms for studying asexual reproduction and paratomy by fission.

Annelids are known to possess a high potential for regeneration in terms of repair or replacement of lost body parts, usually correlated with asexual reproduction and fission (Zattara and Bely 2016, Chen et al. 2020). *Aeolosoma viride* is the only species in which regeneration has been studied in more detail to date (Chen et al. 2020), but it has been demonstrated by a few other species (Brace 1901, Herlant-Meewis 1964). In annelids, the capacity to regenerate lost parts differs greatly among taxa, and *A. viride* is one annelid possessing a very high capacity for regeneration, demonstrating anterior and posterior regeneration. In these experiments, 40–60% of amputated worms could complete anterior regeneration from nine, six, or three body segments, whereas posterior regeneration was significantly more successful, approximately 80% (Chen et al. 2020). Regeneration was completed within 120 h. The regeneration process includes wound healing and the formation of a blastema, mouth, or pygidium. Massive proliferation in the blastema and absence of cell migration indicates that *A. viride* regenerates through epimorphosis.

Biology and ecology

Data on the ecology and biology of Aphanoneura are scarce (Bunke 1988, Rouse and Pleijel 2001, Chen et al. 2020), although faunistic data are more widely available (e.g., Rota and de Jong 2015, Timm 2020). Most *Aeolosoma* spp. live interstitially or epibenthically in freshwater habitats and can be found in ponds, lakes, brooks, and streams (Bunke 1967, 1988, Rota and De Jong 2015). One species, *A. variegatum*, has exclusively been found in peat bogs (Bunke 1967). Some species inhabit the humid litter of forest soils, where they may also be found in an encysted state and thus may resist desiccation or otherwise hostile conditions (Herlant-Meewis 1950). Besides resistance to nonfavorable conditions, it is discussed whether aeolosomatids are dispersed by other animals in encysted state (Stout 1956). Individuals of species living interstitially in limnetic sediments may be found to 70 cm depth. Some of the interstitial species extend their distribution to brackish waters of estuaries or marine beaches with up to 5‰ salinity (*A. litorale*), and one species, *A. maritimum* Westheide and Bunke, 1970, is known from entirely marine habitats: sandy beaches with up to 29.3–34.6‰ salinity in the zone of damp sand above the groundwater level at a maximum of 60 to 110 cm depth (Westheide and Schmidt 1974). *Rheomorpha neizvestnovae* is only known from the limnetic mesopsammal (Bunke 1967, 1988). *Hystricosoma* spp. live epizoically on crayfish. In contrast to all other aphanoneurans, it moves using its body musculature, and cilia are not involved in locomotion. *Potamodrilus fluviatilis* is exclusively found in the interstices of coarse and medium-fine sands (Bunke 1967, 1988), mostly from the bottom of streams and rivers (Jouin 1973) but occasionally in certain oligotrophic lakes and the shore of the Baltic Sea (Collado et al. 1999, Rota and de Jong 2015). Because of their small size, interstitial or epibenthic mode of life, Aphanoneura species do not burrow or build permanent tubes except for *Aeolosoma corderoi* Ev. Marcus, 1944 and *Aeolosoma travancorense* Aiyer, 1926, reported to build tubes formed from sediment particles and detritus stabilized by glandular secretion (Marcus 1944, Bunke 1967).

Species most likely feed on algae and decaying organic matter and are found in well-oxygenated habitats (Bunke 1967, 1988). Many species occur in detritus-rich localities, whereas others seem to be restricted to detritus-poor habitats (Bunke 1967). Interestingly, all species investigated are very sensitive to oxygen deficiency (Singer 1978). Species occurring in decaying plant material have been found in the mesophyll of decaying leaves, where they may feed on soft plant tissue, protists, bacteria, and algae. They have been described as suction feeders in which the prostomium and the ventral ciliation plays an important part (Singer 1978). In *Potamodrilus*, the tongue is used to scrape and gather food particles from the substrate (Bunke 1967). Studies on population dynamics are rare and mainly report data from laboratory cultures (Herlant-Meewis 1951, Suzuki and Kurihara 1981, Falconi et al. 2006, 2015).

Distribution

Species of Aphanoneura have been recorded from all parts of the world except for certain oceanic islands and the Antarctic (Glasby and Timm 2008). There are many reports of the *Aeolosoma* species from these regions, but records of the remaining three genera are currently restricted to Europe. This preponderance might largely reflect sampling activity rather than true distributional patterns as shown by the record of a yet undescribed *Potamodrilus* species in North America (Strayer 2001, Rota and de Jong 2015). Some species are reported to be cosmopolitan such as the oldest nominal species, *Aeolosoma hemprichi*. However, it can be speculated that misidentifications

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occurred or cryptic species complexes exist (Glasby and Timm 2008, Glasby et al. 2009). The same is assumed for several other *Aeolosoma* species with widespread or disjunctive occurrence such as *A. aureum* Marcus, 1944; *A. niveum*; *A. sawayai* Marcus, 1944; *A. tenebrarum* Vejdovský, 1882; and *A. travancorense* (see Glasby et al. 2009). The marine species *A. maritimum* is known from the Mediterranean and Atlantic European coasts (Westheide and Bunke 1970, Westheide 1972), and its subspecies *A. maritimum dubiosum* Westheide and Schmidt, 1974 has been described from the Galapagos archipelago (Westheide and Schmidt 1974). Several authors have reviewed faunistic data (e.g., Bunke 1967, Van der Land 1971, Glasby et al. 2009, Christoffersen 2012a, Rota and de Jong 2015, Gil et al. 2019, Spiller 2020, Timm 2020). However, there may be numerous records hidden in the literature where especially *Aeolosoma* spp. have been recorded (see Paxton 2000), unfortunately often without a determination to species level (e.g., Jouin 1973, Westheide 1979).

Phylogeny and taxonomy

Aeolosomatidae have been known since 1828, when the first species, *Aeolosoma hemprichi*, was described by Ehrenberg (1882). Subsequently, the genera *Hystricosma* Michaelsen, 1926; *Potamodrilus* Lastochkin, 1935; and *Rheomorpha* Ruttner-Kolisko, 1955 were erected in the past century and united in the single family Aeolosomatidae (Rouse and Pleijel 2001, Read and Fauchald 2020). Traditionally, these annelids were classified as oligochaetes (e.g., Michaelsen 1928, Stephenson 1930, Avel 1959) mainly based on their simple sigmoid or hairlike chaetae, hermaphroditism and clitellum-like structure, freshwater habitat, and absence of parapodia. Within oligochaetes, they were considered to be related to Naididae either as their most primitive group ("Archioligochaeta") or in a highly derived position (Michaelsen 1928, 1929, Stephenson 1930). Because of significant morphological differences between *Potamodrilus fluviatilis* and the remaining Aeolosomatidae, as a first step, Bunke (1967) formed the family Potamodrilidae for this species and also raised the initial doubts on their affiliation as oligochaetes. They were finally excluded from Clitellata in the early 1970s because of the absence of any clitellate key character (synapomorphies) (Brinkhurst and Jamieson 1971). Likewise, a close or even sister-group relationship between these two families has been debated and was excluded by Bunke (1967, 1985, 1986). However, Bunke's view was not generally accepted, and Timm (1981) again united both groups in the single taxon Aphanoneura by resurrecting the taxon name originally coined by Vejdovsky (1884). Subsequent ultrastructural analyses of spermiogenesis, nervous system, and sensory organs in *Aeolosoma* spp. and *Potamodrilus* found no support for separating the two families (Hessling and Purschke 2000, Purschke and Hessling 2002, Marotta et al. 2003). Moreover, whenever *Potamodrilus* and Aeolosomatidae were included in the same molecular analysis, their sister group relationship was confirmed, supporting the Aphanoneura hypothesis (Struck and Purschke 2005, Zrzavý et al. 2009), which is now generally accepted.

After excluding Aphanoneura from Clitellata, they were still regarded as closely related to this group and possibly evolved from a common freshwater ancestor (Brinkhurst and Jamieson 1971, Timm 1981). Although their relationships were debated, they were at that time subsequently placed as *incertae sedis* within polychaetes (e.g., Rouse and Fauchald 1997, Rouse and Pleijel 2001). This placement was validated by several morphological studies that found no shared derived characters typical of Clitellata (Bunke 1985, 1986, Hessling and Purschke 2000, Purschke and Hessling 2002, Marotta et al. 2003). For instance, the spermatozoa of Clitellata bear several characters not present in other annelids and are thus seen as autapomorphies (Jamieson and Ferraguti 2006). However, Christoffersen (2012b) again proposed a closer relationship with Clitellata (as Euclitellata) as a sister of *Hrabeiella* and Euclitellata (forming the emended clade Oligochaeta), but this hypothesis did not receive much attention. The first molecular studies addressing this question also could not clarify the position of Aphanoneura. These studies found Aeolosomatidae was never closely related to clitellates but in various positions in the respective phylogenetic hypotheses (Rota et al. 2001, Struck et al. 2002, Struck and Purschke 2005, Rousset et al. 2007). However, in several studies, a sister group relationship with *Hrabeiella*, another annelid with uncertain affinities (see Purschke 2020; chapter Hrabeiellidae in Volume 2), was found (Rota et al. 2001, Rousset et al. 2007, Zrzavý et al. 2009). Notably, Zrzavý et al. (2009) were the first to identify a sister group relationship of the clade *Hrabeiella*/Aphanoneura with Clitellata with strong statistical support. This placement was further confirmed by a recent phylogenomic study focusing on clitellate phylogeny (Erséus et al. 2020). Thus, the old view of a closer relationship with Clitellata is currently strongly supported, and the issue is again under discussion. With these hypotheses in mind, the common characters of Aeolosomatidae and Hrabeiellidae must be evaluated anew with respect to their phylogenetic importance as probable synapomorphies of these taxa and with Clitellata.

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The family Aeolosomatidae was described as new on two occasions, and there has been some confusion in the literature (Read and Fauchald 2020). The first description was by Levinsen (1884), but most other authorities have overlooked this publication for many years, including Beddard (1895), who again described the family as new to science, most likely unaware of Levinsen's (1884) description. The same happened to Bunke (1967), who also overlooked Levinsen (1884) and named the family Aeolosomatidae Beddard, 1894. Most recent authorities have repeated this oversight (e.g., Fauchald and Rouse 1997, Rouse and Pleijel 2001, Glasby et al. 2009, Spiller 2020).

Because of their delicate body, minute size, and character paucity, the taxonomy of Aeolosomatidae is difficult (Bunke 1988, Gil et al. 2019, Timm 2020). Most species will shrink, burst, or become opaque during fixation, leaving only the chaetae visible under a microscope (Bunke 1988, Timm 2020). Thus, determination from fixed material alone is almost impossible and only reliable with the observation of live organisms. A lack of material might be overcome when living animals are available since many species are easily cultured (Bunke 1988). Nevertheless, these difficulties might be the main reason for the extraordinary number of invalid or uncertain species almost exceeding the number considered valid (Read and Fauchald 2020). As mentioned above, several species commonly accepted and regarded valid may, in fact, be groups of cryptic species. Genetic fingerprints might help to clarify the taxonomic problems in the future, especially widely distributed species.

Aeolosomatidae Levinsen, 1884

Type genus: *Aeolosoma* Ehrenberg, 1828

Diagnosis: Small, mostly freshwater animals, living interstitially, epibenthically, in forest litter, or epizoic. Cosmopolitan. Body comprising prostomium, peristomium, a limited number of segments, pygidium. Segment borders usually indistinct. Hermaphroditic but mostly reproducing asexually by paratomy, chains with generally not more than four zooids; depending on species first zooid with 5–17 segments. Sexual individuals not known in every species. Prostomium flattened with dense cilia ventrally, ciliary field used for locomotion and feeding, cilia continue into the mouth. Most species have yellow, orange, red, or green epidermal so-called oil glands. Parapodia lacking, chaetae capillaries or sigmoid, arranged in four bundles per segment, seldom absent. Nervous system intraepithelial, brain situated in prostomium with double circumesophageal roots, ventral nerve cord with widely separated main connectives and an additional median nerve; nuchal organs and simple photoreceptor-like ciliary sense structures present, no eyes. Alimentary canal with simple weakly muscularized pharynx, esophagus, stomach, and midgut. Coelom present, septa, and mesenteries reduced, blood vascular system simple, metanephridia. Usually, only one functional ovary in midbody, two to five pairs of simple receptacula, clitellum-like accumulation of gland cells around unpaired ventral female opening. Testes in segments anterior and posterior to ovaries, sperm filiform, discharged through posterior nephridia (Stephenson 1930, Bunke 1967, Van der Land 1971, Rota and de Jong 2015).

3 Genera: *Aeolosoma* Ehrenberg, 1828; *Hystricosoma* Michaelsen, 1926; and *Rheomorpha* Ruttner-Kolisko, 1955. A fourth genus *Derostoma* Duges, 1830, is mentioned but contains only uncertain species (Read and Fauchald 2020) and is not further considered here.

Aeolosoma Ehrenberg, 1828

Type species: *Aeolosoma hemprichi* Ehrenberg, 1828

Synonyms: *Aeolonais* Gervais, 1838; *Chaetodemus* Leidy, 1852

Diagnosis: Small species, usually around 1 mm, exceptionally up to 10 mm, usually dorsoventrally flattened, intersegmental furrows hardly visible, colored epidermal glands usually present (Figs. 1A and 2A, B); each chaetiger with two pairs of capillaries, sigmoid chaetae present in certain species, number and length varying among species (Fig. 3A–D). Cosmopolitan. Main references: Stephenson (1930), Bunke (1967), Van der Land (1971), Glasby et al. (2009), Gil et al. (2019), Rota and de Jong (2015), Read and Fauchald (2020), Timm (2020).

26 species and 27 additional species considered as taxa inquirenda or uncertain (Read and Fauchald 2020).

Hystricosoma Michaelsen, 1926

Type species: *Hystricosoma chappuisi* Michaelsen, 1926

Two species

Diagnosis: Small animals, less than 1 mm, freshwater, epizoic on crayfish; trunk cylindrical with flat prostomium, peristomium and segments distinct; chaetae of dorsal bundles arranged in two transverse rows or an elliptical row, colored epidermal glands in the chaetigers around chaetal bundles (Fig. 1C); ciliated prostomial pits (nuchal organs) present. Only known from Europe and Colombia. Main references: Stephenson (1930), Van der Land (1971), Glasby et al. (2009), Rota and de Jong (2015), Gil et al. (2019), Read and Fauchald (2020), Timm (2020).

Remarks: *Hystricosoma pictum* (Schamarda, 1861) is poorly described, and its status is discussed (Timm 2020). *Hystricosoma insularum* Michaelsen, 1933 is regarded as uncertain (Read and Fauchald 2020, Timm 2020).

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Rheomorpha Ruttner-Kolisko, 1955

Type species: *Rheomorpha neizvestnovae* (Lastochkin, 1935) as *Aeolosoma neizvestnovae* Lastochkin, 1935
Monotypic
Diagnosis: Small animals, approximately 1 mm, interstitial in freshwater; chaetae absent with segmental adhesive papillae, intersegmental furrows hardly visible, colored epidermal glands usually present, pygidium with two adhesive lobes (Fig. 1B); ciliated prostomial pits (nuchal organs) present, asexual and sexual reproduction. Only known from European lakes, rivers, and springs. Main references: Ruttner-Kolisko (1955), Bunke (1967), Van der Land (1971), Glasby et al. (2009), Rota and de Jong (2015), Gil et al. (2019), Read and Fauchald (2020).

Potamodrilidae Bunke, 1967

Type genus: *Potamodrilus* Lastochkin, 1935
Diagnosis: Small, interstitial freshwater animals with constant segment number. Body comprising prostomium, peristomium, six chaetigerous segments, pygidium. Prostomium large with ventral ciliation, used for locomotion. Pygidium with funnel-shaped appendage, anus ventral, subterminally. Oil glands absent. Chaetae capillaries with fine serration (Fig. 3E). Stomodaeum with dorsal tongue. Protandric hermaphrodite: one pair of ovaries (chaetiger 4), two pairs of testes (chaetigers 4 and 5), male pores united to unpaired longitudinal furrow, female pore in furrow between chaetigers 5 and 6, receptaculum in chaetiger 5. Nervous system intraepidermal, nuchal organs present, internalized, unpigmented ciliary photoreceptor-like sense organ present, eyes absent. Coelom present, septa, and mesenteries reduced, simple blood vascular system (Fig. 1D). Main references: Bunke (1967), Rota and de Jong (2015).

Potamodrilus Lastochkin, 1935

Type species: *Potamodrilus fluviatilis* (Lastochkin, 1935)
Original combination: *Stephensoniella fluviatilis* Lastochkin, 1935
Monotypic
Diagnosis: as for the family
Remarks: Currently only known from Europe and Asia (Bunke 1967, Jouin 1973, Rota and de Jong 2015), one undescribed species from North America (Strayer 2001).

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https://doi.org/10.1515/9783110647167-022

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